INTEGR. COMP. BIOL., 44:163–176 (2004)

Polar Bears in a Warming Climate[1]

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SYNOPSIS. Polar bears (*Ursus maritimus*) live throughout the ice-covered waters of the circumpolar Arctic, particularly in near shore annual ice over the continental shelf where biological productivity is highest. However, to a large degree under scenarios predicted by climate change models, these preferred sea ice habitats will be substantially altered. Spatial and temporal sea ice changes will lead to shifts in trophic interactions involving polar bears through reduced availability and abundance of their main prey: seals. In the short term, climatic warming may improve bear and seal habitats in higher latitudes over continental shelves if currently thick multiyear ice is replaced by annual ice with more leads, making it more suitable for seals. A cascade of impacts beginning with reduced sea ice will be manifested in reduced adipose stores leading to lowered reproductive rates because females will have less fat to invest in cubs during the winter fast. Non-pregnant bears may have to fast on land or offshore on the remaining multiyear ice through progressively longer periods of open water while they await freeze-up and a return to hunting seals. 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 maintain contact with the remaining preferred habitats. The effects of climate change are likely to show large geographic, temporal and even individual differences and be highly variable, making it difficult to develop adequate monitoring and research programs. All ursids show behavioural plasticity but given the rapid pace of ecological change in the Arctic, the long generation time, and the highly specialised nature of polar bears, it is unlikely that polar bears will survive as a species if the sea ice disappears completely as has been predicted by some.

INTRODUCTION

Polar bears (*Ursus maritimus*) are a classic *K*-selected species having delayed maturation, small litter sizes, and high adult survival rates (Bunnell and Tait, 1981). Sea ice is the platform on which polar bears travel and hunt so that changes to its distribution, characteristics, and timing have the potential to have profound affects (Stirling and Derocher, 1993). Most populations rely on terrestrial habitats for maternity denning and some take refuge on land in areas where the sea ice melts completely during summer. Some higher latitude populations, such as those in the Chukchi and Beaufort seas, retreat to the multiyear ice of the polar basin each summer. Polar bears are a specialised predator of phocid seals in the ice-covered Arctic seas. While there is some geographic variation in their diet, their main prey are ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) (Smith, 1980; Stirling and Archibald, 1977). Other prey such as harp seals (*P. groenlandica*), white whales (*Delphinapterus leucas*), narwhal (*Monodon monoceros*), and walrus (*Odobenus rosmarus*) are sometimes taken (Smith, 1985; Smith and Sjare, 1990; Calvert and Stirling, 1990; Derocher *et al.*, 2002) but currently appear to be a less important energy source for most populations.

Polar bears have successfully occupied virtually all available sea ice habitats throughout the circumpolar Arctic and the global population was last estimated at 21,500–25,000 individuals (IUCN/SSC Polar Bear Specialist Group, 2002). The main threat to polar bears in the recent past was over-harvest but this has been largely corrected through various management regimes (Prestrud and Stirling, 1994). For the most part, the circumpolar habitat of polar bears has experienced a relatively small amount of impact from human development. Consequently, they retain a higher proportion of their original range than any other extant large carnivore. During periods of climatic cooling, polar bears ranged much further south than they do at present (Kurtén, 1964; Aaris-Sørensen and Petersen, 1984) but their fossil record is scant and there is little information on how they may have responded or adapted during earlier climatic fluctuations. However, it is clear that because of the speed with which the climate continues to warm, particularly in the Arctic, and the correspondingly rapid reduction in the abundance of sea ice, the prognosis for polar bears is uncertain.

A growing body of studies suggests that climatic warming is well underway in Arctic areas and the rate of change may increase (Serreze *et al.*, 2000; Parkinson and Cavalieri, 2002; Comiso, 2002*a*, *b*). Most of the characteristic mammals in the arctic marine ecosystem are specifically adapted to the sea ice environment. Sea ice is a vital substrate for both pagophilic (''ice-loving'') mammals and epontic marine communities so that significant reduction or disappearance of the ice from some areas will fundamentally alter the arctic marine ecosystem as we know it today. In particular, the disappearance of sea ice from the biologi-

[1] From the Symposium *Biology of the Canadian Arctic: A Crucible for Change in the 21st Century* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 4–8 January 2003, at Toronto, Canada.

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cally productive areas of the continental shelf or the inter-island channels of the various archipelagos will fundamentally change the marine ecosystems there. Other changes that are likely to occur, but are difficult to model, include reduced total sea ice area, reduced sea ice duration, thinner ice, smaller floe sizes, more open water, altered snow cover, and increased rates of ice drift.

It is well known that climate is a principal factor determining the life history patterns of animals (Stearns, 1992). Furthermore, it is also well documented that arctic ecosystems and populations exhibit large-scale fluctuations in relation to natural climatic cycles in their environment (*e.g.*, Vibe, 1967; Stirling *et al.*, 1999; Stirling, 2002; Post and Forchhammer, 2002). However, the concern now is not that the climate will exhibit fluctuations but that the changes will be unidirectional (*i.e.*, progressively warmer) and that this will result in negative changes to arctic pagophilic species on an ecosystem-wide basis.

Possible impacts of climatic warming on polar bears were first discussed by Stirling and Derocher (1993). Since then, additional perspectives on how climate may affect polar bears have developed as we have learned more about their interrelationships with both their prey species and their sea ice habitats in different parts of the Arctic. In this paper, we examine how climatic warming in the Arctic to date has influenced polar bears and speculate on how projected future changes may affect the sea ice and consequently polar bears and their prey. We also assess the ability of research to detect changes.

DISCUSSION

The most fundamental characteristic of polar bears, in relation to any discussion of their ecology, is that they are highly pagophilic. They evolved from terrestrial brown bears (*U. arctos*) to exploit the available, biologically productive, but unoccupied niche for a large predator (Stirling and Derocher, 1990; Talbot and Shields, 1996; Shields *et al.*, 2000). Although females from most populations use snow dens on land for parturition, polar bears are almost completely dependent on sea ice for sustenance. Thus, anything that significantly changes the distribution, abundance, or even the existence of sea ice will have profound effects on polar bears.

