

Forecasting the relative influence of environmental and anthropogenic stressors on polar bears

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Citation: Atwood, T. C., B. G. Marcot, D. C. Douglas, S. C. Amstrup, K. D. Rode, G. M. Durner, and J. F. Bromaghin. 2016. Forecasting the relative influence of environmental and anthropogenic stressors on polar bears. *Ecosphere* 7(6):e01370. 10.1002/ecs2.1370

Abstract. Effective conservation planning requires understanding and ranking threats to wildlife populations. We developed a Bayesian network model to evaluate the relative influence of environmental and anthropogenic stressors, and their mitigation, on the persistence of polar bears (*Ursus maritimus*). Overall sea ice conditions, affected by rising global temperatures, were the most influential determinant of population outcomes. Accordingly, unabated rise in atmospheric greenhouse gas (GHG) concentrations was the dominant influence leading to worsened population outcomes, with polar bears in three of four ecoregions reaching a dominant probability of decreased or greatly decreased by the latter part of this century. Stabilization of atmospheric GHG concentrations by mid-century delayed the greatly reduced state by ≈ 25 yr in two ecoregions. Prompt and aggressive mitigation of emissions reduced the probability of any regional population becoming greatly reduced by up to 25%. Marine prey availability, linked closely to sea ice trend, had slightly less influence on outcome state than sea ice availability itself. Reduced mortality from hunting and defense of life and property interactions resulted in modest declines in the probability of a decreased or greatly decreased population outcome. Minimizing other stressors such as trans-Arctic shipping, oil and gas exploration, and contaminants had a negligible effect on polar bear outcomes, although the model was not well-informed with respect to the potential influence of these stressors. Adverse consequences of loss of sea ice habitat became more pronounced as the summer ice-free period lengthened beyond four months, which could occur in most of the Arctic basin after mid-century if GHG emissions are not promptly reduced. Long-term conservation of polar bears would be best supported by holding global mean temperature to $\leq 2^\circ\text{C}$ above preindustrial levels. Until further sea ice loss is stopped, management of other stressors may serve to slow the transition of populations to progressively worsened outcomes, and improve the prospects for their long-term persistence.

Key words: Arctic; Bayesian network; climate change; conservation; greenhouse gas emissions; influence analysis; mitigation; stressor evaluation; *Ursus maritimus*.

Received 16 July 2015; revised 14 February 2016; accepted 4 March 2016. Corresponding Editor: G. Chapron.

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INTRODUCTION

The Arctic ice cap has provided critical habitat for ice-adapted marine mammals, including

polar bears (*Ursus maritimus*) (Kovacs et al. 2011), for millenia (Polyak et al. 2010). Over the last two decades, increased air temperature (Lindsay and Zhang 2005) and advection processes that have

moved warm Pacific water into the Arctic Ocean (Shimada et al. 2006) and transported older and thicker sea ice out through Fram Strait (Serreze et al. 2007) have driven a rapid decline in sea ice volume and summer extent (Arrigo et al. 2008, Wang and Overland 2009, Kovacs et al. 2011, Stroeve et al. 2014). These changes have negatively impacted some populations of ice-adapted species such as polar bears (e.g., Stirling and Derocher 1993, 2012, Amstrup et al. 2008, Derocher et al. 2013). In 2008, the polar bear was listed as globally threatened under the U.S. Endangered Species Act (ESA) based on projections suggesting that continued reductions in sea ice habitat, along with other stressors from changing environmental conditions and anthropogenic activities, presented a cumulative threat to the species' long-term persistence (U.S. Fish and Wildlife Service 2008).

Polar bears preferentially forage in first-year sea ice that occurs over biologically productive continental shelf (shallow) waters (Durner et al. 2009). Declines in the extent and temporal availability of ice over such areas reduces their access to ringed (*Pusa hispida*) and bearded (*Erignathus barbatus*) seals, their preferred prey (Thiemann et al. 2008), and represents a loss of preferred habitat. Throughout the Arctic, the annual period of reduced ice availability (i.e., the open-water season) has lengthened 13 d/decade since 1979, with a modest trend toward an earlier mean date of break-up and a pronounced trend toward later freeze-up (Stroeve et al. 2014). In some polar bear populations, the longer open-water season has been linked to declines in body condition (Stirling et al. 1999, Obbard et al. 2006, Rode et al. 2010), reproductive indices (Stirling and Parkinson 2006), and survival (Regehr et al. 2007, 2010). Moreover, energy budget models suggest a 30-d increase in the length of the open-water season could lead to a significant rise in reproductive failure and starvation for populations already experiencing protracted open-water periods (Molnár et al. 2010, 2014, Robbins et al. 2013).

While reduced sea ice availability has been linked to declining vital rates of some polar bear populations, geographic variation in sea ice persistence and ecosystem productivity has modulated the global population response. For example, an increase in the Davis Strait polar bear population has been attributed to greater

availability of secondary prey (i.e., harp seals; *Pagophilus groenlandicus*) concurrent with the lengthening open-water season (Peacock et al. 2013). Likewise, in the biologically productive Chukchi Sea, polar bear body condition and reproduction have remained relatively unchanged despite a substantial reduction in the extent of sea ice (Rode et al. 2014). The Northern Beaufort Sea polar bear population was considered stable through 2006 despite a trend of declining sea ice, probably due to the tendency of some sea ice to persist during summer over the continental shelf (Stirling et al. 2011). Collectively, these studies indicate that geographic variation in sea ice dynamics and ecosystem productivity are important determinants of polar bear population dynamics, as Bromaghin et al. (2015) concluded.

Historically, polar bears throughout their range spent most of their annual life cycle on the sea ice. With the lengthening open-water season, however, more bears will spend a greater amount of time on shore where they are likely to be exposed to increasing levels of human activities such as extraction of oil and gas, and trans-Arctic shipping (Amstrup et al. 2006, Gautier et al. 2009, Smith and Stephenson 2013, Stephenson et al. 2013) and tourism, as well as industrial chemicals and effluents (Amstrup et al. 1989, Derocher and Stirling 1991, Smit et al. 2008) and human–bear conflict, all of which raise the potential for lethal outcomes for bears. Similarly, the extensive sea ice cover of the past may have functioned as a physical barrier to disease agents by limiting contact between polar bears and vectors. Exposure to disease and parasites is not thought to represent a current threat to polar bears (Vongraven et al. 2012). However, climate change is expected to alter host–pathogen associations, transmission dynamics, and pathogen resistance (Burek et al. 2008) and increase interactions among marine mammal species (Kovacs et al. 2011). All are cause for concern given the relatively naïve immune system of polar bears (Weber et al. 2013).

Emission of greenhouse gases (GHG) at current or increased rates will cause further warming, additional sea ice declines, and other changes to the Arctic marine ecosystem (IPCC 2014), and likely result in substantial declines in polar bear abundance (Amstrup et al. 2008, 2010). Future temperatures, and thus Arctic sea ice extent, will

depend on both past and future GHG emissions (Allen and Stocker 2013). The Representative Concentration Pathways (RCP; IPCC 2014) describe future GHG emission scenarios reflecting different patterns of energy use and climate policy (van Vuuren et al. 2011). RCP 2.6 represents a stringent mitigation scenario where global warming does not increase by more than 2°C above preindustrial levels and emissions peak around the year 2020 and decline significantly thereafter. RCP 4.5 is considered a stabilization scenario where emissions significantly decrease after 2040 and radiative forcing plateaus by mid-century and remains stable through the end of the century. RCP 8.5 represents an unabated rise

of GHG over the 21st century, resulting in 4–5°C projected rise in average global temperature. Our goal here was to determine the extent to which these emission pathways, and their interactions with other potential stressors, are likely to affect future polar bear populations. To understand how threats to the long-term persistence of polar bears may best be mitigated, we constructed a Bayesian network (BN) model that allowed us to (1) characterize the effect of different GHG emission scenarios on the relative influence of various stressors, and (2) identify the source and implications of uncertainties in forecasting the response of polar bears to those stressors and their potential mitigations.

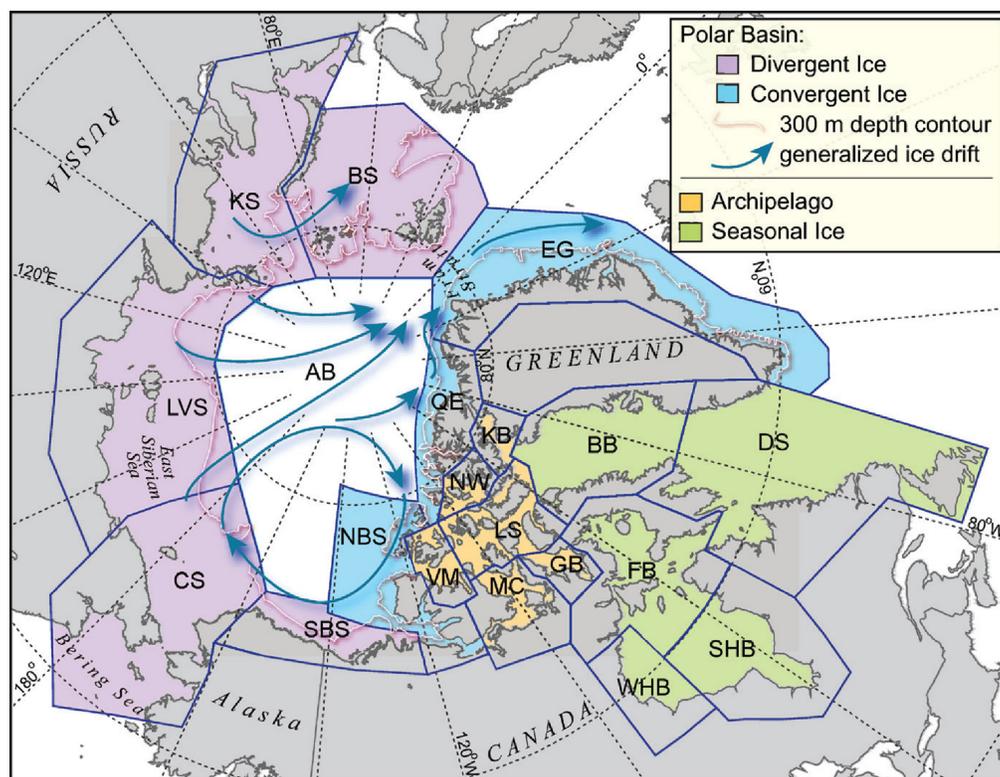


Fig. 1. The four polar bear ecoregions defined by Amstrup et al. (2008), including a 300-m bathymetry contour denoting the continental shelf, and a depiction of seasonal patterns of ice motion and distribution. Polar bear populations comprising the Polar Basin Divergent Ice Ecoregion (PBDE) includes Southern Beaufort Sea (SBS), Chukchi Sea (CS), Laptev Sea (LVS), Kara Sea (KS), and the Barents Sea (BS). The Polar Basin Convergent Ice Ecoregion (PBCE) includes East Greenland (EG), Queen Elizabeth (QE), and Northern Beaufort Sea (NBS) populations. The Seasonal Ice Ecoregion (SIE) is comprised of southern Hudson Bay (SHB), western Hudson Bay (WHB), Foxe Basin (FB), Davis Strait (DS), and Baffin Bay (BB) populations. The Archipelago Ecoregion (AE) includes populations from the Gulf of Boothia (GB), M'Clintock Channel (MC), Lancaster Sound (LS), Viscount-Melville Sound (VM), Norwegian Bay (NW), and Kane Basin (KB) populations (figure source: Amstrup et al. 2008).

