# Chapter 23
# Polar Bears and Sea Ice Habitat Change

**George M. Durner and Todd C. Atwood**

**Abstract** The polar bear (*Ursus maritimus*) is an obligate apex predator of Arctic sea ice and as such can be affected by climate warming-induced changes in the extent and composition of pack ice and its impacts on their seal prey. Sea ice declines have negatively impacted some polar bear subpopulations through reduced energy input because of loss of hunting habitats, higher energy costs due to greater ice drift, ice fracturing and open water, and ultimately greater challenges to recruit young. Projections made from the output of global climate models suggest that polar bears in peripheral Arctic and sub-Arctic seas will be reduced in numbers or become extirpated by the end of the twenty-first century if the rate of climate warming continues on its present trajectory. The same projections also suggest that polar bears may persist in the high-latitude Arctic where heavy multiyear sea ice that has been typical in that region is being replaced by thinner annual ice. Underlying physical and biological oceanography provides clues as to why polar bear in some regions are negatively impacted, while bears in other regions have shown no apparent changes. However, continued declines in sea ice will eventually challenge the survival of polar bears and efforts to conserve them in all regions of the Arctic.

## 23.1 Introduction

The evolution of extant Arctic marine mammals is tightly linked to climatic factors that influenced the formation and development of sea ice, and as such current climate factors may threaten their persistence. The Arctic Ocean became seasonally ice covered due to a cooling environment beginning in the mid-Eocene (~45 million

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A. Butterworth (ed.), *Marine Mammal Welfare*, Animal Welfare 17,
DOI 10.1007/978-3-319-46994-2_23

years ago, mya; Moran et al. 2006) with further cooling leading to the development of perennial sea ice ~14 mya (Darby 2008; Moran et al. 2006). This new sea ice habitat that persisted throughout the annual cycle presented ecological opportunities for the radiation of Arctic marine mammals. Phocid seals, which likely originated in southern latitudes ~20 mya, expanded their range to northern Atlantic waters at least 15 mya (Harington 2008)—largely coinciding with the appearance of perennial sea ice. This resulted in some northern hemisphere phocids becoming sea ice specialists, isolating them from their southern counterparts and causing their radiation into six species that fill sea ice niches today (Harington 2008). Arctic phocids are widespread and abundant, with at least one species comprising up to two million individuals (i.e., ringed seals, *Pusa hispida*; Kelly et al. 2010). The early adaptation and success by these seals to utilize Arctic sea ice presented opportunities for a new apex predator, the polar bear (*Ursus maritimus*).

The polar bear evolved as a specialist predator of ice-adapted seals (Fig. 23.1), primarily ringed seals but also bearded seals (*Erignathus barbatus*; Stirling and Archibald 1977; Stirling and Øritsland 1995). Polar bears are believed to have diverged from a brown bearlike ancestor sometime from as recently as 160 kya to as long ago as 5 mya (Hailer et al. 2012; Lindqvist et al. 2010; Miller et al. 2012). Regardless of which divergence estimate is used, the ancestor of present-day polar bears clearly entered a sea ice environment with abundant resources and few, if any, competitors. Despite periodic hybridization with brown bears (*U. arctos*; Bidon et al. 2014; Edwards et al. 2011; Miller et al. 2012), selective drivers in the Arctic have resulted in the genotypic and phenotypic traits in modern polar bears that are largely absent of brown bear ancestry (Cahill et al. 2015).

The present-day distribution of polar bears is concordant with the extent of Arctic and sub-Arctic marine waters that are normally covered by sea ice for at least 7–8 months of the year. The Arctic undergoes large seasonal fluctuations in sea ice extent, from a winter maximum of ~15.5 million km$^2$ to a summer minimum of ~6.3 million km$^2$ (1981–2010 average; National Snow and Ice Data Center (2016a, b). As a result, polar bears in much of their range change their distribution with the seasonal changes in sea ice. Despite the necessity for polar bears to adjust their distribution to this labile substrate, and the continuity of Arctic sea ice during most of the year, individuals show such strong philopatry (Amstrup et al. 2004; Paetkau et al. 1999) to regions that the entire world's population can be divided into 19 relatively discrete subpopulations (Fig. 23.2; Obbard et al. 2010).

These subpopulations, however, may be grouped into four ecoregions (please see Chap. 22; Fig. 23.2), each of which has distinct seasonal composition and dynamics of sea ice, underlying oceanography, and influence of adjacent land masses. Following the convention put forth by Amstrup et al. (2008), these include:

1. Seasonal Ice Ecoregion—sea ice typically melts completely and is absent 3–4 months during summer (subpopulations: Baffin Bay, Davis Strait, Foxe Basin, Southern Hudson Bay, and Western Hudson Bay [WH]). In the Seasonal Ice Ecoregion, polar bears are forced to summer on land where food consumption is negligible and activity is reduced.

**Fig. 23.1** Typical hunting modes used by polar bears on the spring sea ice in the Beaufort Sea. (**a**) An adult male polar bear still hunting at a seal hole (15 April 2009) and (**b**) an adult female with her 2-year-old young at a ringed seal lair adjacent to a pressure ridge, where they successfully captured an adult seal (12 April 2000). *Image credits:* **(a)** *Michael Lockhart, United States Geological Survey (USGS);* (**b**) *George Durner, USGS*

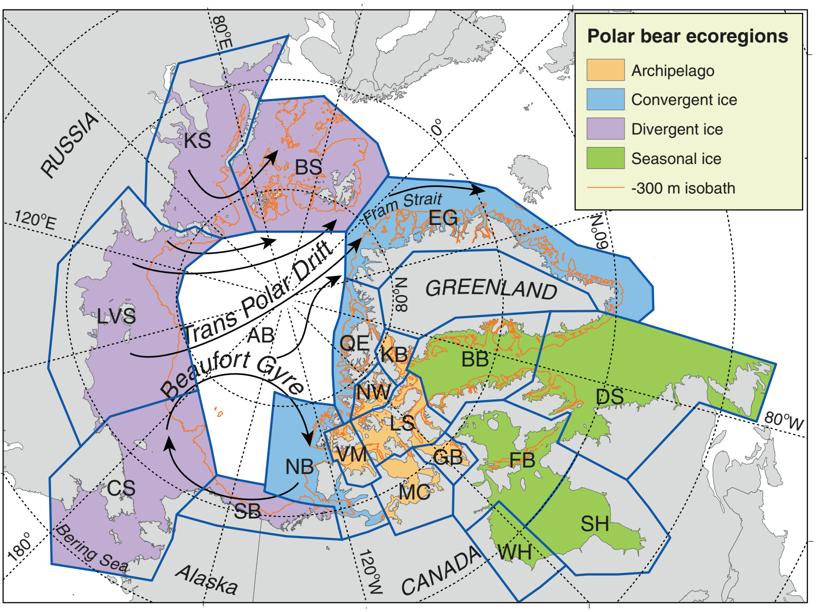

**Fig. 23.2** Distribution of 19 polar bear subpopulations and four ecoregions. Southern Beaufort Sea (SB), Chukchi Sea (CS), Laptev Sea (LVS), Kara Sea (KS), Barents Sea (BS), East Greenland (EG), Queen Elizabeth (QE), Northern Beaufort Sea (NB), Southern Hudson Bay (SH), Western Hudson Bay (WH), Foxe Basin (FB), Davis Strait (DS), Baffin Bay (BB), Gulf of Boothia (GB), M'Clintock Channel (MC), Lancaster Sound (LS), Viscount-Melville Sound (VM), Norwegian Bay (NW), and Kane Basin (KB). Note the location of subpopulations relative to the 300 m bathymetric contour and ice drift patterns. *Black arrows* indicate generalized path of primary currents (*Source*: Amstrup et al. (2008) *Geophysical Monograph 180:213–268*)