It is important also to consider that there are different types of sea ice and that its distribution over water of varying depths and locations has significant effects on the ecology of polar bears. Their preferred habitat is the annual sea ice over the continental shelf and inter-island archipelagos that encircle the polar basin. Recent research has indicated that the total sea ice extent has declined over the last few decades, particularly in both near shore areas and in the amount of multiyear ice in the polar basin (Parkinson and Cavalieri, 2002; Comiso, 2002*a*, *b*). These changes have been attributed to climatic warming and current modelling suggests the climate will continue to warm into the foreseeable future. Regardless, of the eventual end point, it is clear that significant change is already underway and is continuing in both the regional availability and the total abundance of sea ice. This will have a significant effect on all pagophilic species in the arctic marine ecosystem, including polar bears.

In the following discussion, we have attempted to separate possible effects of climatic warming on polar bears into a series of categories, though obviously there is overlap and linkage between them. We start with the most obvious: increased melting of ice and subsequent changes in seasonal patterns of distribution and abundance. We then speculate about the ecological consequences of these changes, some of which are evident now while others have varying degrees of conjecture. Lastly, we discuss possible management changes and the degree to which aspects of polar bear biology may lend themselves to monitoring the predicted changes.

DECREASE IN THE OVERALL EXTENT OF ARCTIC SEA ICE

Overall decreases in the distribution and abundance of both annual and multiyear sea ice have already been recorded and are projected to continue (Maslanik *et al.*, 1996; Serreze *et al.*, 2000; Parkinson and Cavalieri, 2002). Since 1978, the total amount of ice cover has declined by about 14% (Vinnikov *et al.*, 1999). Comiso (2003) reported that the longer term *in situ* surface temperature data show that the 20-year trend is 8 times larger than the 100-year trend, suggesting a rapid acceleration in warming. Further, because of this, he further suggested that by 2050, except for the most northerly parts of the Canadian Arctic Archipelago and Greenland, the average minimum extent of sea ice will be several hundred km north of the continental coastlines. In many areas, that means the remaining ice will no longer lie over the continental shelf but over the much deeper waters of the polar basin. In more southerly areas such as Hudson Bay, using coupled atmosphere-ocean climate model, Gough and Wolfe (2001) suggested that ice might be gone by the middle of the present century.

DECREASES IN MULTIYEAR ICE

Rothrock *et al.* (1999) reported significant thinning of the multiyear ice in the polar basin. Similarly, Comiso (2002*b*) reported that the perennial sea ice cover in the Arctic is declining at a rate of about 9% per decade and, if that rate is sustained, the multiyear ice cover may be gone by the end of this century. Extensive multiyear ice is a principal feature of the inter-island channels of the Sverdrup Basin in the Canadian High Arctic Archipelago. Melling (2002) recently reported that the ice in the Sverdrup Basin is strongly influenced by a heat flux that originates in the Atlantic-derived waters of the Arctic Ocean. The drift of ice through the basin is controlled at present by the formation of relatively stable ice bridges across connecting channels. However, relaxation of these controls in a warmer climate may cause deterioration in ice conditions in Canadian arctic waters.

There are of course variations in some of the results projected by different climate models and studies (*e.g.*, comparison in Vinnikov *et al.*, 1999) but the most sobering aspect is that most projections go in the same direction (*i.e.*, warmer in the relatively near future). The differences are primarily only in the rate of change and occasionally geographic variation in the strength and timing of effects. Regardless of variations in individual models or papers that deal with different parts of the Arctic, the overwhelming consensus appears to be that the climate is warming, total ice cover is decreasing at a significant rate, and that large parts of the polar basin may be largely or completely ice-free in as little as 100 years. How factors like increased albedo or precipitation may affect the rate of melting are as yet largely unknown thus difficult to model, as is whether the anthropogenic contribution to steadily increasing greenhouse gasses may in future slow, stop, or decline.

TIMING OF ICE FORMATION AND BREAK-UP

The first changes that might be predicted in a steadily warming climate would be for break-up of the annual ice to become progressively earlier while the timing in freeze-up may be delayed. In general, one might also expect such changes to first be documented in more southerly latitudes such as Hudson Bay although, as noted by Skinner *et al.* (1998), the eastern side of Hudson Bay and the Labrador sea were cooling between 1950 to 1990 while the western side was warming.

Much of the life history of polar bears is tied to storing large quantities of adipose tissue when hunting conditions are good and subsequently using these stores during periods of low food availability (Watts and Hansen, 1987; Ramsay and Stirling, 1988). Studies on polar bears in the Canadian Arctic have shown evidence of substantial variation in body size and reproductive output over short periods (2–3 years) mediated by varying ice conditions (Kingsley, 1979; Stirling, 2002) and for longer term changes (10+ years) in reproduction and body mass (Derocher and Stirling, 1995*b*; Stirling *et al.*, 1999). In western Hudson Bay, break-up of the annual ice is now occurring approximately 2.5 weeks earlier than it did 30 years ago (Stirling *et al.*, 1999 and I.S. and N.J.L., unpublished data). This shortens the amount of time that bears are able to feed on seals during the most important time of year—late spring and early summer. There is a highly significant relationship between break-up of the sea ice and condition of the bears when they come ashore (*i.e.*, the earlier they are forced to come ashore, the less fat they have been able to store and fast upon during the 4-month open water period). Declining reproductive rates, subadult survival, and body mass were postulated to be affected by the progressively earlier break-up of the sea ice caused by an increase in spring temperatures (Stirling and Derocher, 1993; Stirling *et al.*, 1999). It is likely that in the future, trends toward either earlier break-up or later freeze-up, or both, will occur in other areas where polar bears seek seasonal refuge on land, such as Foxe Basin or south-eastern Baffin Island.

A key element for understanding and detecting the impacts of climate warming centres on how various elements of polar bear ecology may change, the order and time frame of change, and the patterns of change (*e.g.*, linear, non-linear, or chaotic). We predict both sudden short-term and longer-term changes in both the ecosystem and in polar bears. Short-term fluctuations are likely less important given the *K*-selected nature of polar bears so we are largely concerned with long-term directional changes.