METHODS

Study area

Following Amstrup et al. (2008), we grouped the 19 polar bear subpopulations (Aars et al. 2006) into four ecoregions based on polar bear life history and observed and forecasted patterns of sea ice dynamics (Fig. 1). Two of the ecoregions—the Polar Basin Convergent Ice (Convergent; three subpopulations) and Archipelago (six subpopulations)—are characterized by persistent multiyear sea ice that has allowed polar bears to remain on the ice year-round (e.g., Ferguson et al. 2000). The Polar Basin Divergent Ice Ecoregion (Divergent; five subpopulations) historically has been characterized by annual sea ice that retreats from the coast during summer (Durner et al. 2009), advects toward the central polar basin, and aggregates in the Convergent. Bears in the Divergent historically spent $\leq 7\%$ of their time on land (Amstrup et al. 2000, Amstrup 2003), but with recent prolonged sea ice retreats more bears now come ashore for longer periods during summer (Ovsyanikov and Menyushina 2007, Schliebe et al. 2008). The Seasonal Ice Ecoregion (Seasonal; five subpopulations) is characterized by annual sea ice that melts entirely each summer (Derocher and Stirling 1990), during which time bears come ashore and experience food deprivation while waiting for sea ice to reform in the fall (Stirling and Archibald 1977).

Model structure and parameterization

Our model represents the second generation of the polar bear BN model originally created to project the probability of persistence of the circumpolar population through the 21st century (Amstrup et al. 2008). We convened a team of subject matter experts to identify the relative influence of individual stressors on population outcomes. We reviewed and restructured the first generation BN model based on information that had become available since its creation (i.e., since 2007). Following established BN modeling guidelines (Marcot et al. 2006), we parameterized the new model with conditional probabilities informed by published literature, empirical and projected data, expert knowledge, and peer reviews. We reviewed and edited each node's conditional probability table in a

spreadsheet, sequentially among all team members, until consensus was reached for all probability values. We also evaluated behavior of an initial draft model using sensitivity analyses on model subsets and whole-model response, and adjusted targeted nodes to reconcile unrealistic model behavior based on our research experience or as matched in hindcasting model results to known conditions in prior time periods (Jay et al. 2011; also see Appendix S1).

Bayesian network models consist of input, intermediate, and output nodes. Input nodes are not informed by other nodes, and their states are parameterized by probabilities pertinent to specific scenarios of time period, climate conditions, climate change model set, and ecoregion. Input nodes are initially parameterized with uniform probability distributions (Fig. 2) but are updated for each specific scenario; however, if information is lacking for an input node for any scenario, its uniform distribution is retained to represent complete uncertainty for that scenario run. Intermediate and output nodes are conditioned on the preceding nodes they are linked to, which can be both input and other intermediate nodes (Jay et al. 2011). Node states are parameterized by conditional probabilities. In our model, input and intermediate nodes were organized into submodels, consisting of various stressors (e.g., sea ice conditions, seal prey conditions, shipping, hunting, resource extraction) and polar bear demographic processes. We used data available from the literature to assign conditional probabilities at each intermediate and summary node to reflect the range of possible outcomes from each combination of input stressors. Where data were lacking, we used expert knowledge to determine the range of likely outcomes as well as the degree of certainty. We incorporated uncertainty by prescribing a broader distribution of probabilities across possible outcomes. Where outcomes had greater certainty as a result of existing data and well-understood relationships, the prescribed probabilities were distributed across outcomes more narrowly. The final output node represented the cumulative effect of all input and intermediate nodes, expressed as relative influence on polar bear population trend.

We structured the model with 10 interlinked submodels comprised by a total of 49 nodes (Fig. 2). General descriptions of the submodels are presented below, and with greater detail in Appendix S1.

full spread of uncertainty among different GCM, we chose to report the BN results where the variance among the GCM for each ice metric was represented as a frequency distribution that was proportionally allocated across the prior probabilities of each sea ice input node (Atwood et al. 2015a). We also found little difference among three subsets of the GCMs, and we chose to report BN results based on the full ensemble of all 13 models (Appendix S1: Table S1).

Three quantitative sea ice habitat metrics (i.e., nodes) were calculated in a manner analogous to Amstrup et al. (2008) for each year and ecoregion in both the modeled and observed time series of monthly sea ice concentration. We calculated an annual metric of total ice habitat, represented by the input node “Foraging Sea Ice Area,” by calculating the 12-month sum of monthly optimal habitat area as defined by Durner et al. (2009). The input node “Foraging Sea Ice <50% Absence” quantified information about duration of the summer melt period from the preferred continental shelf foraging areas (Durner et al. 2009), calculated as the number of reduced ice months per year over shelf waters. The input node “Sea Ice Shelf Distance Change” represented the potential importance of how far the ice retreats away from the preferred continental shelf foraging areas each year. We calculated the shelf-to-ice distance metric during the month of minimum (but non-zero) ice extent as the mean distance from every shelf pixel in the respective ecoregion to the nearest pack ice pixel. The pack ice was defined as the largest contiguous region of ice with >50% concentration. “Foraging Sea Ice <50% Absence” and “Sea Ice Shelf Distance Change” were not calculated for Seasonal and Archipelago because we considered all sea ice in those ecoregions to be over shelf waters.

The node “Foraging Sea Ice Quality” expressed a subjective assessment of the quality of sea ice for foraging by polar bears. Recent observations of sea ice characteristics in several Arctic seas and regions (e.g., southern Beaufort and Chukchi seas [Mahoney et al. 2012], Hudson Bay [Gagnon and Gough 2005]) suggest that changes in sea ice phenology

have resulted in thinner ice that more easily deforms and more frequently rafts over itself. We incorporated the potential for these changes to reduce the quality of sea ice as a foraging substrate in the Divergent and Seasonal, as extensive ice deformation can limit access to prey (Stirling et al. 2008). Conversely, we incorporated the potential for thinning of thick, multiyear ice in the Archipelago and portions of the Convergent to increase foraging opportunities in the early- and mid-century periods, and reduced foraging opportunities in the late century periods. In both of these cases, due to uncertainty about how sea ice characteristics might affect foraging habitat quality, we allowed for a range of negative, negligible, and positive impacts that varied with sea ice conditions and ecoregion. We used the intermediate node “Foraging Sea Ice Distribution” to express how the spatiotemporal retreat of sea ice may affect availability of continental shelf habitats. Similarly, we used the intermediate node “Overall Sea Ice Conditions” to characterize the combination of the quantitative and qualitative ways the sea ice changes may affect use of continental shelf habitats by polar bears.

- (3) Marine prey and conditions submodel: We used the “Ringed Seal Abundance” and “Bearded Seal Abundance” input nodes to express the probability that changes in abundance of primary prey are likely to occur as sea ice cover declines and its character changes. We incorporated evidence that earlier spring break-up of sea ice in western Hudson Bay has been related to declining pup survival (Ferguson et al. 2005). We used the “Secondary & New Prey Abun” input node to express changes in the abundance of alternative marine mammal prey, and to allow northward range expansion (into Arctic waters) by novel prey species as sea ice extent declines and ice phenology and characteristics change over time (e.g., Lowry and Boveng 2009, Kovacs et al. 2012). We used the “Primary Prey Abundance” intermediate node to summarize changes in ringed and bearded seal abundance over time, and then linked to the “Marine Prey Base Quality” intermediate node, which

expressed cumulative changes in primary and secondary prey abundance likely to occur over time. As with the prey abundance nodes, “Marine Prey Base Quality” was based largely on expert judgment because there was little information available to suggest how the prey base quality is likely to change in the future.

- (4) Terrestrial food/prey and conditions submodel: We constructed three input nodes to describe the use of terrestrial habitat and food resources. “Human Provisioned Food Abundance” was used to express the availability of human-harvested marine mammals and other foods to polar bears in terrestrial habitats. The “Terr. & Marine Prey/Food Access” node expressed the availability of terrestrial prey and other food resources that may be available in a terrestrial environment, including beach-cast marine mammals (e.g., Derocher et al. 1993, Smith et al. 2010). We used the intermediate node “Overall Terrestrial Prey/Food” to characterize the availability of food resources relative to requirements of bears during their stay on shore, while noting that the availability of human-provisioned food was mostly relevant to portions of the Divergent and Seasonal. We used the intermediate node “Bears on Shore” to express the length of time each year that bears may spend on shore using terrestrial habitat as influenced by changes in overall sea ice conditions, terrestrial prey, and ecoregion. We used the input node “Terrestrial Refugia Quality” to characterize stability in habitat structure and extent of human and natural disturbance over time. The node intermediate “Overall Terrestrial Conditions” was used to depict changes in onshore habitat suitability as a function of habitat quality and the length of time bears spend on shore.
- (5) Overall habitat suitability submodel: This single-node submodel summarizes overall marine conditions (“Overall Marine Conditions”) and overall terrestrial conditions (“Overall Terrestrial Conditions”; described above) as the intermediate node “Overall Habitat Suitability”.
- (6) Event-driven mortality submodel: We depicted mortality as a function of specific

known and hypothesized lethal stressors including hunting (input node “Hunting Mortality [legal]”) and take resulting from human–bear conflict (input node “Human-Bear DL Lethal Interactions”). The hunting input node had three states and we considered same as recent and reduced to represent hunting at or below sustainable levels; increased represented hunting above a level we considered sustainable. Additional input nodes used to depict mortality risks included oil spills due to small and large exploration and extraction operations, and a catch-all node encompassing multiple risks such as those resulting from management and research activities and catastrophic storm events. We assumed future conditions might be related to sea ice extent and duration of the ice-reduced period, and also considered the potential for these stressors to have no effect on future conditions. The intermediate node “Event-Driven Mortality” then summarized these various risks and informed adult and subadult survival nodes.