2. Archipelago Ecoregion—the channels and bays within the island complex of northern Canada (subpopulations: Gulf of Boothia, Kane Basin, Lancaster Sound, M'Clintock Channel, Norwegian Bay, and Viscount Melville Sound). In the Archipelago Ecoregion, some sea ice survives the summer melt, resulting in a high proportion of ice >1 year old (i.e., multiyear ice) in subsequent seasons. Because of the proximity of islands and larger land masses, a high proportion of ice in the Archipelago Ecoregion does not drift as it is frozen to land (i.e., landfast ice) from autumn to spring. Polar bears in the Archipelago Ecoregion have access to sea ice throughout the year as summer ice concentration remains relatively high (>50%) (Canadian Ice Service 2016a, b).
3. Divergent Ice Ecoregion—seas within the Arctic Ocean proper, primarily over the continental shelves of northern Eurasia, northern Alaska, and mainland northwest Canada (subpopulations: Barents Sea, Chukchi Sea, Kara Sea, Laptev Sea, and Southern Beaufort Sea [SB]). Historically, some sea ice over continental shelves was retained during summer and persisted into autumn freeze-up, providing hunting habitat for polar bears throughout the year. More recently, sea

ice over continental shelves in the Divergent Ice Ecoregion melts nearly to completion or is advected to other regions by currents of the Transpolar Drift and the Beaufort Gyre (Fig. 23.2). Recent patterns of sea ice melt and freeze now force most bears in this ecoregion to follow sea ice into the deep waters of the Arctic Ocean, or, to a lesser extent, onto land.

4. Convergent Ice Ecoregion—spanning northern and eastern Greenland and the northern edge of the Canadian Archipelago (subpopulations: Northern Beaufort Sea, Queen Elizabeth, and East Greenland). In the Convergent Ice Ecoregion, summer sea ice melt is minimal, and ice is received via the Transpolar Drift and the Beaufort Gyre from the Divergent Ice Ecoregion. Entrainment of ice by the Beaufort Gyre in the Northern Beaufort Sea and Queen Elizabeth subpopulations results in those waters consisting of the oldest and thickest sea ice in the Arctic.

There is commonality among ecoregions because polar bears are an ice obligate species that depend on sea ice for fulfilling life history requirements (e.g., hunting seals, traveling, seeking mates). However, variation in the composition, distribution, and pattern in the annual formation of sea ice influences polar bear distribution, life history, and demography. Climate-mediated displacement from preferred sea ice habitat, as is considered later, can have significant consequences for polar bear subpopulations.

## 23.2 Sea Ice Selected by Polar Bears Throughout Their Range

To appreciate how climate change is influencing polar bear habitat, it is helpful to understand how polar bears distribute themselves relative to sea ice extent and composition. Research on polar bear habitat use has been conducted on most of the 19 subpopulations. With few exceptions (Stirling et al. 1993; Pilfold et al. 2014), the bulk of these studies became possible through the advent of satellite radiotelemetry (Fig. 23.3; Fancy et al. 1988), which has provided location data of individual polar bears across the annual sea ice cycle (e.g., Amstrup et al. 2004). Satellite-derived locations of polar bears, when coupled with environmental data (e.g., sea ice attributes) and analyzed with statistical models (i.e., Resource Selection Functions, RSFs; Manly et al. 2002), have revealed broad-scale spatial and temporal characteristics of sea ice that are important for polar bears—aspects which researchers were largely unable to identify and quantify due to difficulty of making visual observations of bears across their range and throughout the year. In addition to pinpointing important habitat characteristics, RSFs have the added benefit, due to the wide spatial extent and frequent collection of satellite-collected environmental data, of providing information on the distribution of optimal sea ice habitats of polar bears across most of their range. The development of RSFs to describe important polar bear habitat has revealed how optimal habitat changes seasonally and across years and is likely to change decades beyond the present (Fig. 23.4; Durner et al. 2009).

**Fig. 23.3** Placing a satellite radio collar on an adult female polar bear in the southern Beaufort Sea, 12 April 2005. *Image credit: Eric Regehr, USGS*

### *23.2.1 The Importance of Sea Ice Concentration and Composition*

In subpopulations where RSF models have been developed, sea ice concentration (SIC; i.e., the areal extent of ice-covered versus ice-free waters within a defined area) can be one of the most important environmental variables affecting polar bear distribution. In other words, the mere presence or absence of sea ice is insufficient for predicting the distribution of optimal habitats and likely distribution of bears. The reasons for this are that polar bears require sea ice with characteristics that enable them to hunt efficiently, and which provides security against inclement weather. With the possible exception of the Archipelago Ecoregion, a stable ice platform is necessary for bears to avoid being swept into open ocean (Mauritzen et al. 2003). For this discussion we focus on polar bear habitat patterns modeled from SIC, as estimated largely from passive microwave (PMW) imagery. Since 1978, PMW estimates of Arctic SIC and extent (Cavalieri et al. 1996) have been disseminated as daily and monthly means in raster format (25 × 25 km pixel size) from the National Snow and Ice Data Center (NSIDC; http://nsidc.org/). These data provide a consistent long-term data source to measure changes in polar bear habitat.