In the following, we apply data collected from polar bears in western Hudson Bay to estimate when further effects of climatic warming and earlier ice break-up might be demonstrable. Adult polar bears lose approximately 0.85–0.9 kg of body mass per day during fasts (Derocher and Stirling, 1995*b*; Polischuk *et al.*, 2002). Given that the sea ice season has shortened by 0.5 days/year in a large part of the coastal annual ice preferred by polar bears in recent years (Parkinson, 2000) this means that the on-ice feeding period is shortened and the fasting period is lengthened. In autumn 1982–90, the mean mass of pregnant females in western Hudson Bay was 283 kg (Derocher *et al.*, 1992). The same study concluded that females below 189 kg in the autumn were unable to successfully reproduce. Starting from the mean mass of 283 kg and assuming the sea ice period shortening by 0.5 days per year, resulting in reduced energy intake and increased energy use, projects that most female polar bears in western Hudson Bay will be unable to reach the minimum mass required to rear viable offspring in roughly 100 years. However, the recorded mass loss of pregnant females in western Hudson Bay was much greater at 4.71 kg/year up until 1992 (Derocher and Stirling, 1995*b*). Using this rate of mass loss, most females would be below the minimum required mass for successful parturition by 2012 assuming a linear decline. Although these estimates are greatly simplified, they illustrate a possible range of time for effects.

There are indications that sea ice changes induced by climate warming will have a greater degree of inter-annual variability. For example, Parkinson (2000) noted that annual variability is high, both in the sea ice season length and monthly distribution. This study also noted that during a period with 18 years of remote sensing data, the September average sea ice cover was lowest in 1995 but was followed in 1996 by one of the highest years. This high variation will lead to highly variable population responses. Of greater concern, however, is the possibility of successive years of poor ice conditions that result in low food intake or high energy output resulting in inadequate adipose stores to undertake successful reproduction. Because polar bears are a long-lived species, they can forgo reproduction during poor environmental conditions for a single or small number of years without a significant population decline but if sufficiently prolonged, a population decline would ensue. Our overall prediction is one of a gradual decline in population-related parameters but this decline may be difficult to detect in the initial phases given the possible increased variance in the environment. In general, population losses can be precursors of extinction and habitat loss is a primary cause of species extinction (Beissinger, 2000; Ceballos and Ehrlich, 2002); as polar bear habitat is altered or reduced, the conservation concerns will increase.

EFFECTS ON DENNING

Female polar bears show fidelity to specific den areas, most of which are on land within a few km of the coast (*e.g.*, Harington, 1968; Schweinsburg *et al.*, 1984; Garner *et al.*, 1994; Ramsay and Stirling, 1990). However, this requires either that the ice drifts or freezes early enough in the fall for pregnant females to be able to either walk or swim to the coast in time to dig a den (late October to early November) in wind-drifted snow before parturition, as they currently do in the Beaufort Sea or Svalbard. As the distance increases between the southern edge of the pack ice, where some polar bear populations spend the summer, and coastal areas where pregnant females den, it will become progressively more difficult for them to reach their presently preferred locations. Considerable inter-annual variation in the distance between ice and terrestrial denning areas is already occurring. For example, in 1995, the distance between the Beaufort Sea coast and the southern limit of the pack ice in September was about 300 km. In Svalbard, the number of maternity dens on the most southern of the denning islands, Hopen, has varied from 0 to over 35 and was strongly correlated with the date that the sea ice arrived the previous autumn (A.E.D., unpublished data). Furthermore, Comiso (2002*b*) suggested that by the 2050s, the mean minimum extent of the sea ice in the polar basin would be about 600 km from the north coast of Alaska or western Siberia and 100 or so km north of Svalbard. Two of the three largest known polar bear denning areas are on Wrangel Island and the Svalbard Archipelago. It seems likely that if this prediction is correct, pregnant females will likely not be able to reach either of these areas or several other coastal locations (such as the north slope of Alaska) where polar bears also have maternity dens, though at much lower densities.

In northern Alaska, between 1981 and 1991, approximately 53% of polar bear maternity dens were found on drifting multiyear ice several hundred km north of the coast (Amstrup and Gardner, 1994). While these bears appeared to successfully raise cubs, between den entry and emergence, those dens drifted 19 to 997 km from the point where the females first entered them (Amstrup and Gardner, 1994). If sea ice thins and becomes more dynamic, it is likely that drift rates of floes with dens will increase. If so, this will require females accompanied by small cubs to travel longer distances, while expending additional energy, to return to the core of their normal home range. One can also speculate that cubs emerging from dens in sub-optimal habitats would experience reduced survival. It is uncertain how quickly bears might learn to exploit alternate denning habitat such as the drifting pack ice if they were unable to access areas they were familiar with on land, or if bears in all populations would respond in this way.

In some areas, an alternative strategy for coping with large expanses of open water separating terrestrial denning areas from residual pack ice in the fall might be for pregnant females to leave the ice at break-up and summer in such locations and then den there. This is the pattern in Hudson Bay at present. This strategy would require that the females were able to accumulate sufficient fat stores to fast for up to 8 months or so before they could return to the sea ice to feed on seals. If the sea ice these bears were using before leaving the ice were over the deep polar basin (as seems to be suggested by Comiso, 2002*b*) where the density of seals is lower than over the continental shelf, it seems less likely that pregnant females would be able to meet the nutritive requirements for such a long period of fasting and nursing cubs.

Even within areas females are familiar with, there may be changes in the habitat available for maternity denning. For example, in Hudson Bay, pregnant female polar bears make extensive use of terrestrial dens dug into permafrost peat banks under black spruce (*Picea mariana*) (Jonkel *et al.*, 1972; Clark *et al.*, 1997). Dens may exist at specific sites for over 200 years because they are periodically re-excavated (Scott and Stirling, 2002). Gough and Leung (2002) predicted that the permafrost along the coast of western Manitoba may be reduced by 50% due to climatic warming by 2100. Also, as temperatures warm, the vegetation within the denning area is likely to become drier and more combustible, thus increasing the risk of fire, after which such areas are unused and unsuitable for polar bear maternity denning for several decades (Richardson, 2004). Fires follow the riparian areas where the permafrost peat is overlaid with black spruce resulting destabilization of the banks in which female polar bears den. The long-term effects of these habitat changes are unknown.