- (7) Anthropogenic stressors submodel: We included several input nodes that allowed for potential effects of sub-lethal stressors and pollutants associated with different forms of anthropogenic activities. Sub-lethal stressors, such as the input nodes “Human-Bear Sub-Lethal Interactions,” “Oil, Gas, & Mining Activity,” “Shipping,” and “Tourism” were summarized in the intermediate node “Sub-lethal Human Disturbance” to reflect the potential displacement from foraging and refugia habitat. We used the input nodes “Hydrocarbon/Oil Spill” and “Contaminants” to characterize potential patterns of sub-lethal exposure to specific local (e.g., associated with drilling operations and shipping) and transported (e.g., organic compounds) pollutants. We used the “Pollution (sub-lethal)” intermediate node to summarize the effects of exposure to hydrocarbons and contaminants. The “Anthropogenic Stressors (sub-lethal)” intermediate node summarized the potential cumulative effects of “Human-Bear Sub-Lethal Interactions” and “Pollution (sub-lethal),” and was linked to the intermediate node “Adult Female Body Condition” given the potential for cumulative stress to

- adversely affect fitness (Love et al. 2013, Sheriff and Love 2013).
- (8) Other biotic stressors submodel: We summarized the probabilities of potential effects of disease and parasites and intraspecific predation (input nodes “Parasites & Disease” and “Predation”) with an intermediate node (“Other Biotic Stressors”) which was linked to subadult survival. We also linked parasites and disease to an intermediate node characterizing adult female body condition, based on the documented relationship between the two for other species (e.g., Møller et al. 2003, Irvine et al. 2006).
- (9) Demographic submodel: This submodel represents the cumulative influence of stressors on polar bear vital rates. The “Adult Survival” intermediate node represented the sum of effects on survival as influenced by “Overall Habitat Suitability,” “Parasites and Disease,” and “Event-Driven Mortality.” Based on the link between sea ice habitat, body condition, and survival (Regehr et al. 2007, 2010, Rode et al. 2010), we assumed that declines in habitat suitability would adversely affect condition and survival. Likewise, we acknowledged the supposition that sublethal stressors (e.g., parasites and disease, pollution, human disturbance) are likely to increase as the Arctic continues to warm (Moore and Huntington 2008), and adversely affect female body condition. Because there is no information to establish a direct relationship between sublethal effects and disease to polar bear body condition, we relied on literature from other species (e.g., Pioz et al. 2008, Sheriff et al. 2013) to inform the conditional probability table for the intermediate node “Adult Female Body Condition” and we distributed table probabilities to reflect our uncertainty. The “Recruitment” intermediate node reflected the effect of stressors on numbers of cubs produced and weaned, and on the ability of females to reach traditional denning areas (i.e., “terrestrial maternal den access” node; e.g., Derocher et al. 2011).
- (10) Polar bear persistence submodel: The output node “Relative Influence on Population Trend” represented the projected population outcome given the hypothesized strength of individual and cumulative threats

potentially affecting polar bears. The node was informed by “Adult Survival,” “Subadult Survival,” and “Recruitment,” and in creating the conditional probability table, we attributed the greatest weight to “Adult Survival” because it is the most important stressor affecting population trend and also the least sensitive to change (Wielgus et al. 2008).

The output node had four response states:

- increased: polar bears occur in numbers that are increased compared to the recent period (i.e., 2007–2012), and their distribution is at least the same, although stressors may cause local variation in abundance and distribution;
- same as recent: polar bears occur in numbers and distribution similar to the recent period. While stressors may cause local variation in abundance and distribution, they are not expected to induce an increasing or decreasing trend at the ecoregional scale.
- decreased: polar bears occur in numbers and distributions decreased compared to the recent period, with ecoregional-scale populations susceptible to stressors that may cause further declines in abundance and/or occupancy; and
- greatly decreased: polar bears occur in numbers and distributions substantially decreased compared to the recent period, with ecoregional-scale populations highly vulnerable to stressors that may lead to further reductions in abundance and to polar bears being restricted to a fraction of their historic range.

Analyses

We conducted separate model runs for combinations of the four ecoregions detailed above and six time periods, including four future periods extending to the end of the 21st century. A 1985–1995 period represented historic relationships and a 2007–2012 period represented recent conditions (i.e., immediately prior and subsequent to polar bears being listed under the ESA). Four future periods (2020–2030, 2045–2055, 2070–2080, 2090–2100) represented projected conditions through the end of the century. We used spans of decadal time periods, rather than single years

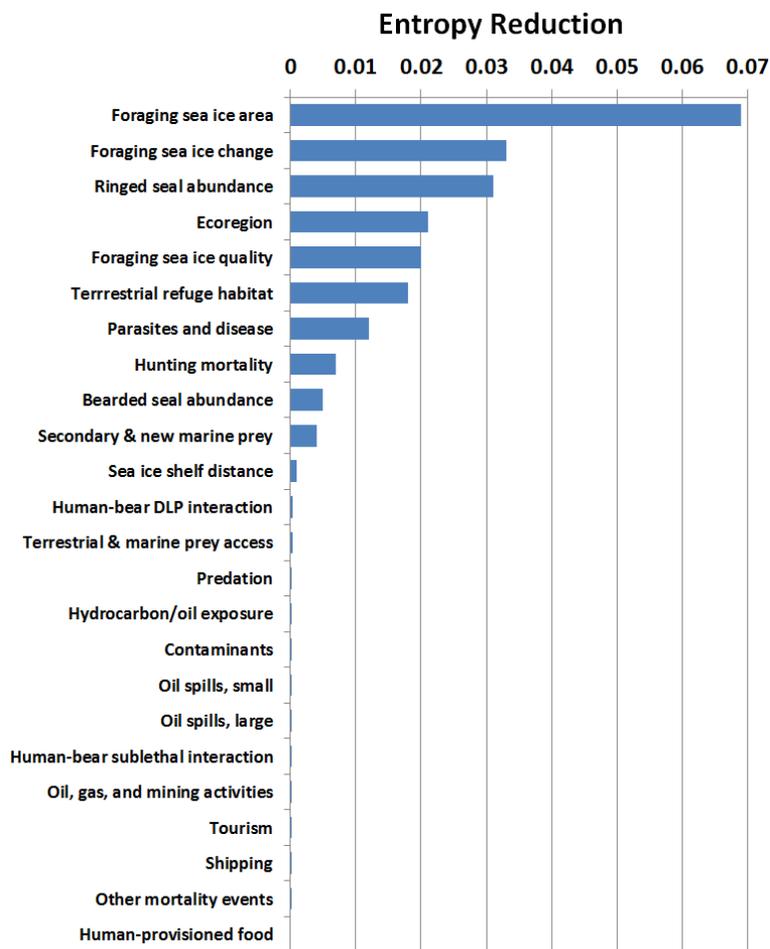


Fig. 3. Sensitivity of the final outcome node “relative influence on population trend” to all input (parentless) model nodes, and the Ecoregion treatment node. Sensitivity is measured as entropy reduction (also called mutual information), which denotes the degree to which polar bear outcome probabilities are sensitive to a given model input node.

or individual-year time series, to pool across inherent natural variability in the environmental inputs to the model (Jay et al. 2011). For each of the future time period model runs, we evaluated three scenarios of GHG emission pathways (RCP 2.6, RCP 4.5, and RCP 8.5). By taking an ecoregion- and time period-specific approach, we were able to represent geographic and temporal variation in RCP and stressor effects, potential mitigation influences, and uncertainties. A detailed description of model nodes, including definitions of node states and key assumptions, is presented in Atwood et al. (2015a).

We conducted sensitivity and influence analyses with the modeling shell Netica using methods

and interpretations described in Marcot et al. (2006), Amstrup et al. (2008), Jay et al. (2011), and Marcot (2012). Sensitivity analyses were used to provide information on the inherent underlying conditional probability structure of the model (Morgan and Henrion 1990, Darwiche 2009). We used influence runs (Morgan and Henrion 1990) to determine the relative importance of stressors and to examine the effect that mitigation may have on relative population trend. The latter was useful for ascertaining the potential benefits (or detriments) of mitigation of those stressors that are most easily controlled by management, including much of event-driven mortality and anthropogenic stressors. For influence runs, we

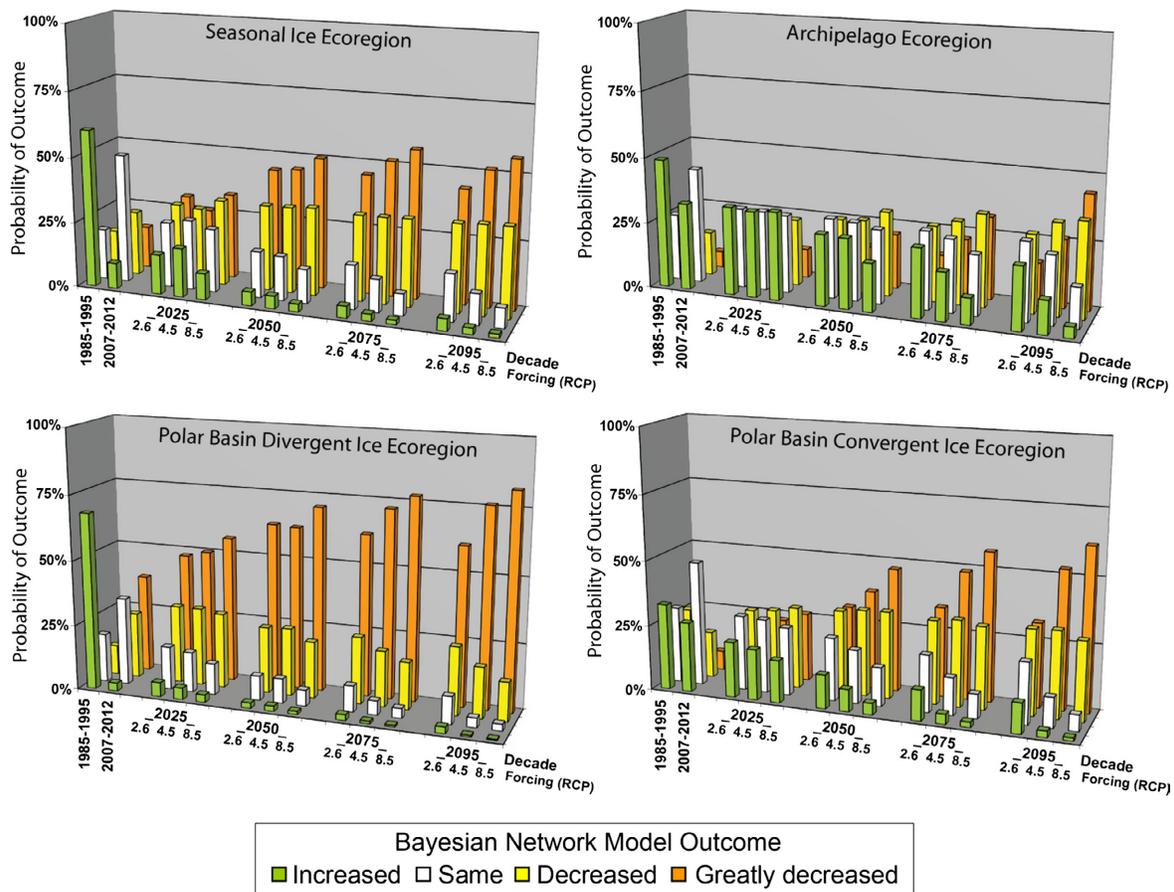


Fig. 4. Probabilities of polar bear population outcome states from the updated Bayesian network model. Results are from normative model runs for four ecoregions at six decadal time periods (historic and future). Historic sea ice conditions were based on observed data. Future sea ice conditions were from an ensemble of 13 GCM forced with each of three (RCP 2.6, 4.5, and 8.5) GHG emission scenarios.

assigned select input nodes to best- and worst-case scenarios (e.g., setting nodes to best and worst states) and compared outcomes between the two cases. We also conducted influence runs on the event-driven mortality and anthropogenic stressor submodels, both individually and collectively. We then qualitatively compared the outcomes of influence runs to the normative model outcomes (i.e., outcomes based on our best estimates of values of input variables; e.g., Jay et al. 2011) to determine the relative influence that managing the strength of select stressors may have on model outcomes. Because normative outcomes are expected results given our current understanding of the effects of managed and unmanaged stressors on polar bear populations,

they provided a standard expectation to which controlled influence runs could be compared.