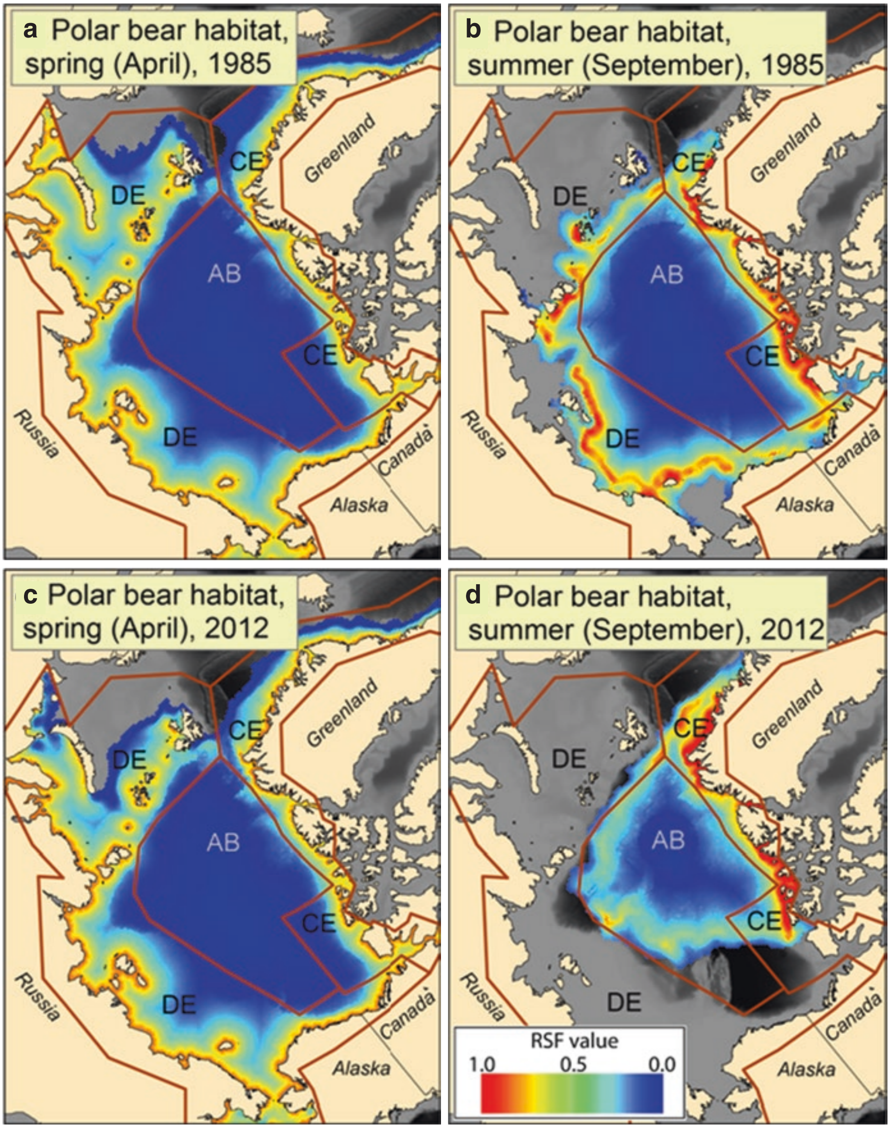

**Fig. 23.4** A polar bear resource selection function comparing the distribution of polar bear sea ice habitat quality in the Arctic Basin (AB) and the Convergent (CE) and Divergent (DE) ecoregions (see Fig. 23.2) (1985 and 2012) during spring (**a** and **c**) and summer (**b** and **d**), based on Durner et al. (2009). Habitat quality ranges from poor (*blue tone* RSF) to optimal (i.e., the upper 20% of RSF-valued habitat, indicated by *yellow-red tone* RSF). *Gray tones* indicate ocean depth, where *light gray* indicates continental shelves and *dark gray* to *black* indicates deep polar basin waters. *Source*: Durner et al. (2009)

Additionally, habitat indices developed from PMW data, when coupled with twenty-first-century projections of sea ice made with general circulation models (GCMs), present a view of the potential impacts of future greenhouse gas-induced warming. Although other sea ice charts (e.g., National Ice Center 2016; Canadian Ice Service 2016a, b) are available that provide estimates of ice stage (thickness) and form (e.g., floe size), those data are more limited temporally and spatially, precluding their use in estimating decadal trends in polar bear sea ice habitat and making projections into the twenty-first century.

Arthur et al. (1996) first demonstrated the response of polar bears to SIC using satellite telemetry data from five adult female polar bears in the Chukchi Sea. By analyzing telemetry and PMW data with RSFs, they found polar bears were most selective of 51–75% SIC during spring and 21–50% SIC during summer. Studies in several other subpopulations have shown selection by polar bears for ~50–90% SIC (Fig. 23.5; Durner et al. 2004, 2006, 2009; Ferguson et al. 2000; Laidre et al. 2015; Mauritzen et al. 2003; Pilfold et al. 2014; Wilson et al. 2014). While patterns of habitat selection relative to SIC are clearly elucidated by RSFs, models also show

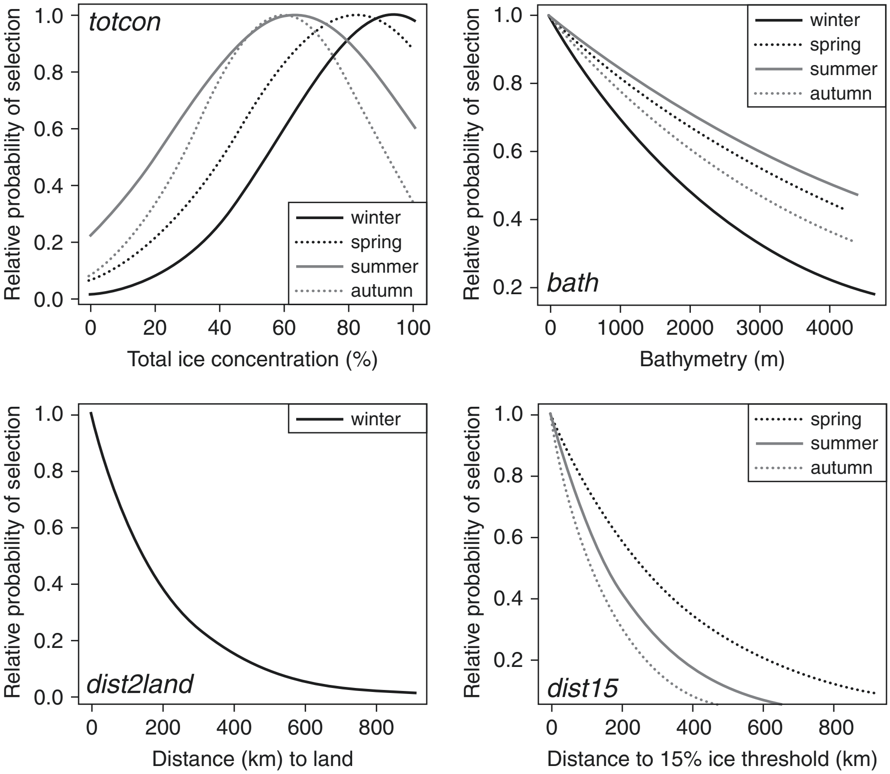

**Fig. 23.5** Resource selection function results for the response of polar bears to habitat variables in the polar basin (1985–1995). Total ice concentration is the percent of ocean surface covered by sea ice. Bathymetry is ocean depth. *Source*: Durner et al. (2009)

that polar bears select relatively high SIC in close proximity to areas with low SIC (i.e., <15–50%) and near land (Fig. 23.5; Durner et al. 2009; Laidre et al. 2015; Pilfold et al. 2014). However, habitat selection is seasonally dependent (Durner et al. 2004, 2009; Ferguson et al. 2000; Laidre et al. 2015; Wilson et al. 2014), with lower concentrations of sea ice being selected during spring breakup (i.e., time when sea ice begins to fragment) and summer (Fig. 23.5; Durner et al. 2004, 2009; Ferguson et al. 2000; Laidre et al. 2015; Wilson et al. 2014). But in subpopulations whose sea ice is composed of a high proportion of landfast ice (i.e., sea ice attached to land, as in the Canadian Archipelago) or where sea ice converges (i.e., east Greenland Sea), concentrations near 100% are highly selected by polar bears during winter months (Ferguson et al. 2000; Laidre et al. 2015).