In those populations where females den in snow, significant changes in the distribution and timing of snowfall may alter when suitable snow is available, both in the autumn and in the spring. Insufficient snow will preclude den construction or result in use of poor sites where the roof may collapse. In contrast, excessive snow could influence oxygen flux through the snow layer, necessitating reconfiguration of the dens by females through the winter. Further, changes in snowfall may alter the thermal properties of dens because of the insulative value of the overlying snow layer (Watts and Hansen, 1987). The exact nature of this type of impact on polar bears is difficult to assess but given the altricial nature of cubs at birth (*ca*. 600

g) (Ramsay and Dunbrack, 1986) and their need to be nursed for about three months before they are able to leave the maternity den with their mothers, we suggest that a major change in the thermal properties of dens would have a detrimental effect on cub survival.

An additional concern specific to female polar bears in dens with altricial cubs is the possibility that rain might become more frequent in late winter and cause the snow cover over dens to collapse and suffocate the occupants (Clarkson and Irish, 1991).

MOVEMENTS OF BEARS ON THE SEA ICE

Increasing temperatures are likely to reduce sea ice thickness with the result that it will become more labile. For example, in the Barents Sea, polar bears spend most of year the moving against the direction of the ice drift (Mauritzen *et al.*, 2003*b*). If the ice begins to move more quickly, polar bears may have to use more energy to maintain contact with preferred habitats. Ultimately, increased energy use could result in both lower survival and reproductive rates. In a parallel with fragmentation in terrestrial habitats, it is likely that climate change will result in landscape-scale alteration of habitat connectivity. If the width of leads increases, the transit time for bears to move across the habitat will increase due to the increased need to swim or to travel around the lead. While capable of crossing large areas of open water, polar bears show a marked preference for sea ice (Mauritzen *et al.*, 2003*a*). Polar bears quickly abandon sea ice for land once the sea ice concentration drops below 50% (Stirling *et al.*, 1999) likely because hunting success declines and the energetic costs of locomotion increase because moving through highly fragmented sea ice is difficult and likely more energy demanding than walking over consolidated sea ice. While data are unavailable to compare the energetic costs of walking compared to swimming, it is likely that swimming is energetically even more expensive. We speculate that as habitat patch sizes decrease, the available food resources are likely to decline resulting in a reduced residency time and thus increased movement rates.

Treadmill studies of polar bear energetics revealed that polar bears had higher costs of walking than predicted from general equations for mammals and that polar bears only reach maximum efficiency of walking as adults (Hurst *et al.*, 1982). This suggests that if alterations to the movement patterns cause polar bears to travel further, or move more to remain in a particular area, there will be a greater requirement for energy. Further, the relative impacts of such effects are likely to differ with the age class of the animals and have greater impacts on younger animals. Another related impact is that if the sea ice becomes more labile due to decreased ice thickness and increased winds, then it is possible that some bears near the edge or southern limit of the pack may lose contact with the main body of ice and subsequently drift into inappropriate habitats from which return may be difficult. Southwest Greenland and the island of Newfoundland are examples of where this already occurs. If such events became more frequent and widespread, they could negatively affect survival rates and contribute to population declines.

Female polar bears demonstrate a wide range of space-use patterns, both within and between populations, with annual home ranges as small as 500 km^2 to over 300,000 km^2 (Garner *et al.*, 1991; Ferguson *et al.*, 1997; Ferguson *et al.*, 1999; Mauritzen *et al.*, 2001). In association with this variation in range sizes, the habitat use patterns, diet, and energetics of various populations vary widely. In consequence, we suggest that the impacts of climatic warming on demographic processes will show large geographic variation but even within a population, females with different space-use patterns may be differentially affected.

AVAILABILITY OF PREY

Sea ice is the essential platform from which polar bears hunt. Changes in the distribution of areas of high or low biological productivity will likely alter seal distributions which will in turn result in changes in the distribution of polar bears. A key issue will be how accessible prey species are within an altered sea ice environment. Polar bears are at the top of this ecosystem and track changes in their prey populations (Stirling and Øritsland, 1995; Stirling, 2002). However, increased amounts of open water may reduce the hunting efficiency of polar bears because seals may become less restricted in their need to maintain breathing holes and haul-out sites and thus become less predictable for foraging polar bears. Only rarely has a bear been reported to capture a ringed seal in open water (Furnell and Oolooyuk, 1980) so it is unlikely that hunting in ice-free water will compensate for loss of ice to provide access to ringed seals. Bearded seals, walrus, and occasionally harbour seals (*Phoca vitulina*) are captured by polar bears when hauled out on land but such opportunities tend to be quite local and learned by a limited number of individuals. It is unlikely that predation on these other species would completely compensate for loss of opportunities to hunt ringed seals in most areas. In some areas, such as southern Davis Strait and the Barents Sea, it appears that harp seals are an important component of the diet so it is likely that polar bears would continue to prey on them as long as there was ice in areas occupied by these seals.

Throughout their range, the distribution of polar bears is centred on areas of good hunting habitat so an initial response to a reduction in sea ice could be an increase in bear densities resulting in more competition for the available prey. Reduction in sea ice area may allow increased hunting efficiency by polar bears if seals are restricted to smaller areas of suitable habitat. Concentration of seals in fjords or areas with freshwater influx that may continue to freeze over for longer periods could create a concentrated food resource for polar bears. However, there is an increased likelihood of competition for prey with subordinate animals likely suffering more than dominant bears that can confiscate or monopolize prey. Because polar bears are not territorial, loss of habitat may not result in an immediate loss hunting opportunity through loss of individual home ranges as it would for terrestrial ursids. Regardless, it seems logical overall to predict that a major loss of sea ice habitat will result in a decline in polar bear abundance over time.

Polar bears preferentially feed on the blubber of their prey and adult bears in particular often leave much of the protein behind (Stirling and McEwan, 1975) and do not typically remain with prey (Stirling, 1974; Stirling and Archibald, 1977). Immature bears are not as efficient at catching seals (Stirling and Latour, 1978) and the remains of kills made by other bears may be important for this age class. It is possible that if polar bears experience decreased kill rates, greater use of kills may occur and result in relatively less food for younger bears to scavenge. Scavenging dynamics and competition for prey suggest age-related differences in response to climate warming.