RESULTS

Sensitivity analysis

Sensitivity analysis of all input nodes indicated that the outcome node (i.e., “Relative Influence on Population Trend”) was most sensitive to the input nodes pertaining to sea ice, marine prey (ringed seal abundance), and differences among ecoregions, with sea ice and marine prey being directly or indirectly tied to climate change (Fig. 3). Sensitivity to “Foraging Sea Ice Area” and “Foraging Sea Ice < 50% Absence” was likely due to the importance of the continental

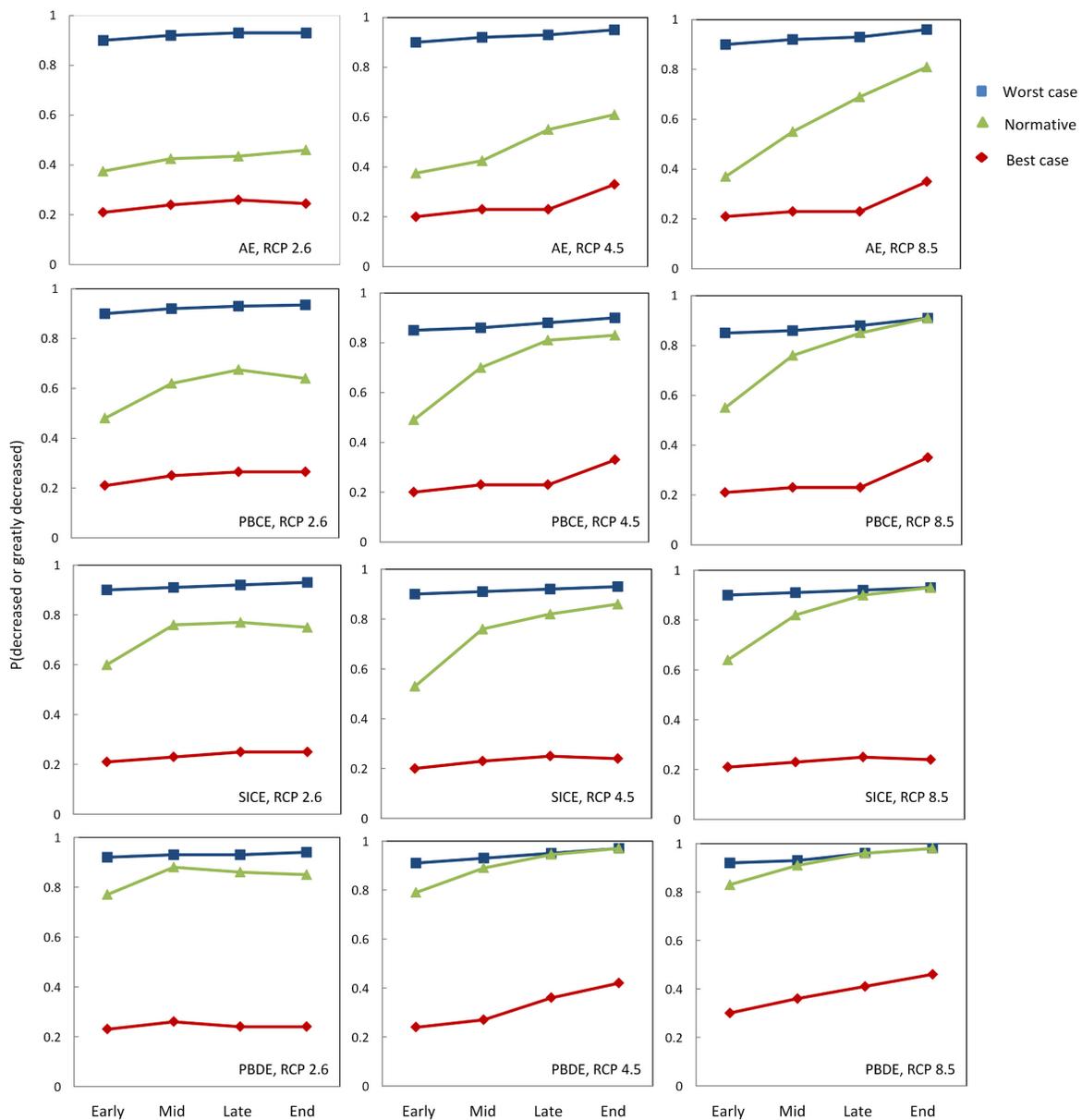


Fig. 5. Influence of “Overall Sea Ice Conditions” on the probability of a decreased or greatly decreased outcome for polar bears from the four ecoregions (see Fig. 1) at four future time periods for each of three GHG emission scenarios: RCP 2.6, 4.5, and 8.5. Time periods are 2020–2030 (early century), 2045–2055 (mid-century), 2070–2080 (late century), and 2090–2100 (end of century).

shelf in deriving those metrics, and the importance of ice-covered shelf waters to the availability of prey to polar bears.

Normative model results

For the normative model runs, polar bear outcomes from the historic and recent observation

periods (1985–1995 and 2007–2012) were similar for the Archipelago, Seasonal, and Convergent, with each of the three having dominant probabilities of either increased or same as recent (Fig. 4). There was considerable uncertainty in the Divergent outcome for the recent time period, with probabilities closely distributed among same

as recent, decreased, and greatly decreased, though the probability of greatly decreased was greater than the probabilities of the other states. For future outcomes, the remaining three ecoregions reached dominant probabilities of greatly decreased at different time periods (Fig. 4). The Divergent attained a clearly dominant probability of greatly decreased at all future decadal time periods for all three GHG forcing scenarios: RCP 2.6, 4.5, and 8.5. The Convergent transitioned to a dominant probability of greatly decreased at the mid-century (2045–2055) period for the three scenarios, although there was notable uncertainty for outcomes associated with RCP 2.6. The Seasonal was also characterized by uncertainty in the early century (2020–2030) outcome, and attained a clearly dominant probability of greatly decreased at mid-century (2045–2055) for all three forcing scenarios. Outcomes for the Archipelago were characterized by the most uncertainty, with the greatest probabilities occurring for the increased and same as recent outcome states early on and transitioning to decreased or, in the case of RCP 8.5, greatly decreased by the end of the century (2090–2100). The spread of probabilities among outcome states decreased over time for all models, and likely reflected the stronger signal of greater GHG forcing among the 13 GCM relative to natural climate variability in the system (Fig. 4). Probabilities of increased and same as recent states declined, while probabilities of decreased and greatly decreased states rose. As a result, uncertainty among future outcome states was mostly distributed between those latter two, with the exception of the Archipelago where uncertainty was also distributed among same as recent. Overall, uncertainty in polar bear outcomes was greatest for the Archipelago, and least for the Divergent.

Influence runs

Influence runs conducted on all combinations of emission pathways, ecoregions, and time periods suggested that “Overall Sea Ice Conditions” (Fig. 5) and “Marine Prey Base Quality” consistently had the greatest influence on polar bear outcomes, followed by “Event-Driven Mortality,” “Hunting Mortality (legal),” and “Human-Bear Lethal Interactions” (Appendix S2: Figs. S1–S4). Other potential stressors, such as “Pollution

(sub-lethal),” “Shipping,” “Tourism,” and “Oil, Gas, & Mining Activity” had minimal influence on polar bear outcomes. The influence of “Overall Sea Ice Conditions” and “Marine Prey Base Quality” on adverse population outcomes increased over time, while the influence of in situ anthropogenic stressors (e.g., “Hunting Mortality (legal),” “Human-Bear Lethal Interactions,” “Pollution (sub-lethal),” “Shipping”) decreased. Below, we report the results of influence runs as the probability of decreased or greatly decreased, i.e., $\text{Pr}(\text{decreased}) + \text{Pr}(\text{greatly decreased})$, and probability of greatly decreased alone, for worst-case and best-case scenarios relative to normative runs.

Setting “Overall Sea Ice Conditions” or “Marine Prey Base Quality” to worst-case states (greatly reduced) caused probabilities of decreased or greatly decreased population outcomes to rise by 5–51% and 3–32%, respectively, depending on the RCP, ecoregion, and future time step. The disparity between worst-case and normative probabilities of these two adverse outcomes was greatest for the Archipelago, followed by the Convergent, Seasonal, and Divergent, and the disparity between the worst-case and normative probabilities mostly decreased over time and with larger RCP forcing. Minimizing those stressors (setting stressors to best-case states) lowered probabilities of decreased or greatly decreased by 17–60% (for “Overall Sea Ice Conditions;” Fig. 5) and $\approx 15\%$ (for “Marine Prey Base Quality;” Appendix S2: Fig. S1) from normative levels through the end of the century. The Divergent experienced the greatest decline in probabilities of decreased or greatly decreased, followed by the Seasonal, Convergent, and Archipelago, and mostly rose over time and with higher RCP (i.e., greater GHG forcing). The efficacy of minimizing adverse stress from “Overall Sea Ice Conditions” or “Marine Prey Base Quality” was most pronounced on the probability of greatly decreased which, in some cases, resulted in projected probabilities 75% (“Overall Sea Ice Conditions;” Divergent) and 20% (“Marine Prey Base Quality;” Divergent) lower than normative levels.