*The distribution of sea ice relative to the continental shelves*—Aside from the reliance on moderate to high SIC adjacent to low SIC, the spatial and temporal distribution of sea ice is also a determinant of habitat quality for polar bears. In general, the sea ice that we described in the prior paragraph can occur anywhere in the Arctic during some point in the annual cycle. However, the most biologically rich regions across the range of polar bears are in the Arctic's peripheral seas and over the continental shelves (<300 m deep). Several factors contribute to the relative richness of shelf waters. As pack ice is a dynamic substrate that drifts due to winds and currents (Spreen et al. 2011), the motion of ice next to landfast ice or shorelines creates regions of stress in the pack ice (i.e., shear zones) where fracturing of ice creates long cracks in the ice that remain open for hours to days (i.e., leads) and larger areas of open water (i.e., polynyas; Stirling 1997). Shelf waters are adjacent to basins with depths up to 3000 m (Jakobsson et al. 2008). This combination of shelf and basin results in a unique distribution of upwellings that mix deep-origin nutrient-rich waters with current-influenced waters near and over the continental shelf (Carmack and Wassmann 2006; Christensen 2008; Horner and Schrader 1982; Piatt and Springer 2003; Sigler et al. 2011). Seals remain in these productive shelf waters, even as the summer melt reduces or completely removes sea ice (Harwood and Stirling 1992; Harwood et al. 2012). Hence, biologically rich waters near and over the continental shelf coincide with an abundance of leads and polynyas to provide necessary habitat for several marine mammals, including polar bears (Stirling 1997).

RSFs for polar bears indicate a distribution of optimal sea ice habitat that is consistent with our understanding of primary productivity and prey habitat use. Arctic marine waters, with drifting ice of mid-to-high concentration over continental shelves, provide the nexus for optimal polar bear habitat (Fig. 23.4; Durner et al. 2009; Pilfold et al. 2014; Wilson et al. 2014).

### *23.2.2 Observed Changes in Optimal Habitat*

Arctic sea ice extent has been substantially reduced and is projected to continue to decline during the twenty-first century (Comiso 2012; Meier et al. 2007; Overland and Wang 2013; Stroeve et al. 2007). PMW estimates of sea ice extent show multidecadal declines in sea ice both during the winter maximum and the summer minimum (Fig. 23.6). Likewise, polar bear habitat in most of the Arctic basin subpopulations and in the Seasonal Ice Ecoregion declined during the decade following 1995 (Durner et al. 2009; Stirling et al. 1999; Stirling and Parkinson 2006). Between the years 1985–1995 and 1996–2006, the total number of months of optimal sea ice habitat (i.e., the upper 20% of RSF-valued habitat) declined ~14% in the Barents Sea, ~12% in the Chukchi Sea, ~10% in the east Greenland Sea, and ~6% in the southern Beaufort Sea (Fig. 23.7; Durner et al. 2009). The greatest declines in

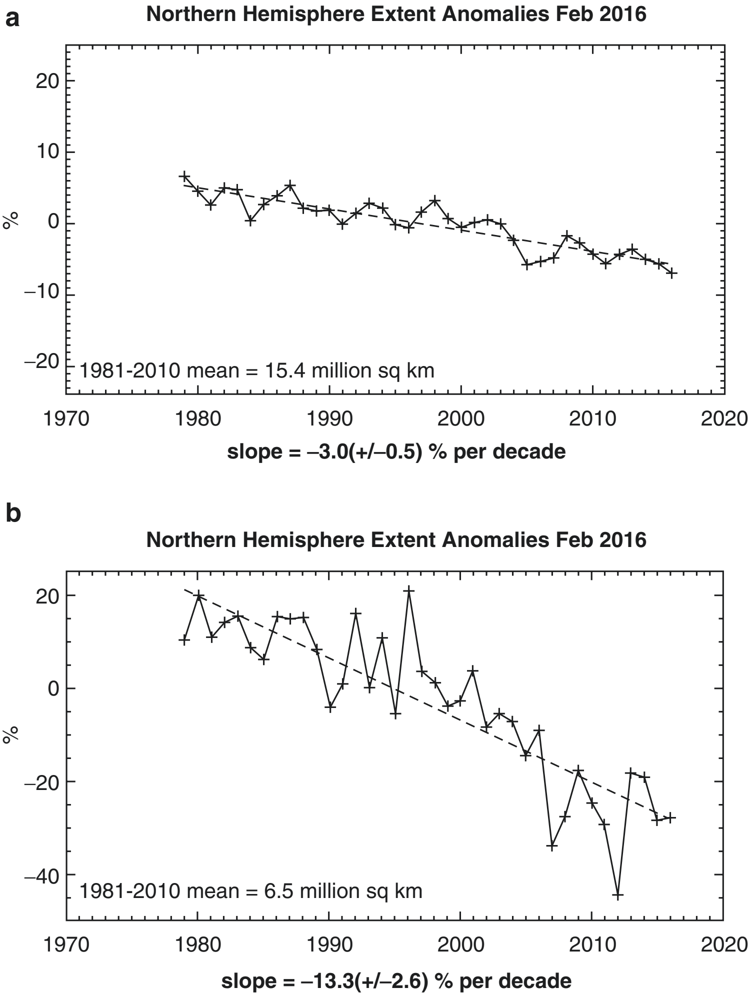

**Fig. 23.6** Sea ice anomalies for (**a**) February (winter) and (**b**) September (summer) 1979–2015, relative to the 1981–2010 mean sea ice extent for the respective month (February, 15.4 million km$^2$; September, 6.5 million km$^2$). Arctic sea ice extent has been declining 3.0% decade$^{-1}$ (winter maximum) and 13.4% decade$^{-1}$ (summer minimum). *Source*: *NSIDC, ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/, accessed 3 December 2016*

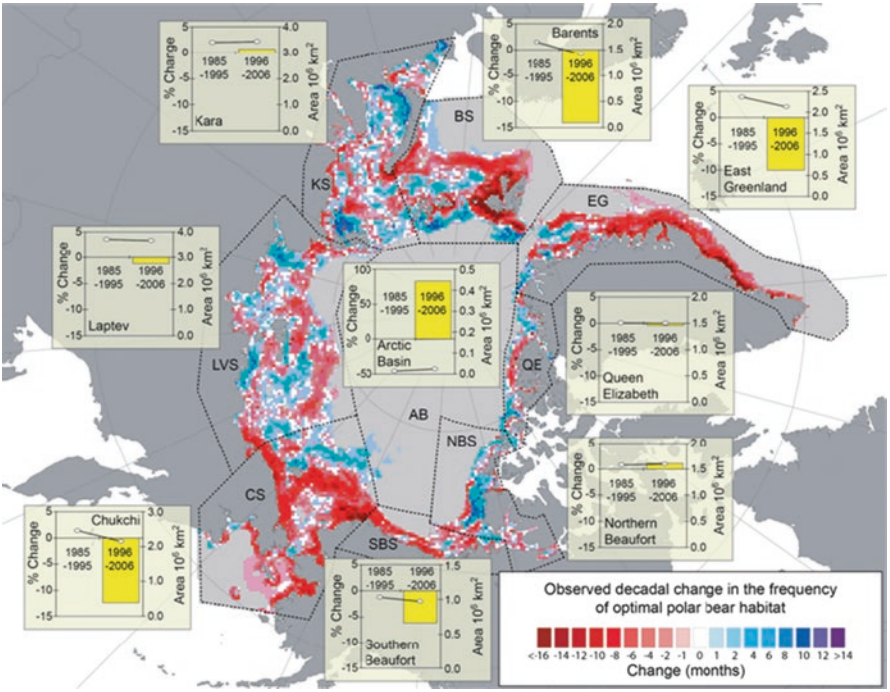

**Fig. 23.7** Observed changes in polar bear optimal habitat (i.e., the upper 20% of RSF-valued habitat) in the polar basin, comparing the total number of months of optimal habitat in 1985–1995 compared to 1996–2006. Loss (gain) in optimal habitat is indicated by *red* (*blue*) colors. *Gray* indicates no optimal habitat was present in either decade. *Source*: Durner et al. (2009)