How the primary prey species of polar bears (ringed and bearded seals) will be affected by climatic warming is also uncertain but it appears possible that habitat for ringed seals in particular may be reduced. Both these seal species are territorial during the breeding season (Smith and Hammill, 1981; Van Parijs *et al.*, 2001) and as suitable sea ice habitats are reduced, seal productivity will probably be reduced. Changes to the distribution and timing of sea ice formation can have a significant impact on ringed seal productively. For example, years of very heavy ice in the 1970s and 1980s in the eastern Beaufort Sea resulted in markedly lower productivity of ringed seals and resulted in reduced polar bear productivity (Stirling, 2002). In 1998, ringed seal pup development in Prince Albert Sound, Northwest Territories, was significantly retarded by either reduced area of suitable breeding habitat or an unusually early break-up (Smith and Harwood, 2001). What effect, if any, this may have had on polar bear productivity is unknown. However, unusual climatic events are likely to have major impacts on polar bear-prey dynamics. For example, during unusually mild conditions in 1979 in SE Baffin Island, warm temperatures and rain resulted in ringed seal birth lairs being covered by very soft snow and exposure of some pups resulting in predation success by polar bears three times higher than normal (Hammill and Smith, 1991; Stirling and Smith, 2004). It is likely that if the climate continues to warm, early season rain will become more frequent and will wash away the birth lairs that hide and protect newborn ringed seal pups from predation by polar bears and arctic foxes (*Alopex lagopus*). Without the protection afforded by intact subnivean lairs until the pups are mobile enough to escape from predators by swimming to different breathing holes, it is likely that increased predation resulting from lair collapse or disappearance with warm weather or rain when pups are young, will have a significant negative effect on population size and recruitment of ringed seals and subsequently of bears. Beyond this, it is difficult to project trends with confidence as our knowledge of how ringed and bearded seals use and depend on sea ice is limited as is our ability to forecast their responses to changes in climate and ice conditions.

There are several species of seals whose current distributions lie at the southern edge of polar bear range and could expand northward if ice conditions are altered. In the north Atlantic, harp seals and hooded seals (*Crystophora cristata*), both ice-breeding species, already migrate to the ice edge in summer and currently form a part of the polar bear's diet. It is possible that these species could expand northward and come into greater contact with polar bears particularly if whelping areas are relocated to higher latitudes. In the Barents Sea, a portion of the harp seal population in the White Sea migrates to the sea ice edge in summer (Haug *et al.*, 1994). However, if the ice edge migrates too far north, harp seals may not reach the sea ice where they are vulnerable to predation by polar bears and the seals may shift to a more pelagic distribution already shown by part of the population (Haug *et al.*, 1994). However, this assumes that both harp and hooded seals are able to find suitable pupping habitat. Loss of southern pupping areas due to inadequate or highly variable ice conditions may reduce these species as polar bear prey.

Harbour seals, spotted seals (*P. largha*), ribbon seals (*Histriophoca fasciata*), and gray seals (*Halichoerus grypus*) populations already exist at the edges of the range of polar bears and are not currently common prey. Woolett *et al.* (2000) showed from archaeological data that during periods of warmer weather and presumably less ice, harbour seal bones had a higher frequency of occurrence relative to ringed seals along the coast of northern Labrador and south-eastern Baffin Island and that the opposite was true when the weather was colder and there was more ice. This suggests that as the climate warms and there is more open water in the ice, harbour seals are likely to become more abundant. In western Hudson Bay, preliminary data from the Inuit harvest data and fatty acid signatures in polar bears suggest that harbour seals may already be increasing (I.S. and S. Iverson, unpublished data) and becoming more important prey items for the bears there. Predation attempts on harbour seals have been also observed in Svalbard (Derocher *et al.*, 2002). Over the long term, harbour seals are unlikely to replace ringed and bearded seals as prey for polar bears because they will become most abundant when open water predominates in a region. However, if their numbers increase among the floes and leads as the amount of open water in winter increases they could become more important as prey.

Walrus are a relatively minor prey species of polar bears in most areas but may be locally important in areas such as Foxe Basin, the central High Arctic, and the Bering Sea. Kelly (2001) postulated that walrus might be more vulnerable to polar bear predation if the extent of summer sea ice is reduced by climate warming so that walrus were forced to concentrate in smaller areas. This is of possible benefit to some polar bears but assumes that they will be able to access these walrus haul-out sites and be able to predictably kill walrus. Given the large size of even subadult and young walrus, it is likely that only adult male polar bears would be able to exploit walrus as prey (*e.g.*, Calvert and Stirling, 1990). Furthermore, walrus are aware of the danger represented by polar bears and are capable of threatening and possibly killing polar bears themselves (Kiliaan and Stirling, 1978; Stirling, 1984).

One possible source of alternate prey for polar bears over the short term at least, as a consequence of greater inter-annual fluctuation in environmental conditions, could be an increase in the frequency of ''sassats'' which are entrapments of variable numbers of whales (usually belugas and narwhals) at breathing holes in the ice from which they are unable to escape. They are vulnerable to predation by polar bears at these sites and the amount of nutrition available to both hunting and scavenging polar bears can be substantial, if unpredictable (Lowry *et al.*, 1987). We speculate that such events may become more frequent if sea ice patterns become less predictable. However, the importance of such events to polar bears is difficult to evaluate because the majority of occurrences are likely never observed, regardless of frequency, because areas where sassats might occur are rarely travelled in.

Further difficulty in predicting climate warming impacts is that the behavioural plasticity of polar bears and their prey are unknown. We have assumed that a reduction in sea ice area is largely detrimental to ice-breeding seals but it is conceivable that, similar to their more temperate relatives, they may move to land-based haul-outs, moulting, and pupping areas. Using land may be more likely for bearded seals that occasionally haul-out on land but how ringed seals, which rarely haul out on land, would respond is unknown. Other temperate seals species have a more land-based life cycle and it is conceivable that the polar bear–seal system could become more land-based as the climate warms. Polar bears will use terrestrial resources such as blueberries (*Vaccinium uliginosum*) (Derocher *et al.*, 1993), snow geese (*Anser caerulescens*) (Russell, 1975), and reindeer (*Rangifer tarandus*) (Derocher *et al.*, 2000) but the frequency of occurrence recorded to date indicate that these are relatively unimportant energy sources compared to seals.