In situ anthropogenic stressors had less influence on population outcomes than environmental stressors. The lowest levels (i.e., best case) of “Event-Driven Mortality,” (e.g., “Hunting Mortality (legal)” and “Human-Bear Lethal Interactions”) caused probabilities of decreased

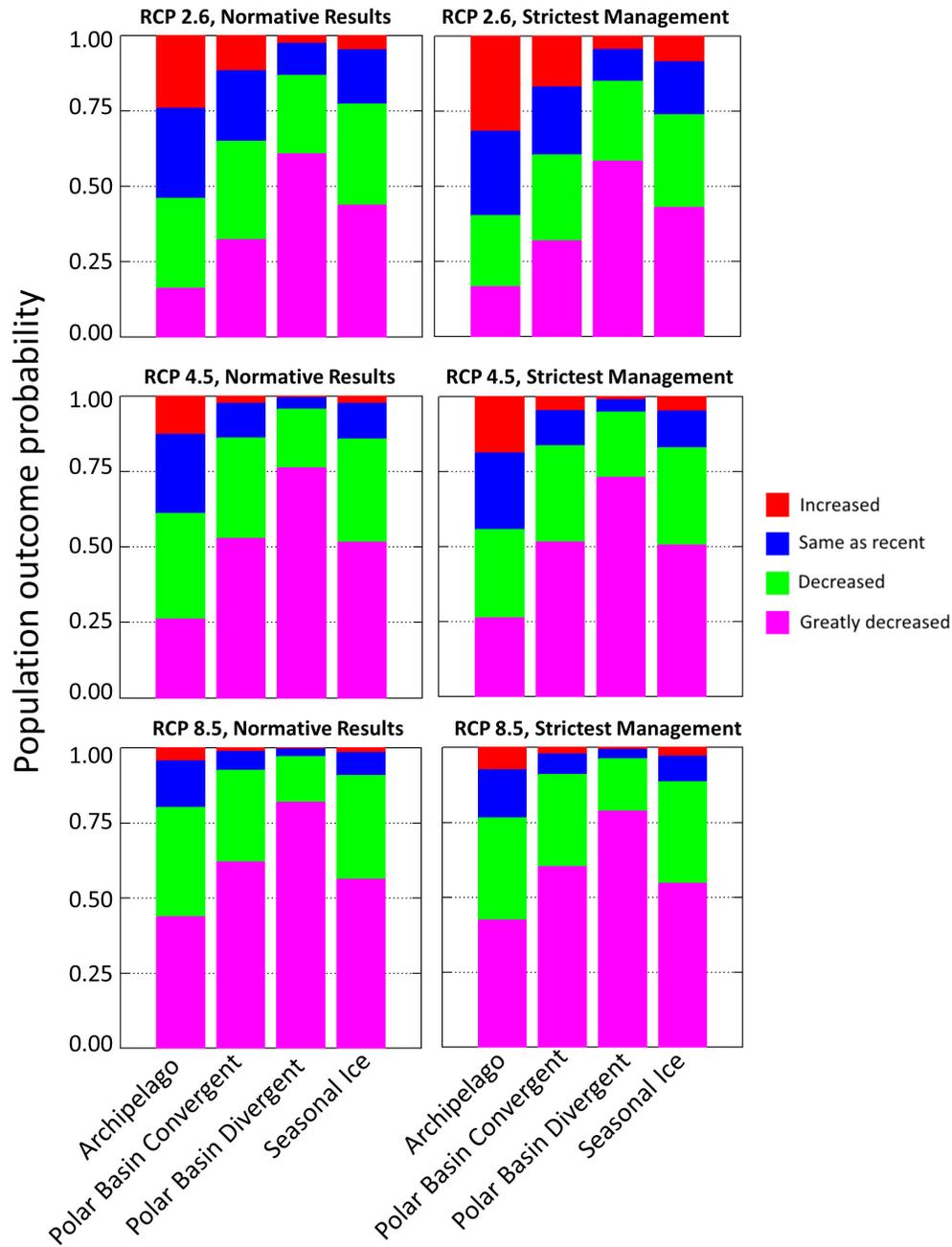


Fig. 6. Probabilities of polar bear population outcome states for the normative model runs and the “strictest management” influence runs for the four ecoregions, three RCP emission scenarios, and the end-of-the-century time period. “Strictest management” refers to simultaneously minimizing the influence of the “Shipping,” “Tourism,” “Oil, Gas, & Mining Activity,” “Human-Bear Sub-Lethal Interactions,” “Pollution (sub-lethal),” and “Event-Driven Mortality” stressor nodes.

or greatly decreased to be 1–9% lower than normative values, depending on the ecoregion and future time step. Similar to the environmental stressors, the disparity between the best-case and normative probabilities was greatest for the Archipelago, followed by the Convergent, Seasonal, and Divergent, was greater with larger RCP, and mostly declined over time. For example, minimizing the level of “Event-Driven Mortality” lowered probabilities of decreased or greatly decreased by \approx 3–5% below normative values, while maximizing the level raised probabilities by 3–8% (Appendix S2: Fig. S2). Setting the “Hunting Mortality (legal)” node to the maximal value (i.e., worst case) resulted in probabilities 2–7% greater, whereas minimizing it resulted in probabilities 2–5% lower (Appendix S2: Fig. S3). Setting the other individual stressor nodes to maximal and minimal values had negligible effects on outcomes. Last, we conducted a “strictest management” influence run by simultaneously minimizing all manageable stressors on population outcomes (i.e., “Shipping,” “Tourism,” “Oil, Gas, & Mining Activity,” “Human-Bear Sub-Lethal Interactions,” “Pollution (sub-lethal),” and “Event-Driven Mortality”), which collectively lowered probabilities of decreased or greatly decreased by up to \sim 9% below normative values by the end-of-the-century time period, depending on the GHG forcing scenario (Fig. 6).

DISCUSSION

A salient feature of any approach to assess threats to populations must be the portrayal of an appropriate level of ecological complexity. Bayesian network models have the capacity to integrate environmental, ecological, and anthropogenic processes, along with an explicit representation of uncertainties, into a unified analytical framework (Jensen and Nielsen 2007, Barton et al. 2012). The Amstrup et al. (2008, 2010) polar bear BN model represented the relationships of sea ice habitat and a select group of threats with polar bear demography to project the future worldwide status of polar bears. A central conclusion of that effort was that mitigating GHG emissions, along with managing anthropogenic activities, could result in the maintenance of polar bear numbers at reduced but sustainable levels throughout the 21st century

(Amstrup et al. 2010). We revised that model, using updated (CMIP5) sea ice forecasts and new information about a wide range of stressors to polar bear populations, and found that intensive management of threats other than GHG may slow, but are unlikely to stop, the transition of polar bear populations to progressively worsened outcomes. We concur with the previous modeling effort that GHG effects on sea ice are the main threat to polar bear persistence.

Polar bear population outcomes were projected to worsen with larger GHG forcing and, for RCP 4.5 and 8.5, also worsen over time. It is important to consider model projections within the context of uncertainties we attempted to characterize. To the extent practicable, we represented uncertainty in the estimation of probabilities associated with individual nodes (Marcot et al. 2006, Marcot 2007, Pollino et al. 2007). For example, we reflected uncertainty (including potential for interactions between stressors) in some nodes by specifying uniform probabilities for outcome states in the conditional probability tables. It is also worth noting that we did not consider threshold or tipping point effects of rapid reductions in polar bear populations given progressively incremental increases in the various stressors (see Drake and Griffen 2010 and Guntenspergen 2014, for examples in other ecosystems and theoretical discussions) because there is a lack of empirical understanding of how and when such responses might manifest. However, the most influential determinant of population outcomes was overall sea ice conditions, a node whose states become more certain over time as the signal of greater GHG forcing becomes more discernible from natural variation (Swart et al. 2015).

Normative model runs

Population outcomes for all ecoregions were highly sensitive to sea ice metrics, most notably “Foraging Sea Ice Area,” which expressed the proportional change over time in extent of optimal sea ice habitat (as determined in Durner et al. 2009) in the Divergent and Convergent, and in total ice extent in the Seasonal and Archipelago. The Arctic-wide sea ice melt season (i.e., period between the onset of sea ice melting in summer and freeze-up in fall) has increased at a rate of \approx 5 d/decade since 1979 (Stroeve et al. 2014). The lengthening melt season has

been driven primarily by later autumn freeze-up dates in the southern Beaufort, Chukchi, Kara, and Laptev seas (Perovich et al. 2011, Stroeve et al. 2014), all of which are included within the Divergent. Change in the availability of sea ice foraging habitat has been linked to declines in body condition, recruitment, survival, and abundance in the southern Beaufort Sea (Regehr et al. 2010, Rode et al. 2010). Thus, the finding of worsening population outcomes through time is consistent with historic observations, though there is little data available from the Kara and Laptev sea subpopulations (Obbard et al. 2010). Recent data from the Chukchi Sea suggest that polar bears have maintained body condition and reproduction despite initial levels of sea ice loss (Rode et al. 2014). While we considered these results when prescribing the conditional probability table for the female body condition node, the long-term model outcomes suggested that polar bears in the Divergent ecoregion will be the most sensitive to continued sea ice loss.

Polar bears in portions of the Seasonal have been accustomed to spending upwards of four months on shore fasting each summer/autumn, when the sea ice melts completely (Deroyer and Stirling 1990). The Hudson Bay portion of the Seasonal has experienced an increase in the length of the melt season (approximately 3 weeks over three decades as of the mid-2000s; Gagnon and Gough 2005) with evidence of adverse effects on bears (e.g., Stirling et al. 1999, Regehr et al. 2007, Rode et al. 2012). However, Seasonal outcomes were characterized by greater uncertainty than Divergent outcomes. Uncertainty in Seasonal outcomes might be attributed to the mediating effects of changing primary and secondary prey availability in some areas. In the portion of the Seasonal adjacent to the Atlantic Ocean, a marked increase in the abundance of harp seals, concomitant with declines in sea ice (DFO 2010), has been posited as contributing to an increase in the size of the Davis Strait subpopulation (Peacock 2009). In the Hudson Bay system, where the regional increase in the length of the melt season has been greatest (Stroeve et al. 2014), energetic modeling has predicted that 16% of adult males and females could die of starvation if the onshore fasting period lasts upwards of five months (Molnar et al. 2011, Robbins et al. 2013, Molnár et al. 2014).