optimal habitat occurred during spring breakup and summer—largely as a result of sea ice melting beyond continental shelves and into the deep waters of the Arctic Ocean (Fig. 23.4d). Within the Seasonal Ice Ecoregion, a region that typically loses sea ice every summer, increasing duration of the ice-free season has displaced bears from preferred sea ice habitat to land for longer periods (Stirling et al. 1999; Stirling and Parkinson 2006). This is illustrated in Hudson Bay where from 1971 to 2003, annual breakup and freeze-up dates became 40 days earlier and 18 days later, respectively (Gagnon and Gough 2005).

### *23.2.3 Projections of Future Polar Bear Optimal Sea Ice Habitat*

Current and future climate change is “extremely likely” to be linked to human activities, most notably from industrial emissions of carbon dioxide and methane (Intergovernmental Panel on Climate Change, IPCC; IPCC 2013). The IPCC (2013) projects that ≥5 consecutive years of nearly ice-free conditions (i.e., sea ice extent $<1 \times 10^6$ km$^2$ of SIC >15%) in the Arctic during September are likely before 2050. Beyond 2050, the IPCC (2013) projects that Arctic sea ice is "very likely" to decrease through the remainder of the twenty-first century. The shoulder months of August and October will likely see Arctic-wide ice-free conditions by 2070 (Laliberté et al. 2016), resulting in an earlier breakup and later freeze-up. Observed and projected sea ice loss is driven in a large part by an ice cover that is becoming thinner and by the increased vulnerability of this thinning ice to complete summertime melt (Holland et al. 2010). Climate models (i.e., GCMs) from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Coupled Model Intercomparison Project (2016) utilized emission scenarios based on different radiative forcings (i.e., Representative Concentration Pathways (RCP), expressed as watts per m$^2$ above preindustrial levels at year 2100) imposed by different levels of greenhouse gas (GHG) emissions. As expected, high GHG emissions result in higher radiative forcing and increased likelihood of sea ice loss during the latter part of the twenty-first century (Fig. 23.8). With one notable exception, hindcasts from GCMs agree well with satellite observations of sea ice extent, and this lends confidence in the use of GCMs for projecting future conditions. The exception is that observed summertime declines in sea ice exceed that projected by GCMs (Fig. 23.8; Overland and Wang 2013). Hence, projections of the twenty-first-century sea ice declines made with CMIP5 GCMs can be considered conservative.

Since 1979, when satellite data on sea ice distribution first became available, six of the lowest September sea ice minimums have occurred after 2006, resulting in ice-free waters in most regions of the Divergent Ice Ecoregion, the entire Seasonal Ice Ecoregion, and parts of the Archipelago Ecoregion during those years (National Snow and Ice Data Center 2012). Of interest to the future status of polar bears is how the ice-free period may become longer in future years and how this may vary among regions. By using CMIP5 twenty-first-century projections of sea ice, Laliberté et al. (2016) demonstrated the advancement of the ice-free season to earlier months for the coming decades varies by region. Arctic seas adjacent to northern Asia (i.e., Kara Sea and Laptev Sea) may experience ice-free conditions in July as early as 2050. Near Alaska, projections of ice-free waters in the Chukchi and Beaufort seas during July are not expected until ~2080 and 2095, respectively, likely due to advection of thick multiyear ice from the central Arctic (Laliberté et al. 2016). At the extremes, ice-free conditions in the central Arctic Ocean and the Canadian Archipelago are not expected to occur until ~2070 during August; however, an ice-free Hudson Bay for July has been possible since 2010. The study by Laliberté et al. (2016) provides additional evidence that polar bear response to habitat loss will be regionally specific (Atwood et al. 2016).

Projections of the twenty-first-century polar bear habitat have included all ecoregions (Castro de la Guardia et al. 2013; Durner et al. 2009; Hamilton et al. 2014). In Hudson Bay 30–50% SIC has been identified as a critical threshold below which bears begin moving on to land during spring breakup, or 10% SIC, above which bears move from land to back to the sea ice during autumn freeze-up (Cherry et al. 2013; Stirling et al. 1999). This presents an important distinction between the standard of <15% SIC used by geophysicists (see, e.g., National Snow and Ice Data

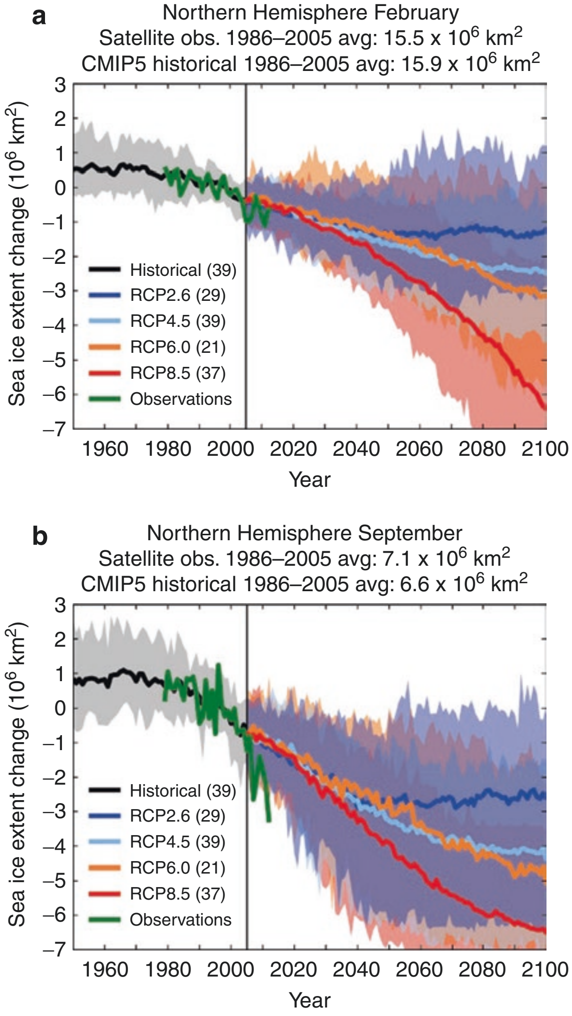

**Fig. 23.8** The late twentieth- and twenty-first-century Arctic sea ice extent change (defined by concentration >15%) simulated by CMIP5 (Coupled Model Intercomparison Project) ensembles under Representative Concentration Pathways (RCP)2.6, RCP4.5, RCP6.0, and RCP8.5 for (**a**) February and (**b**) September, relative to conditions during 1986–2005. Solid lines represent multi-model means, and shading indicates the 5–95% range of the ensemble. Sample sizes for each RCP are indicated in the legend. Observational data of sea ice extent (1979–2012) are indicated by the *green solid line*. Note the greater observed loss of sea ice relative to that projected by GCMs after 2005. *Source*: *Fig. 12.28 in Collins et al. (2013). Chap. 12. Long-term climate change: projections, commitments and irreversibility (IPCC 2013)*