CHANGES IN TROPHIC DYNAMICS

The Arctic Ocean is possibly the world's least productive major water body (Pomeroy, 1997). Because the arctic marine system has relatively low species diversity it may be particularly vulnerable to climate mediated changes in species composition (Chapin *et al.*, 1997). Reduced sea ice extent or the timing of sea ice formation and break-up will impact the lower trophic levels of the ecosystems upon which polar bears depend. However, it is significant that climate change may result in both increased and decreased biological productivity in different areas depending upon the changes in sea ice characteristics, snow cover, circulation patterns and other factors which will have ramifications in the food web. The present trophic pathways in arctic marine ecosystems are reasonably well understood (Hobson and Welch, 1992) but the effects of a change in the productivity of lower trophic levels have not been directly linked to higher trophic levels such as ringed and bearded seals. These missing elements make it difficult to determine possible bottom up effects of ecosystem change.

As noted earlier, much of the most biologically productive habitat for polar bears is the annual ice overlying the continental shelf and inter-island channels of archipelagos around the rim of the arctic basin, and more southerly relatively shallow water areas such as Foxe Basin and Hudson Bay. These are the most important areas for polar bears because that is where biological productivity, and hence seals, are most abundant. If as projected by Comiso (2002*b*), a large amount of the pack ice in the polar basin retreats to the north and lies over the deep polar basin, then it is likely that productivity will be less than over the continental shelves. However, with thinner ice and more open water, productivity may be greater than it presently is. This dichotomy makes accurate predictions difficult.

Bearded seals and walrus, feed in relatively shallow waters and rely on benthic prey (Lowry *et al.*, 1980; Kraft *et al.*, 2000; Hjelset *et al.*, 1999) associated with continental shelf areas and rely on annual sea ice for pupping (Burns, 1981). A likely effect of reduced sea ice over the continental shelf is that bearded seals and walrus may be forced offshore to try to find ice suitable for pupping and feeding in areas where the water may be too deep or lack the productivity of near shore habitats. The net result may be reduced bearded seal and walrus abundance and condition with subsequent negative effects on polar bears.

Over the shorter term at least, if the multiyear ice that prevails over the relatively shallow waters of the inter-island channels of the Canadian High Arctic Islands, including Sverdrup Basin, is largely replaced by annual ice as suggested by Melling (2002) and the polynyas in the area (Stirling, 1997) became more numerous and larger it is likely that biological productivity might increase. If so, it is likely the resident populations of ringed seals, bearded seals, and walrus would increase and the area would become better habitat for polar bears.

HUMAN-BEAR INTERACTIONS

Increased polar bear-human interactions were predicted as an impact of climate warming (Stirling and Derocher, 1993), but there is only limited evidence of this occurring to date. However, at Churchill, Manitoba, there were more problem bears handled in town by the Conservation Officers in years when break-up was earlier resulting in bears being thinner than in years when break-up was late (Stirling *et al.*, 1999). In the Beaufort Sea, following the heavy ice winter of

1974 which caused ringed seal productivity to plummet, bears were significantly thinner (Kingsley, 1979) than in earlier years and two humans were killed and eaten by starving bears. Given the widespread distribution of polar bears and the relatively low human density this element of impact may not be detected quickly in some areas and, overall, the number of reported problem bears killed do not show any clear indications of increase (IUCN/SSC Polar Bear Specialist Group, 2002). However, we predict that western Hudson Bay may be one of the first places where polar bear-human problems show signs of increasing.

Demographic Effects

The demographics of polar bears are relatively well understood. Similar to other large mammals, polar bear populations are most sensitive to events that alter adult female survival rates (Bunnell and Tait, 1985; Eberhardt, 1990; Taylor *et al.*, 1987). While studies vary in terms of the relative importance of specific factors associated with high extinction risk, species with small populations, small ranges, and many of the traits of polar bears such as specialized diet, habitat specialisation, large body size, low fecundity, long-lifespan, and low genetic variability are often cited (McKinney, 1997; Beissinger, 2000; Owens and Bennett, 2000). In general, we speculate that climate warming will result in demographic impacts that will affect female reproductive rates and juvenile survival and only affect adult female survival rates under severe conditions.

Declines in body condition (*i.e.*, adipose stores) of polar bears at critical times will result in a cascade of demographic impacts. A decline in body condition will reduce the proportion of pregnant females that are able to initiate denning. Further, females with lower adipose stores will likely produce fewer cubs (more singleton litters) and smaller cubs with lower survival rates because body mass in adult females is correlated with cub mass at den emergence which in turn, is correlated with cub survival (Derocher and Stirling, 1996; Derocher and Stirling, 1998). For those females with adequate adipose stores to initiate denning, it is likely that the proportion abandoning the attempt will increase and result in more females emerging mid-winter after aborting the reproductive event. If maternal resources are insufficient or the hunting conditions in the early spring after den emergence are poor, then this could lead to increased cub mortality post den emergence. In addition, polar bear cub mortality was thought to be high in some areas of Svalbard owing to extensive areas of open water (Larsen, 1985) in part due to the rapid chilling of cubs exposed to cold water (Blix and Lentfer, 1979). If sea ice conditions are poor and females with new cubs are forced to swim from den areas to the pack ice then cub mortality may increase.

Body mass in female polar bears increases until roughly 15 years of age (Derocher and Stirling, 1994) suggesting that females slowly accrue body fat. It is also likely that the age of first reproduction, or at least the age of first successful reproduction, will be delayed as growth rates and adipose stores of females are reduced. Reduced reproductive success in females will be an early indicator of climate change but not distinctly so because such effects can also be related to other processes such as a density-dependent response, pollutants, or diseases. Reduced cub survival will result in shorter inter-birth intervals and may result in more solitary adult females in any given year. For this reason, den surveys are unlikely to yield meaningful insight into population trends unless cub survival and recruitment can be monitored. Overall, we predict a lengthening of the time between successful weaning of offspring.

The decline in reproductive output will likely be highly variable as prey availability fluctuates depending on ice conditions. Time lags in the system, also induced by reproductive failure and possible reproductive synchrony, may obscure temporal trends over short periods. If conditions become sufficiently irregular, adult survival may be reduced and sudden population declines would occur. The timing of mortality in polar bears is poorly documented but we predict it would be most severe in winter when fat stores are low and the availability of prey is limited. Facultative mid- to late-winter use of dens in cold weather (Ferguson *et al.*, 2001) demonstrates the need to conserve energy so the shortening of the spring feeding period is unlikely to be compensated for by additional hunting in winter.