Polar bear outcomes for the Convergent were similar to those from the Seasonal in terms of trend, but uncertainty of outcomes was slightly higher. This is most likely due to more modest projected changes in sea ice metrics and the general lack of data about polar bears from this region. The Convergent is characterized by thick multiyear ice that accumulates along coastlines (Holland et al. 2006, Serreze et al. 2007, Stirling et al. 2011) and persists longer at high latitudes in model projections. The more persistent ice also provides functional connectivity with terrestrial denning habitat, which may have further contributed to the less dire trend in projected population outcomes compared to the Divergent or Seasonal. While information on survival and abundance are available for a portion of the northern Beaufort Sea subpopulation through 2006 (Stirling et al. 2011), the general paucity of data for this ecoregion is reflected in the level of uncertainty in polar bear outcomes. Like the Convergent, the Archipelago is characterized by thick multiyear ice that mostly remains in the region year-round (Amstrup et al. 2008), and projected changes to sea ice metrics were less severe. It is possible that, in the near term, thinning of the multiyear ice may actually improve the quality of foraging sea ice habitat (Arrigo et al. 2008). However, also like the Convergent, there is relatively little data available on polar bear vital rates and stressors from the Archipelago. Nevertheless, our findings support those of others (Amstrup et al. 2008, Hamilton et al. 2015, Peacock et al. 2015) that the Archipelago is likely the most reliable long-term refugium for polar bears.

Stressor evaluation

Our influence analyses focused on stressors, individually and in combinations, that are of greatest concern to managers and that span a spectrum from those that are relatively easy to manage (e.g., “Human-Bear DL Lethal Interactions”) to those for which management requires significant international interventions (e.g., “Overall Sea Ice Conditions”). The most influential individual stressors to polar bear populations were “Overall Sea Ice Conditions” and “Marine Prey Base Quality.” This reflects the fundamental dependence of polar bears on the sea ice ecosystem, and the fact that mitigating GHG rise is critical to long-term persistence of polar bears. “Hunting Mortality (legal)” and

“Human-Bear DL Lethal Interactions” were the most influential stressors that can be managed locally, while other stressors, such as “Shipping,” “Tourism,” and “Oil, Gas & Mining Activity” appeared to have little influence on population outcomes, partly because of the paucity of information linking those stressors to adverse effects on polar bears. None of the stressors we identified, however, can be completely decoupled from the trend of sea ice decline. Reduction in summer sea ice, for example, leads to increased shipping, tourism, and other marine-related anthropogenic stressors, as well as to greater potential for DL-related mortality.

“Overall Sea Ice Conditions” exerted the most influence on polar bear population outcomes with ice-free periods lengthening by 2–7.5 months depending on the emissions scenario and ecoregion considered. The most conspicuous symptom of a longer ice-free period was a decline in habitat suitability. However, the most serious consequence of a longer ice-free period is reduced availability of marine mammal prey. Like “Overall Sea Ice Conditions,” “Marine Prey Base Quality” was a highly influential stressor because without a sea ice substrate, prey will be largely unavailable to polar bears (Stirling and Derocher 1993). Changes in the ice-free duration may or may not be accompanied by near-term changes in the abundance of marine prey. Polar bears in some regions of the Arctic (e.g., the Archipelago) may benefit from changes in primary or secondary prey abundance or availability as sea ice cover declines and physical characteristics change (e.g., Lydersen and Kovacs 1999, Bluhm and Gradinger 2008, Iacozza and Ferguson 2014). However, there is insufficient information available to explicitly model the linkage between changing sea ice conditions and polar bear prey abundance and distribution, particularly over the long term and at ecoregional scales.

A secondary concern of the lengthening ice-free period is the resulting increase in the length of time bears spend on shore. Polar bears appear able to forage effectively over sea ice until ice concentration values dip below a threshold ranging from 30–50% (Stirling et al. 1999, Sahanatian and Derocher 2012, Cherry et al. 2013). At lower ice concentrations, they are displaced to terrestrial habitat where the availability of food resources is highly variable. For example, in western Hudson Bay,

observation of predation by polar bears on snow geese (*Chen caerulescens*) has become more common over time (e.g., Derocher et al. 1993, Rockwell and Gormezano 2009). To the north, in Foxe Basin, polar bear predation at seabird-nesting colonies increased substantially over the last three decades (Iverson et al. 2014). In the Barents Sea and east Greenland, increased predation by polar bears on goose and seabird nests is potentially affecting the reproductive success of the affected species (Prop et al. 2015). In the southern Beaufort Sea, use of terrestrial habitat has increased significantly over the last 15 yr and polar bears are becoming increasingly reliant on scavenging remains left over from subsistence whaling activities (Atwood et al. 2015b). Collectively, these studies illustrate the potential for effects of climate change to restructure the nature of community interactions, and suggest that polar bears from some populations are able to exploit alternative sources of food when available, at least to a limited extent. However, some of these same populations have exhibited trends of declining body condition as use of terrestrial habitat has increased (e.g., Stirling et al. 1999, Rode et al. 2010), and it appears that consumption of terrestrial foods is insufficient to offset lost opportunities to hunt fat-rich seals from the ice (Rode et al. 2015).

Increased use of terrestrial habitat also prolongs exposure to anthropogenic stressors, such as human–polar bear interactions, which could then lead to conflict and an increased likelihood of mortality from DL kills (Stirling and Derocher 2012). Likewise, time spent on shore could serve to mediate exposure to industrial pollutants and infectious agents and parasites that polar bears would not be exposed to in a marine environment (Amstrup et al. 1989, Stirling and Derocher 2012). Indeed, the hypothesized nexus between climate-mediated changes in sea ice characteristics and exposure to a greater array of stressors is a key consideration when attempting to identify most effective management scenarios. That said, in situ anthropogenic stressors like “Hunting Mortality (legal)” and “Human-Bear DL Lethal Interactions” had considerably less individual influence on population outcomes. Minimizing the effect of harvest resulted in a $\leq 6\%$ reduction in the probability of transitioning to decreased or greatly decreased states, while minimizing DL resulted in a $\leq 3\%$ reduction.

Other anthropogenic stressors had less influence on polar bear outcomes (although they may play more salient roles locally). For example, minimizing the effect of pollutants (e.g., hydrocarbons and other persistent organic compounds) resulted in $\leq 2\%$ reduction in the probability of a decreased or greatly decreased outcome, and minimizing sub-lethal stressors such as human-polar bear interaction, resource extraction and exploration activity, shipping, and tourism had minimal influences ($< 1\%$) on outcomes. In some cases, the low degree of influence may be due to a lack of information on population-level effects. Although there is substantial information characterizing exposure of polar bears to pollutants (e.g., Sonne et al. 2012), there is little information linking exposure to population vital rates (Patyk et al. 2015). Also, sub-lethal stressor effects can be cumulative (Holmstrup et al. 2010) and given that some of these stressors are relatively new to the Arctic (e.g., shipping and tourism), they may not have reached a level of intensity that elicits a measurable response from polar bears, or some of those stressors may not actually affect polar bears. While better understanding of these putative stressors could refine conditional probabilities and point to modifications in the structure of our model, we have no evidence their importance could become major drivers of future polar bear status.

Conclusions

Improved condition of sea ice habitat, derived from GHG mitigation, had the greatest positive effect on polar bear population outcomes. Improved availability and accessibility of marine

mammal prey, also linked to sea ice availability, was the second most positive effect. Improved sea ice habitat, alone, could reduce by $\approx 50\%$ the probability of polar bear population status in a given ecoregion reaching a state of decreased or greatly decreased. However, managing for improvements in sea ice habitat and marine mammal prey requires national and international actions to promptly reduce GHG emissions. Peak warmth resulting from emissions occurs approximately 10 yr after the CO_2 is added to the atmosphere (Ricke and Caldeira 2014), and sea ice stabilization requires 20–30 yr (Amstrup et al. 2010). This lag between mitigation of emissions and stabilization of sea ice habitat (sensu Allen and Stocker 2013) means timing of GHG mitigation is critical to the future of polar bears.

While other stressors would be inherently more tractable to manage than sea ice loss, they have substantially less influence and none, individually or in combination, can be targeted with the expectation of achieving long-term improvement in population outcomes. As evidenced by our wholistic “strictest management” influence runs, when all stressor values other than those for sea ice were set to their minimum levels, the probability of an ecoregion reaching the decreased or greatly decreased state was only reduced by $\sim 10\%$. Nevertheless, although there is a fair amount of uncertainty in our population outcomes, a $\sim 10\%$ reduction in the likelihood of a population becoming decreased or greatly decreased is not trivial and may prove important in buying time to achieve a level of GHG mitigation that will stop further sea ice loss.

Table 1. Recommendations for future research to address conservation needs and reduce uncertainties identified by our modeling effort.

Threat	Research need
Global warming induced fragmentation and loss of sea ice habitat	Quantify the effects of habitat fragmentation and loss on polar bear movement and energetics. Quantify the effects of habitat fragmentation and loss, and other factors, on the availability (i.e., abundance and accessibility) of prey species forage and habitat. Determine the factors that mediate differential vulnerability of populations to the immediate effects of sea ice loss.
Human activities	Evaluate the potential for cumulative exposure to local and transported pollutants, contaminants, and zoonotic agents to impact fitness. Identify the factors that increase the risk of human-polar bear conflict, and determine the potential for cumulative lethal removals (legal harvest, illegal harvest, and defense of life kills) to adversely impact populations. Determine the potential for industrial and recreational activities to influence suitability of terrestrial habitats.

Future iterations of our model will benefit from research on ecological processes and stressors whose effects on polar bear vital rates are poorly understood (Table 1). For example, there is a need to better understand relationships between processes that drive the loss of sea ice habitat—e.g., changes in the timing and rates of annual sea ice melt and freeze-up, increasing distance of pack ice retreat, and increasingly dynamic ice conditions (Mahoney et al. 2012)—and influence general marine productivity. The sea ice metric “ice-free days” (similar to our “Foraging Sea Ice < 50% Absence” node) is often used to link changes in the availability of sea ice habitat to declines in body condition and survival (e.g., Regehr et al. 2010, Rode et al. 2010), yet the relationship is likely more nuanced. For instance, Rode et al. (2014) provided evidence that geographic variation in biological productivity, and the ability of polar bears to access that productivity, may moderate the effects of declining sea ice on some population indices. Similarly, climate-mediated expansion of alternate marine prey has been posited as a key factor in maintaining population health of polar bears in Davis Strait (Peacock et al. 2013); range expansion of alternate prey elsewhere may serve a similar role, but to an unknown and, at present, unpredictable extent. Additionally, there is a need to refine understanding of polar bear physiology, particularly processes that influence the allocation of nutrients and that determine the limits of fasting and the corresponding impact on reproduction and health. Energetic models developed for a Seasonal subpopulation of polar bears indicate that fasts approaching five months in length could result in a significant risk of starvation (Molnar et al. 2011, Robbins et al. 2013, Molnár et al. 2014). As polar bears from more regions of the Arctic spend greater amounts of time on shore during summer, better information on nutritional status will be needed to identify thresholds for reproductive failure and starvation. Last, it is possible that the low influence of some stressors (e.g., “Shipping,” “Oil, Gas & Mining Activity,” “Human-Bear DL Lethal Interactions”) reflects our uncertainty about how and when they might be expressed and their population-level impact, which may become clearer after targeted research.