Center 2016a, b) to denote ice-free conditions and what are effectively ice-free conditions for polar bears. In projections of the twenty-first-century polar bear habitat in the Seasonal Ice and Archipelago Ecoregions, ice-free conditions were assumed to include the period when SIC reaches <30–50% in the spring to when SIC became

>10% in autumn (Castro de la Guardia et al. 2013; Hamilton et al. 2014). Using IPCC (2000) GHG emission scenarios for projections of the twenty-first-century WH sea ice (Fig. 23.2), Castro de la Guardia et al. (2013) projected spring SIC to decline from 1.0 to 13.5% decade$^{-1}$ between 2001 and 2100, resulting in 2100 SIC at 20–84% of 2001 levels. They found that between 2035 and 2100, WH trends in breakup dates and ice-free periods range from 1.7 to 13.0 days decade$^{-1}$ earlier and 2.2 to 20.7 days decade$^{-1}$ longer, respectively. The overall effect projected by Castro de la Guardia et al. (2013) was for the 2100 ice-free season in WH to be 4.5–18.7 weeks greater than it would be had GHG emissions remained at 2001 levels.

For the Archipelago Ecoregion (Fig. 23.2), Hamilton et al. (2014) adopted a similar approach to that of Castro de la Guardia et al. (2013) by projecting SIC through the twenty-first century with a worst-case GHG emission scenario (i.e., RCP 8.5; IPCC 2013). In the seven polar bear subpopulations that they examined, none had ice-free conditions in any month during 1992–2005. Even with substantial GHG forcing, the annual pattern of SIC 2040–2060 was largely similar to 1992–2005 levels, albeit with lower summer SIC minima. However, during the last two decades of the century, all seven subpopulations are expected to experience multiple months of ice-free conditions. By the end of the twenty-first century, four subpopulations were projected to be ice-free for up to 5 months and the other three for 2–5 months. This means that bears in those subpopulations would be forced to use land during ice-free months. Hamilton et al. (2014) also show that this threshold SIC required for optimal habitat may be reduced to only 6 months a year, which is below the annual ice-covered duration currently experienced by the most southern polar bear subpopulation (i.e., Southern Hudson Bay).

For the Divergent and Convergent Ice Ecoregions, Durner et al. (2009) extrapolated RSFs to GCM projections of Arctic Ocean SIC to predict trends in the twenty-first-century optimal sea ice habitat for nine subpopulations. Their approach differed from that of Castro de la Guardia et al. (2013) and Hamilton et al. (2014) in that the RSF included, in addition to SIC, explanatory variables of ocean depth, distance to land, and distance to the 15% SIC threshold. Because ocean depth greatly influenced the RSF, the habitat value for a given level of SIC and proximity to the 15% SIC threshold over the continental shelf was greatly diminished for otherwise identical ice characteristics over deep waters beyond the shelf (Fig. 23.4). Because GCMs project that the majority of the twenty-first-century sea ice declines occur between spring and autumn, and that ice continues to return throughout the Arctic Ocean each winter, extrapolation of RSFs to GCM projections reveals high seasonal variability in habitat loss. Whereas Arctic Ocean winter habitat value decreased <10% by the end of the twenty-first century, the habitat value decreased >50% for summer (Durner et al. 2009). Likewise, there was considerable regional variation in the twenty-first-century habitat change, with most showing that the decadal cumulative frequency of optimal habitat occurring in any particular month would decline by between 25 and 50% by 2041–2050 (Fig. 23.9). Only the Arctic Basin, Queen Elizabeth, and the northern-most part of the Northern Beaufort subpopulations are likely to experience an increase in optimal sea ice habitat. Otherwise, the frequency of optimal habitat is projected to decrease in regions that are currently most important for polar bears (Fig. 23.9).

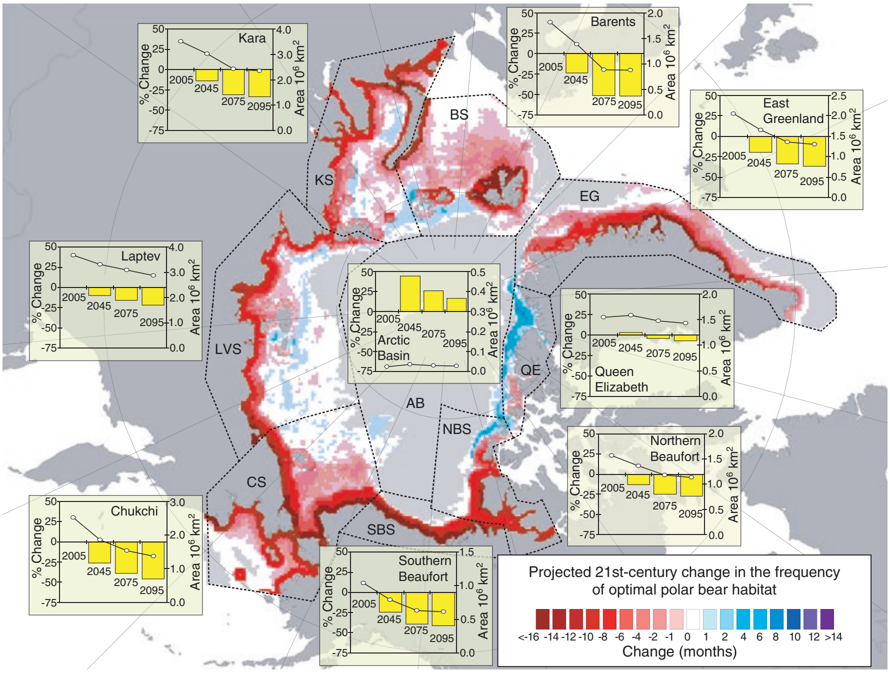

**Fig. 23.9** Projected changes in polar bear optimal habitat (i.e., the upper 20% of RSF-valued habitat) in the polar basin, comparing the total number of months of optimal habitat in 2001–2010 compared to 2041–2050. Loss (gain) in optimal habitat is indicated by *red (blue) colors*. *Gray* indicates no optimal habitat was present in either decade. *Source*: Durner et al. (2009) *Ecol Monogr 79:25–58*

## 23.3 Consequences of Habitat Loss to Polar Bear Health, Reproduction, and Populations

Links between sea ice conditions and polar bear body condition (i.e., an index of health derived from body mass, linear body measurements, fatness estimates, or blood chemistry) have been drawn for several subpopulations from polar bears harvested by indigenous people for subsistence and from bears captured and released by scientists. Within the Seasonal Ice Ecoregion, correlations between declines in polar bear body condition and declining sea ice have been made for the WH (Lunn et al. 2016; Stirling et al. 1999), Southern Hudson Bay (Obbard et al. 2016), Davis Strait, and Baffin Bay (Rode et al. 2012) subpopulations. In the Divergent Ice Ecoregion, polar bears of the SB (Rode et al. 2010, 2014) and Barents Sea (Derocher 2005) subpopulations also appear to be showing declines in body condition that may be related to climatic variation. These studies largely point to a hypothesis of reduced accessibility to seal prey as the primary driver for declines in body condition, although density-dependent effects may have been a contributor in some subpopulations (Derocher 2005; Peacock et al. 2013; Rode et al. 2012).