Pollution and Disease

It is likely that climatic warming will also alter the pathways and concentrations of pollutants entering the Arctic via long-range transport on air and ocean currents (AMAP, 1998; Proshutinsky and Johnson, 2001). Many persistent organic pollutants reach high levels in polar bears due to their high fat diet and high trophic position (Norstrom *et al.*, 1998). Recent studies on polar bears suggest that pollutants impact the endocrine system (Skaare *et al.*, 2001), immune system (Bernhoft *et al.*, 2000), and subsequent reproductive success of polar bears (Derocher *et al.*, 2003). If polar bears become food stressed and their immune system is further challenged, it is possible that they may become more vulnerable to disease or parasites. With the exception of *Trichinella* sp., polar bears are relatively free of parasites (Rogers and Rogers, 1976; Forbes, 2000) and infrequently show signs of disease (but see Taylor *et al.*, 1991; Garner *et al.*, 2000; Tryland *et al.*, 2001). Apparently, polar bears left most diseases and parasites behind when they moved to a marine system and shifted to a diet made up predominantly of fat in which few parasites have intermediate hosts. Whether this apparent lack of disease and parasite exposure makes polar bears more vulnerable to new pathogens is unclear. Also, if bears become more food stressed, they may begin to eat more of the intestines and internal organs of seals and other species than they do at present which may make them more vulnerable to encounter-

TABLE 1. *Hypothetical climate change impacts on polar bears, time scale of impacts (short = <10 years, medium = 10–20 years, long = >20 years), direction of projected change, and potential for monitoring.**

Characteristic	Time frame	Projected change	Monitoring potential
body condition	short	decline, increased variation	good
movement patterns	short	alteration of existing patterns	good
cub survival	short	decline, increased variation	good
reproductive rates	short	variable, increased variation	good
bear-human interactions	variable	increase	good
den areas	medium	change in areas and substrates	good
growth rates	medium	variable	fair
prey composition	medium	change in species, utilisation, age of prey	fair
population boundaries	medium	mixing of adjacent populations	fair
population size	medium	variable	fair
intraspecific aggression	variable	increased	poor
cannibalism	variable	possible increase	poor
adult survival	long	decline, increased variation	poor

* Time frame of impact will vary between populations and is dependent upon rate of change in a given population.

ing parasites or viruses that might be capable of infecting them. It is also possible that new pathogens may expand their ranges northward as the climate warms (Harvell *et al.*, 2002).

ASSESSING AND PREDICTING THE IMPACTS OF CLIMATE CHANGE

Exactly how and when polar bears will respond to climate change in different areas is uncertain but based on life history characteristics we suggest that the species is vulnerable in several areas, at least over the longer term. Our ability to monitor the effects of climate change on specific parameters varies widely (Table 1). Some parameters such as adult survival rates will have a large impact on population trend but are difficult and expensive to measure. Lack of good long-term base-line data in most areas makes interpreting the results of new monitoring programs more difficult. Parameters such as body condition or mass are relatively easy to obtain and provide insight into the underlying mechanisms (*e.g.,* net energy intake). Other parameters such as population boundaries are expensive to study and would require several years to document significant long-term changes because there is substantial annual variability. Monitoring of a suite of parameters will likely yield the greatest insight. We suggest some of the most effective aspects to monitor would include body mass, growth rates, cub survival, and reproductive rates within focal populations, with continuation of monitoring the sex and age composition of the harvest. It may also be possible to sample some tissues over time to obtain further trend data on condition, health, and disease. In cases where sufficient funding exists, it may be possible to maintain more detailed monitoring of population size to provide a quantitative background from which to assess climate change impacts.

There are relatively few polar bear populations that are studied intensively enough to provide information on population trends over time. Of the world's 20 populations, 2 are of unknown population size, 6 have poor estimates of size, 8 have fair estimates, and only 4 are classed as having good population estimates (IUCN/SSC Polar Bear Specialist Group, 2002). One difficulty with the hypothetical northward shift of polar bears is that the High Arctic Islands are almost certain to become an important refuge for polar bears and this area is among the least studied of anywhere in Canada. The polar bear populations in Norwegian Bay, Kane Basin, and Queen Elizabeth are all small (presently numbering less than 200 bears each) (IUCN/SSC Polar Bear Specialist Group, 2002). The current lack of information in these areas means that any increase in these populations would be difficult to detect. Further, monitoring the global population size of polar bears is impractical and not particularly useful in any case because the bears in different regions and populations will respond differently. In many areas, it is likely that the first indications of declining populations, reduced condition, or disease will come from local hunters.

The large amount of inter-annual variability in the sea ice environment will make monitoring of change more difficult over the short term because the statistical power to detect trends will be reduced. Similarly, it is uncertain which changes might occur in either a linear or non-linear fashion. It is not possible to confidently predict whether a reduction in sea ice area would necessarily result in a corresponding reduction in the size of polar bear populations or if under some circumstances, the number might remain similar for some time. Alternatively, in some areas polar bear populations may increase if the changes increased seal populations.

Currently, large data sets exist of the age of captured polar bears for many populations where inventory projects have been conducted. These data sets provide a venue to assess long-term population change but if capture conditions become more difficult with decreasing ice cover, this source of information may be increasingly difficult to collect. Information collected on the age and sex of hunter-harvested animals is another area that could provide long-term trend information but this will be hampered by the likelihood of altered harvest and vulnerability over time. Age- or sex-related changes in vulnerability to harvest may make it difficult to separate behavioural changes from demographic changes. Relatively small harvests in each population may result in low statistical power.

Only a few polar bear populations currently have sufficient long-term data with which a more in-depth assessment into the possible effects of climate change can be made. Western Hudson Bay and the Beaufort Sea are prime candidates for continued research. The southern Hudson Bay, Lancaster Sound, and Svalbard populations are also reasonable candidates but the continuity and time series of information are lower than the two best populations. Most other populations have a much lower level of research activity and lack long-term data. Despite this, a meaningful venue for investigation of the effects of climate change on polar bears would be at the margins of their current range in areas like the Chukchi Sea, Davis Strait, and SE Greenland where distribution patterns are largely determined by annual variation in sea ice. An improved understanding of habitat use and factors affecting the movement patterns of polar bears in these areas may allow insights into how polar bears will respond to climate change.