Our assessment indicates that preserving adequate sea ice availability is key to the long-

term persistence of polar bears, and will be most likely achieved by adhering to a GHG emissions trajectory consistent with the RCP 2.6 scenario. However, even adhering to the RCP 4.5 trajectory, for example, results in a smaller probability of polar bear populations transitioning to worsened outcome states compared to unabated GHG emissions. Until sea ice loss is stabilized, the management of key in situ stressors may serve to slow the transition of populations to progressively more dire outcome states, and thereby improve the prospects of viable polar bear populations when sea ice habitats reach a new equilibrium.

ACKNOWLEDGMENTS

This analysis is part of the U.S. Geological Survey Changing Arctic Ecosystems Initiative, supported by the U.S. Geological Survey Ecosystems Mission Area, with additional in-kind contributions from the U.S. Forest Service, Pacific Northwest Research Station. Additional support was provided by the U.S. Fish and Wildlife Service, Region 7, Marine Mammals Management Office. We acknowledge the World Climate Research Programme’s Working Group on Coupled Modelling, which is responsible for CMIP, and we thank the climate modeling groups (listed in Appendix S1: Table S1) for producing and making available their model output. We thank K. Laidre for providing expertise on polar bear ecology and for valuable insight throughout the course of this study. We thank members of the U.S. Polar Bear Recovery Team, Science and Traditional Ecological Knowledge Working Group for providing feedback on model influence diagrams and structure. We are grateful for the helpful comments and suggestions from T. DeBruyn, J. Wilder, M. Runge, and D. Pierce-Williams at various stages in the development of this work. K. Oakley, S. Ban, G. Wilhere, and A. Derocher provided comments on earlier versions of this manuscript. Use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Aars, J., N. J. Lunn, and A. E. Derocher. 2006. Polar Bears: Proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, Seattle, Washington, June 20–24, 2005. IUCN, Gland, Switzerland and Cambridge, UK.
- Allen, M. R., and T. F. Stocker. 2013. Impact of delay in reducing carbon dioxide emissions. *Nature Climate Change* 4:23–26.

- Amstrup, S. C. 2003. Polar bear. Pages 587–610 in G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America: biology, management, and conservation*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Amstrup, S. C., C. Gardner, K. C. Meyers, and F. W. Oehme. 1989. Ethylene glycol (antifreeze) poisoning of a free-ranging polar bear. *Veterinary and Human Toxicology* 3:317–319.
- Amstrup, S. C., G. M. Durner, I. Stirling, N. J. Lunn, and F. Messier. 2000. Movements and distribution of polar bears in the Beaufort Sea. *Canadian Journal of Zoology* 78:948–966.
- Amstrup, S. C., Durner, G. M., T. L. McDonald, and W. R. Johnson. 2006. Estimating potential effects of hypothetical oil spills on polar bears. U.S. Geological Survey Open-File Report 2006-1337, Anchorage, Alaska, USA.
- Amstrup, S. C., B. G. Marcot, and D. C. Douglas. 2008. A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. Pages 213–268 in E. T. DeWeaver, C. M. Bitz, and L.-B. Tremblay, editors. *Arctic sea ice decline: observations, projections, mechanisms, and implications*. American Geophysical Union Geophysical Monograph, No. 180, Washington, D.C., USA.
- Amstrup, S. C., E. T. DeWeaver, D. C. Douglas, B. G. Marcot, G. M. Durner, C. M. Bitz, and D. A. Bailey. 2010. Greenhouse gas mitigation can reduce sea ice loss and increase polar bear persistence. *Nature* 468:955–960.
- Arrigo, K. R., G. van Dijken, and S. Pabi. 2008. Impact of a shrinking Arctic ice cover on marine prey primary production. *Geophysical Research Letters*. <http://dx.doi.org/10.1029/2008GL035028>
- Atwood, T. C., B. G. Marcot, D. C. Douglas, S. C. Amstrup, K. D. Rode, G. M. Durner, and J. F. Bromaghin. 2015a. Evaluating and ranking threats to the long-term persistence of polar bears. U.S. Geological Survey Open-File Report, 2014-1254, Anchorage, Alaska, USA.
- Atwood, T. C., E. Peacock, M. A. McKinney, K. Lillie, R. Wilson, and S. Miller. 2015b. Demographic composition and behavior of polar bears summering on shore in Alaska. U.S. Geological Survey, Administrative Report, Anchorage, Alaska, USA.
- Barton, D. N., S. Kuikka, O. Varis, L. Uusitalo, H. J. Henriksen, M. Borsuk, A. de la Hera, R. Farmani, S. Johnson, and J. D. C. Linnell. 2012. Bayesian networks in environmental and resource management. *Integrated Environmental Assessment and Management* 8:418–429.
- Bluhm, B. A., and R. Gradinger. 2008. Regional variability in food availability for Arctic marine mammals. *Ecological Applications* 18:S77–S96.
- Bromaghin, J. F., T. L. McDonald, I. Stirling, A. E. Derocher, E. S. Richardson, E. V. Regehr, D. C. Douglas, G. M. Durner, T. Atwood, and S. C. Amstrup. 2015. Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. *Ecological Applications* 25:634–651.
- Burek, K. A., F. M. D. Gulland, and T. M. O'Hara. 2008. Effects of climate change on Arctic marine mammal health. *Ecological Applications* 18:S126–S134.
- Cavaliere, D. J., C. L. Parkinson, P. Gloersen, and H. Zwally. 1996 (updated yearly). Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data, northern hemisphere. National Aeronautics and Space Administration Distributed Active Archive Center at the National Snow and Ice Data Center, Boulder, Colorado, USA.
- Cherry, S. G., A. E. Derocher, G. W. Thiemann, and N. J. Lunn. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *Journal of Animal Ecology* 82:912–921.
- Darwiche, A. 2009. *Modeling and reasoning with Bayesian networks*. Cambridge University Press, New York, New York, USA.
- Department of Fisheries and Oceans (DFO). 2010. Current status of northwest Atlantic harp seals, *Pagophilus groenlandicus*. DFO Canadian Scientific Advisory Secretariat Science Advisory Report 2009/074, Ottawa, Ontario, Canada.
- Derocher, A. E., and I. Stirling. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. *Canadian Journal of Zoology* 68:1395–1403.
- Derocher, A. E., and I. Stirling. 1991. Oil contamination of polar bears. *Polar Record* 27:56–57.
- Derocher, A. E., D. Andriashek, and I. Stirling. 1993. Terrestrial foraging by polar bears during the ice-free period in western Hudson Bay. *Arctic* 46:251–254.
- Derocher, A. E., M. Andersen, Ø. Wiig, J. Aars, E. Hansen, and M. Biuw. 2011. Sea ice and polar bear den ecology at Hopen Island, Svalbard. *Marine Ecology Progress Series* 441:273–279.
- Derocher, A. E., et al. 2013. Rapid ecosystem change and polar bear conservation. *Conservation Letters* 6:368–375.
- Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. *Nature* 467:456–459.
- Durner, G. M., et al. 2009. Predicting 21st-century polar bear habitat distribution from global climate models. *Ecological Monograph* 79:25–58.
- Ferguson, S. H., M. K. Taylor, and F. Messier. 2000. Influence of sea ice dynamics on habitat selection by polar bears. *Ecology* 81:761–772.

- Ferguson, S. H., I. Stirling, and P. McLoughlin. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* 21:121–135.
- Gagnon, A. S., and W. A. Gough. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. *Arctic* 58:370–382.
- Gautier, D. L., et al. 2009. Assessment of undiscovered oil and gas in the arctic. *Science* 324:1175–1179.
- Guntenspergen, G. R. 2014. Application of threshold concepts in natural resource decision making. Springer, New York, New York, USA.
- Hamilton, S. G., L. Castro de la Guardia, A. E. Derocher, V. Sahanatien, B. Tremblay, and D. Huard. 2015. Projected polar bear sea ice habitat in the Canadian Arctic Archipelago. *PLoS ONE* 9:e113746.
- Holland, M. M., C. M. Bitz, and B. Tremblay. 2006. Future abrupt reductions in the summer Arctic sea ice. *Geophysical Research Letters* 33:L23503.
- Holmstrup, M., et al. 2010. Interactions between effects of environmental chemicals and natural stressors: a review. *Science of the Total Environment* 408:3746–3762.
- Iacozza, J., and S. H. Ferguson. 2014. Spatio-temporal variability of snow over sea ice in western Hudson Bay, with reference to ringed seal pup survival. *Polar Biology* 37:817–832.
- Intergovernmental Panel on Climate Change (IPCC). 2014. Climate change: impacts, adaptation, vulnerability. Part A: Global and sectoral aspects. Contribution of the Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, New York, USA.
- Irvine, R. J., H. Corbishley, J. G. Pilkington, and S. D. Albon. 2006. Low-level parasitic worm burdens may reduce body condition in free-ranging red deer (*Cervus elaphus*). *Parasitology* 133:465–475.
- Iverson, S. A., H. G. Gilchrist, P. A. Smith, A. J. Gaston, and M. R. Forbes. 2014. Longer ice-free seasons increase the risk of nest predation by polar bears for colonial breeding birds in the Canadian Arctic. *Proceedings of the Royal Society B*. <http://dx.doi.org/10.1098/rspb.2013.3128>
- Jay, C. V., B. G. Marcot, and D. C. Douglas. 2011. Projected status of the Pacific walrus (*Odobenus rosmarus divergens*) in the twenty-first century. *Polar Biology* 34:1065–1084.
- Jensen, F. V., and T. D. Nielsen. 2007. Bayesian networks and decision graphs. Springer, New York, New York, USA.
- Kovacs, K. M., C. Lydersen, J. E. Overland, and S. E. Moore. 2011. Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity* 41:181–194.
- Kovacs, K. M., et al. 2012. Global threats to pinnipeds. *Marine Mammal Science* 28:414–436.
- Lindsay, R. W., and J. Zhang. 2005. The thinning of Arctic sea ice, 1988–2003: have we passed a tipping point? *Journal of Climate* 18:4879–4894.
- Love, O. P., P. O. McGowan, and M. J. Sheriff. 2013. Maternal adversity and ecological stressors in natural populations: the role of stress axis programming in individuals, with implications for populations and communities. *Functional Ecology* 27:81–92.
- Lowry, L., and P. Boveng. 2009. Ribbon seal. Pages 955–958 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. *Encyclopedia of marine mammals*, Second edition. Academic Press, San Diego, California, USA.
- Lydersen, C., and K. M. Kovacs. 1999. Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. *Marine Ecology Progress Series* 187:265–281.
- Mahoney, A. R., H. Eicken, L. H. Shapiro, R. Gens, T. Heinrichs, F. J. Meyer, and A. G. Gaylord. 2012. Mapping and characterization of recurring spring leads and landfast ice in the Beaufort and Chukchi seas. OCS Study BOEM 2012–067. U.S. Department of the Interior, Bureau of Ocean Energy Management, Alaska Region, Anchorage, Alaska, USA.
- Marcot, B. G. 2007. Biodiversity and the lexicon zoo. *Forest Ecology and Management* 246:4–13.
- Marcot, B. G. 2012. Metrics for evaluating performance and uncertainty of Bayesian network models. *Ecological Modelling* 230:50–62.
- Marcot, B. G., J. D. Steventon, G. D. Sutherland, and R. K. McCann. 2006. Guidelines for developing and updating Bayesian belief networks applied to ecological modeling and conservation. *Canadian Journal of Forest Research* 36:3063–3074.
- Møller, A. P., J. Erritzøe, and N. Saino. 2003. Seasonal changes in immune response and parasite impact on hosts. *American Naturalist* 161:657–671.
- Molnar, P. K., A. E. Derocher, T. Klanjscek, and M. A. Lewis. 2011. Predicting climate change impacts on polar bear litter size. *Nature Communications* 2:186.
- Molnár, P. K., A. E. Derocher, G. W. Thiemann, and M. A. Lewis. 2010. Predicting survival, reproduction and abundance of polar bears under climate change. *Biological Conservation* 143:1612–1622.
- Molnár, P. K., A. E. Derocher, G. W. Thiemann, and M. A. Lewis. 2014. Corrigendum to “Predicting survival, reproduction and abundance of polar bears under climate change”. *Biological Conservation* 143:1612–1622. <http://dx.doi.org/10.1016/j.biocon.2014.07.001>