Variation in polar bear body condition may also be attributed to bottom-up effects of primary productivity, population response of prey, and/or the appearance of alternate prey—all of which are driven by interactions between sea ice and the underlying oceanography. Potential examples of bottom-up effects include (1) changes in the extent and composition of sea ice influencing the productivity of seal populations (Crawford et al. 2015; Harwood et al. 2015; Ferguson et al. 2005), which in turn can directly affect polar bears; (2) polar bears of the Chukchi Sea subpopulation show unchanging body condition, despite sea ice declines, that is likely due to biologically productive waters over a broad continental shelf and a relatively diverse prey base (Rode et al. 2014); and (3) increases in the abundance of harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals in Davis Strait with the resulting increase in bear abundance in that region, again in contrast to reductions in sea ice (Peacock et al. 2013; Stirling and Parkinson 2006). In essence, there is a tight relationship between the productivity of seals and the productivity of polar bears (Stirling and Øritsland 1995), such that the population response of polar bears to climate change can be, to some degree, independent of sea ice abundance.

Maintaining an optimal body condition is necessary for growth, body maintenance, and reproduction. Successful parturition and first-year survival of young are dependent on the condition of pregnant bears immediately prior to den entrance in the autumn, as the burden of gestation, nursing, and fasting can result in a den-bound adult losing 43% of its body mass during the 4–5 months of den tenure (Fig. 23.10; Atkinson and Ramsay 1995). Female polar bears exhibit delayed implantation, and there is evidence that bears <189 kg are unlikely to successfully reproduce (Derocher et al. 1992). To achieve body reserves sufficient for reproduction, female polar bears are dependent on a period of hyperphagia (i.e., near-constant, "super eating," over eating) (Ramsay and Stirling 1988) during late spring and early summer, when newly weaned naïve juvenile seals are abundant and sea ice is present in extent and composition that allows efficient hunting (Stirling et al. 1999). This reaches an extreme within the Seasonal Ice Ecoregion, as pregnant polar bears spend summer on land for 3–5 months, enter maternal dens in autumn, and do not resume hunting until the following March—a potential fasting duration of 8 months (Atkinson and Ramsay 1995; Stirling et al. 1999). For polar bears in other ecoregions, activity data collected from satellite telemetry suggests a similar pattern of hyperphagia during late spring and early summer (high activity) and fasting during summer (low activity) when preys are less available (Ferguson et al. 2001; Messier et al. 1992; Whiteman et al. 2015). Energetic models further support the necessity to polar bears for late spring and early summer sea ice, as advancement of breakup by only 1 month could result in 40–73% of female bears failing to reproduce and a reduction in litter size by 22–67% (Molnár et al. 2011).

Not only is the ability of adult female bears to successfully raise and wean young compromised in an Arctic with diminished sea ice, but other sex and age groups are vulnerable. Subadult bears, because they are likely to still be developing hunting skills, may be especially vulnerable to sea ice habitat loss (Bromaghin et al. 2015; Regehr et al. 2007). But even prime-age adult polar bears, which are the most resilient

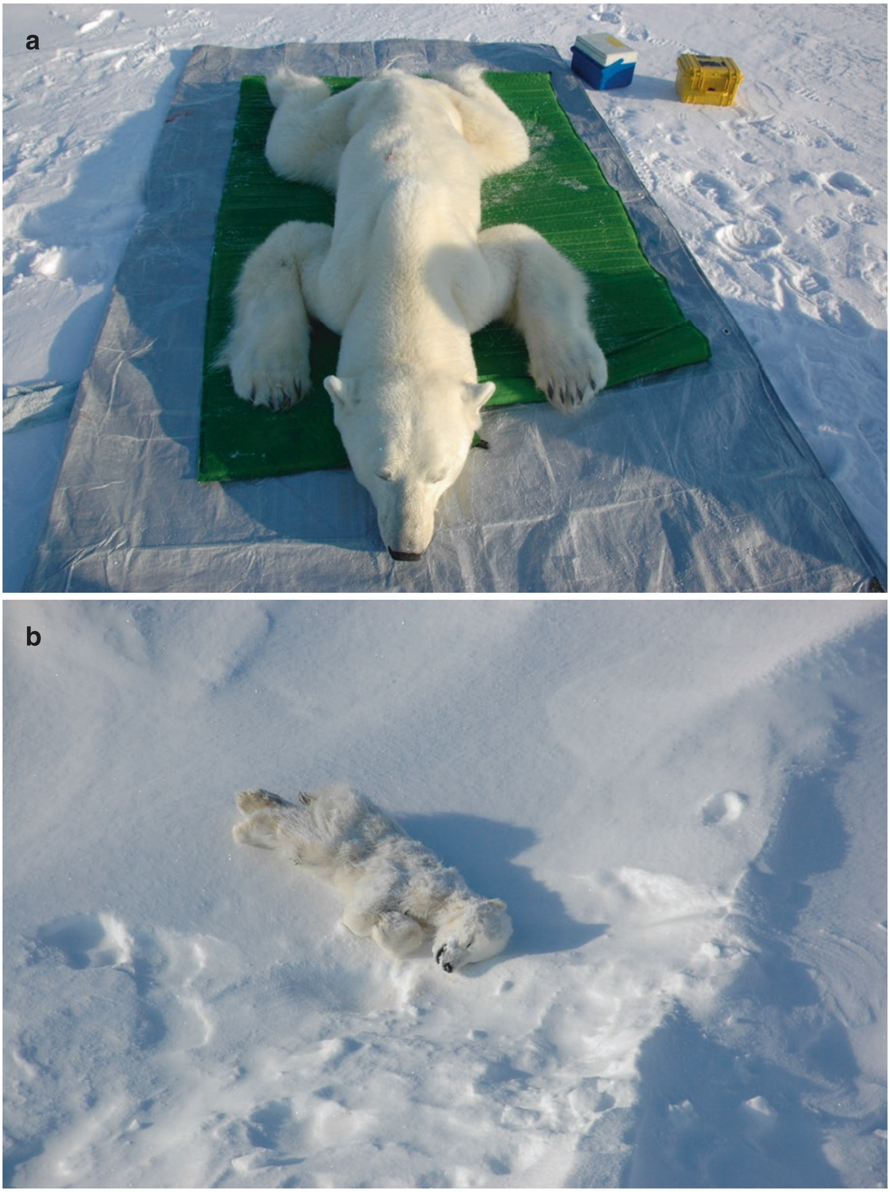

**Fig. 23.10** (**a**) A starving adult female polar bear (137 kg) captured in the Beaufort Sea and (**b**) its emaciated dead cub (9 April 2009). Not shown is the surviving sibling of the dead cub. The adult entered a maternal den in the previous autumn with enough body fat for successful parturition and nursing in the den, but insufficient fat to continue nursing after den departure. Both the adult and surviving cub were observed roaming the pack ice on the following day. Subsequent genetic samples collected at a fur trap in Barrow, Alaska, in February 2011 confirmed survival of the adult. The cub has not been reobserved. *Image credit: George Durner, USGS*