The greatest challenge now is to implement the appropriate studies and infrastructure within the Arctic to monitor and document the sensitive linkages and the ecosystem responses. For example, the role of bottom-up processes on polar bears is largely unknown and will take dedicated research with a multi-disciplinary approach. Specifically, projection models for future conditions of Arctic sea ice are relatively new and uncertainty in these models make it more difficult to predict or assess the possible impacts on polar bears. Extent and duration of annual sea ice is a particularly critical component for understanding impacts on polar bears.

In contrast to many terrestrial and most marine species that may be able to shift northward as the climate warms, polar bears are constrained in that the very existence of their habitat is changing and there is limited scope for a northward shift in distribution. Due to the long generation time of polar bears and the current pace of climate warming, we believe it unlikely that polar bears will be able to respond in an evolutionary sense. Given the complexity of ecosystem dynamics, predictions are uncertain but we conclude that the future persistence of polar bears is tenuous.

MANAGEMENT ADAPTATIONS AND ACTIONS

Polar bears in parts of Russia, Alaska, Canada, and Greenland are harvested on a sustainable basis; some at maximal levels (Lee and Taylor, 1994; IUCN/SSC Polar Bear Specialist Group, 2002). In Canada, 14 polar bear populations have been identified for management purposes based on mark and recapture methods and radio telemetry on adult females (Taylor and Lee, 1995; Taylor *et al.*, 2001). Population structure was also examined using genetic markers and four genetic clusters were identified (Paetkau *et al.*, 1999). The present boundaries of populations are largely dictated by the presence of geographic obstacles such as islands, patterns of break-up and freeze-up of sea ice, bathymetry, maternity denning areas, hunting habitats, and summer retreats during the open water season. We hypothesize that climate change is likely to alter the delineation of polar bear population boundaries as they are currently known due to changes in sea ice distribution leading to altered habitat connectivity and movement patterns. East-west boundaries are more likely to weaken as polar bears shift northward. In some areas, north-south boundaries may weaken if populations seek common refuge areas but may strengthen if habitats become fragmented. For example, in time, we predict that the population in the southern Beaufort Sea will merge with the northern Beaufort Sea and that the Davis Strait population will merge with the Baffin Bay population. The populations in these two areas already have some overlap so that a reduction in sea would likely increase overlap. Similarly, populations in the Canadian High Arctic may merge if animals are forced to retreat into smaller areas. Obviously, if such amalgamations of populations occurs, and is detectable, they should be managed as single units.

If climate change alters the survival and reproductive rates of polar bears, sustainable harvest levels will need to be adjusted or if populations decline, harvest may eventually need to be closed altogether. Further, given that most polar bear harvesting occurs in spring on the sea ice (Lee and Taylor, 1994) it is possible that hunters may shift their harvest to other seasons if sea ice conditions deteriorate and make spring hunting difficult. This already occurs in Hudson Bay. To some degree, harvest of polar bears may be self-regulating as travelling conditions on the sea ice deteriorate, hunters will be less effective at hunting. In Hudson Bay and Foxe Basin, where most hunting currently occurs on land during the open water season in autumn, harvest patterns may be less affected and less likely to be regulated by changes in hunter access. Greater monitoring of harvest impacts will be required in all populations. For example, changes in hunter behaviour may alter age and sex patterns of the bears harvested. Of concern is the potential that the demographics of polar bears in different populations may change with altered ecological conditions induced by climate warming. If survival rates, age of maturity, or reproductive rates shift from historical values, managers must respond appropriately and methods of harvest quota calculation may need to be reassessed. The social and economic implications to local communities of losing this harvest are beyond the scope of this paper but could have serious local economic consequences.

Currently, most hunted polar bear populations are inventoried using mark and recapture methods to determine sustainable harvests (*e.g.*, DeMaster *et al.*, 1980; Furnell and Schweinsburg, 1984; Derocher and

Stirling, 1995*a*; Amstrup *et al.*, 2001) and large sample sizes are required to provide good confidence intervals. With climatic warming, it may be more difficult to conduct such studies because the sea ice conditions could become more difficult for capture (*e.g.*, more open water, thin ice, fog, bears in more remote areas). Further, as individual bears become more stressed by climatic warming (*e.g.*, lower hunting success and poorer condition), capture programs may encounter greater handling mortality although current mortality levels are very low (Stirling *et al.*, 1989). Consequently, new inventory methods may need to be developed. Aerial surveys may provide such an alternative means of population monitoring (McDonald *et al.*, 1999; Wiig and Derocher, 1999; Evans *et al.*, 2004).

Another potential source of long-term impact may result from increased shipping in the Arctic as sea ice retreats northward (Kerr, 2002). As shipping traffic increases, disruption of ice covered areas will occur and the likelihood of dumping and accidents in polar bear habitat will increase. Polar bears are sensitive to oil from spills (Stirling, 1990) and it is likely this source of impact will increase mortality rates of polar bears and their prey. These types of impacts are difficult to quantify but need to be addressed should northern shipping routes become a reality.

Changes to the physical structure and dynamics of sea ice may also impose subtle behavioural interactions in the population. For example, if sea ice becomes more friable and dynamic, it is possible that males may have greater difficulty finding females because males often track oestrous females long distances and tracking ability is reduced if the ice floes are small and in motion. This impact would be reflected in reduced pregnancy rates or an extended breeding season. In contrast, if sea ice area is diminished, the density of breeding bears may increase and males may find oestrous females easier to locate but also result in greater interference and competition for access to them.

Overall, many of the predictions we have made in this paper are subject to a high degree of uncertainty but a highly specialised species such as the polar bear is vulnerable to habitat change and such change has occurred and is continuing to occur through climate warming.

ACKNOWLEDGMENTS

We are grateful to the following for their support of our research over the years which has allowed us to gather the data and experience to write this paper: Canadian Wildlife Service, Churchill Northern Studies Centre, Conservation Manitoba, Northern Ecosystem Initiative, Nunavut Wildlife Management Board, National Sciences and Engineering Research Council of Canada, Norwegian Polar Institute, Parks Canada, Polar Continental Shelf Project, University of Alberta, and World Wildlife Fund (Arctic, Canada, and International).

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