members to environmental perturbations (Regehr et al. 2007), are unlikely to weather consecutive years of sea ice loss. Using a dynamic energy budget model, Molnár et al. (2010, 2014) showed that a 4-month absence of sea ice would result in 2–3% of adult males dying from starvation, but 9–21% could succumb to starvation if the duration of absence were to increase to 6 months. The relationship between adult survival and sea ice conditions is also supported by empirical models: in studies of the SB subpopulation, adult female survival declined precipitously when the number of ice-free days over the continental shelf increased from 3.5 to 4.5 months (Bromaghin et al. 2015; Regehr et al. 2010). For the WH subpopulation, Regehr et al. (2007) found a relationship between early ice breakup and reduced subadult survival but not for adult survival. Even in the northern Beaufort Sea, a region where sea ice has remained stable for three decades, polar bear survival was dependent on the condition of sea ice habitat (Stirling et al. 2011).

Increased displacement from optimal sea ice habitats during late spring and early summer during the hyperphagic feeding period (i.e., periods of very high food intake) has been hypothesized to be the reason for documented downward trends in body condition since the early 1980s (Obbard et al. 2016; Rode et al. 2010, 2012; Stirling et al. 1999). However, the energetic cost of changing sea ice dynamics for polar bears goes beyond displacement from optimal hunting habitat. Simply traveling across a sea ice substrate that, due to thinning, has become more fractured and vulnerable to drifting is likely to increase energy costs for polar bears as they attempt to search for and occupy the most optimal habitat for hunting seals and searching for mates (Castro de la Guardia et al. 2013; Sahanatien and Derocher 2012). Also, because there is a greater duration and extent of ice-free waters in the Arctic during summer, polar bears are increasingly engaging in open-ocean swims (Fig. 23.11) that can involve several hundred kilometers over as much as 9 days (Durner et al. 2011; Pagano et al. 2012; Pilfold et al. 2016). Although polar bears swim well in cold Arctic waters, swimming distances >100 km likely imposes high energetic costs, may result in mortality of the young (Durner et al. 2011), and increases their vulnerability to outright drowning (Monnett and Gleason 2006).

A changing sea ice platform can also affect the ability of polar bears to access suitable denning habitat (Stirling and Derocher 2012). Pregnant polar bears are reliant on

**Fig. 23.11** A male polar bear swimming between ice floes in the Beaufort Sea (26 April 2009). *Image credit: Michael Lockhart, USGS*

**Fig. 23.12** A female polar bear emerges from her maternal den next to a coastal bluff near Prudhoe Bay, Alaska (April 2009). *Image credit: Rusty Robinson, Brigham Young University*

dens of snow to provide a relatively warm and constant environment for parturition and growth of neonates, and the den must occur on a substrate that will remain stable for 3–5 months during the winter (Amstrup and Gardner 1994). Throughout the Arctic, most denning occurs on land (Fig. 23.12), although denning on sea ice occurs in the Beaufort Sea (Amstrup and Gardner 1994). For bears summering on pack ice, the greater extent of summertime open water and thinning sea ice platform that has been observed in recent years is increasing the necessity for pregnant bears to swim long distances or walk over a fractured surface (Pilfold et al. 2016; Sahanatien and Derocher 2012), and these conditions have prevented bears from reaching land traditionally used for denning (Derocher et al. 2011). SB polar bears represent the only subpopulation know to den on pack ice to a large degree (Amstrup and Gardner 1994; Fischbach et al. 2007). However, the suitability of sea ice as a denning substrate has declined since 1998 as Arctic Ocean pack ice has become thinner, younger and less stable (Fischbach et al. 2007). As a result, SB polar bears are increasingly using land for maternal denning (Fischbach et al. 2007), and, hence, an increasing proportion of the population must contend with unfavorable sea ice conditions to reach denning habitat.

Relating habitat loss to changes in population demography has only been possible for a few subpopulations which have received intensive capture-recapture studies. In regions that have high biological productivity and prey abundance

(Rode et al. 2014), have shown little loss of sea ice (Stirling et al. 2011), or have abundant alternate prey (Stirling and Parkinson 2006), the respective subpopulations have shown little apparent change in response to an otherwise warming Arctic. In the future Arctic, high-latitude marine waters including the northern Canadian archipelago and northern Greenland may experience an increase in habitat suitability as thick multiyear sea ice is replaced by thinner annual ice (Durner et al. 2009). This may have benefited some northern subpopulations of polar bears over the past three decades of declining sea ice (Stirling et al. 2011), and the relative persistence of sea ice in northern regions may serve as a refugium for a remnant population during the latter years of the twenty-first century (Atwood et al. 2016; Peacock et al. 2015). However, subpopulation sizes within the peripheral regions of the current circumpolar range of polar bears will likely decline, possibly to the point of extirpation, as sea ice is reduced in both its temporal and spatial extent (Amstrup et al. 2008; Atwood et al. 2016). Indeed, measureable population declines appears to have already begun in some subpopulations, such as the SB (Bromaghin et al. 2015; Regehr et al. 2010) and WH (Regehr et al. 2007).

## 23.4 Conclusions

Rapid loss of sea ice habitat in the twenty-first century brought on by anthropogenic greenhouse gas-driven climate warming presents the greatest stressor on all polar bear subpopulations (Amstrup et al. 2008; Atwood et al. 2016; Stirling and Derocher 2012). The impact of sea ice habitat declines on polar bears is multifaceted and will largely be a combined effect of reduced energy intake through reductions in prey availability; increased energetic costs to bears because of greater ice drift, greater open-water extent and duration, and an increasingly fractured icescape; and interference with the behavior of polar bears that is necessary for reproduction. Ultimately, these factors will reduce the availability of energy polar bears require to successfully reproduce. During the past three decades of warming global temperatures and concomitant declines in sea ice thickness and extent, some polar bear subpopulations have shown no apparent change and, indeed, may have even benefitted from ameliorating multiyear sea ice conditions as primary productivity and prey have increased. However, even those regions with currently stable subpopulations are vulnerable to the impacts of the projected twenty-first-century sea ice loss (Hamilton et al. 2014; Stirling et al. 2011). Continued climate warming-caused habitat loss will negatively impact all polar bear subpopulations by the later decades of the twenty-first century and currently represents the most significant conservation threat to the species (Amstrup et al. 2008; Atwood et al. 2016; Stirling and Derocher 2012).

**Acknowledgments** We thank Evan Richardson (Environment and Climate Change Canada) and Martyn Obbard (Ontario Ministry of Natural Resources) whose input on earlier versions greatly improved this chapter.

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