- Moore, S. E., and H. P. Huntington. 2008. Arctic marine mammals and climate change: impacts and resilience. *Ecological Applications* 18:S157–S165.
- Morgan, M. G., and M. Henrion. 1990. *Uncertainty: a guide to dealing with uncertainty in quantitative risk and policy analysis*. Cambridge Press, Cambridge, UK.
- Obbard, M. E., M. R. Cattet, T. Moody, L. R. Walton, D. Potter, J. Inglis, and C. Chenier. 2006. Temporal trends in the body condition of southern Hudson Bay polar bears, Ontario. Applied Research and Development Branch, Peterborough, Ontario, Canada.
- Obbard, M. E., G. W. Thiemann, E. Peacock, and T. D. DeBruyn. 2010. Polar Bears: Proceedings of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group. Copenhagen, Denmark, 29 June–3 July 2009, IUCN, Gland, Switzerland and Cambridge, UK.
- Ovsyanikov, N. G., and I. A. Menyushina. 2007. Specifics of polar bear surviving ice free season on Wrangel Island in 2007. Wrangel Island State Nature Reserve, Chukotskyi AO, Russia.
- Patyk, K. A., et al. 2015. Establishing a definition of polar bear (*Ursus maritimus*) health: a guide to research and management. *Science of the Total Environment* 514:371–378.
- Peacock, E. 2009. Davis Strait polar bear population inventory. Final Report, Government of Nunavut, Department of Environment Report. Government of Nunavut, Igloolik, Nunavut, Canada.
- Peacock, E., M. K. Taylor, J. Laake, and I. Stirling. 2013. Population ecology of polar bears in Davis Strait, Canada and Greenland. *Journal of Wildlife Management* 77:463–476.
- Peacock, E., et al. 2015. Implications of the circumpolar genetic structure of polar bears for their conservation in a rapidly warming Arctic. *PLoS ONE* 10:e112021.
- Perovich, D. K., K. F. Jones, B. Light, H. Eicken, T. Markus, J. Stroeve, and R. Lindsay. 2011. Solar partitioning in a changing Arctic sea-ice cover. *Annals of Glaciology* 52:192–196.
- Pioz, M., A. Loison, D. Gauthier, P. Gibert, J. M. Jullien, M. Artois, and E. Gilot-Fromont. 2008. Diseases and reproductive success in a wild mammal: example in the alpine chamois. *Oecologia* 155:691–704.
- Pollino, C. A., O. Woodberry, A. Nicholson, K. Korb, and B. T. Hart. 2007. Parameterisation and evaluation of a Bayesian network for use in an ecological risk assessment. *Environmental Modelling and Software* 22:1140–1152.
- Polyak, L., et al. 2010. History of sea ice in the Arctic. *Quaternary Science Reviews* 29:1757–1778.
- Prop, J., et al. 2015. Climate change and the increasing impact of polar bears on bird populations. *Frontiers in Ecology and Evolution* 3:33.
- Regehr, E. V., N. J. Lunn, S. C. Amstrup, and I. Stirling. 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in western Hudson Bay. *Journal of Wildlife Management* 71:2673–2683.
- Regehr, E. V., C. M. Hunter, H. Caswell, S. C. Amstrup, and I. Stirling. 2010. Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. *Journal of Animal Ecology* 79:117–127.
- Ricke, K. L., and K. Caldeira. 2014. Maximum warming occurs about one decade after a carbon dioxide emission. *Environmental Research Letters* 9:124002.
- Robbins, C. T., C. Lopez-Alfaro, K. D. Rode, Ø. Tøien, and L. O. Nelson. 2013. Hibernation and seasonal fasting in bears: the energetic costs and consequences for polar bears. *Journal of Mammalogy* 93:1493–1503.
- Rockwell, R. F., and L. J. Gormezano. 2009. The early bear gets thegoose: climate change, polar bears and lesser snow geese in western Hudson Bay. *Polar Biology* 32:539–547.
- Rode, K. D., S. C. Amstrup, and E. V. Regehr. 2010. Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecological Applications* 20:768–782.
- Rode, K. D., E. Peacock, M. Taylor, I. Stirling, E. W. Born, K. L. Laidre, and Ø. Wiig. 2012. A tale of two polar bear populations: ice habitat, harvest, and body condition. *Population Ecology* 54:3–18. <http://dx.doi.org/10.1007/s10144-011-0299-9>
- Rode, K. D., E. V. Regehr, D. C. Douglas, G. Durner, A. E. Derocher, G. W. Thiemann, and S. M. Budge. 2014. Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. *Global Change Biology* 20:76–88.
- Rode, K. D., C. T. Robbins, L. Nelson, and S. C. Amstrup. 2015. Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities? *Frontiers in Ecology and Evolution* 13:138–145.
- Sahanatien, V., and A. E. Derocher. 2012. Monitoring sea ice habitat fragmentation for polar bear conservation. *Animal Conservation* 15:397–406.
- Schliebe, S., K. D. Rode, J. S. Gleason, J. Wilder, K. Proffitt, T. J. Evans, and S. Miller. 2008. Effects of sea ice extent and food availability on spatial and temporal distribution of polar bears during the fall open-water period in the Southern Beaufort Sea. *Polar Biology* 31:999–1010.
- Serreze, M. C., M. M. Holland, and J. Stroeve. 2007. Perspectives on the Arctic's shrinking sea-ice cover. *Science* 315:1533–1536.

- Sheriff, M. J., and O. P. Love. 2013. Determining the adaptive potential of maternal stress. *Ecology Letters* 16:271–280.
- Shimada, K., T. Kamoshida, M. Itoh, S. Nishino, E. Carmack, F. McLaughlin, S. Zimmerman, and A. Proshutinsky. 2006. Pacific Ocean inflow: influence on catastrophic reduction of sea ice cover in the Arctic Ocean. *Geophysical Research Letters*. <http://dx.doi.org/10.1029/2005GL025624>
- Smit, M. G., R. G. Jak, H. Rye, T. K. Frost, I. Singsaas, and C. C. Karman. 2008. Assessment of environmental risks from toxic and nontoxic stressors; a proposed concept for a risk-based management tool for offshore drilling discharges. *Integrated Environmental Assessment and Management* 4:177–183.
- Smith, L. C., and S. R. Stephenson. 2013. New Trans-Arctic shipping routes navigable by midcentury. *Proceedings of the National Academy of Sciences of the USA* 110:4871–4872.
- Smith, P. A., K. H. Elliott, A. J. Gaston, and H. G. Gilchrist. 2010. Has early ice clearance increased predation on breeding birds by polar bears? *Polar Biology* 33:1149–1153.
- Sonne, C., et al. 2012. Two decades of biomonitoring polar bear health in Greenland: a review. *Acta Veterinaria Scandinavica* 54:S15.
- Stephenson, S. R., L. C. Smith, L. W. Brigham, and J. A. Agnew. 2013. Projected 21st-century changes to Arctic marine access. *Climatic Change* 118:885–899.
- Stirling, I., and W. R. Archibald. 1977. Aspects of predation of seals by polar bears. *Journal of the Fisheries Board of Canada* 34:1126–1129.
- Stirling, I., and A. E. Derocher. 1993. Possible impacts of climatic warming on polar bears. *Arctic* 46:240–245.
- Stirling, I., and A. E. Derocher. 2012. Effects of climate warming on polar bears: a review of the evidence. *Global Change Biology* 18:2694–2706.
- Stirling, I., and C. L. Parkinson. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59:261–275.
- Stirling, I., N. J. Lunn, and J. Iacozza. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52:294–306.
- Stirling, I., E. Richardson, G. W. Thiemann, and A. E. Derocher. 2008. Unusual predation attempts of polar bears on ringed seals in the southern Beaufort Sea: possible significance of changing spring ice conditions. *Arctic* 61:14–22.
- Stirling, I., T. L. McDonald, E. S. Richardson, E. V. Regehr, and S. C. Amstrup. 2011. Polar bear population status in the northern Beaufort Sea, Canada, 1971–2006. *Ecological Applications* 21:859–876.
- Stroeve, J. C., T. Markus, L. Boisvert, J. Miller, and A. Barrett. 2014. Changes in Arctic melt season and implications for sea ice loss. *Geophysical Research Letters* 41:1216–1225.
- Swart, N. C., J. C. Fyfe, E. Hawkins, J. E. Kay, and A. Jahn. 2015. Influence of internal variability on Arctic sea-ice trends. *Nature Climate Change* 5:86–89.
- Thiemann, G. W., S. J. Iverson, and I. Stirling. 2008. Polar bear diets and arctic marine food webs: insights from fatty acid analysis. *Ecological Monographs* 78:591–613.
- U.S. Fish and Wildlife Service. 2008. Endangered and threatened wildlife and plants; 12-month petition finding and proposed rule to list the polar bear (*Ursus maritimus*) as threatened throughout its range. *Federal Registry* 72:1064–1099.
- Vongraven, D., et al. 2012. A circumpolar monitoring framework for polar bears. *Ursus* 23(sp2):1–66.
- van Vuuren, D. P., et al. 2011. The representative concentration pathways: an overview. *Climatic Change* 109:5–31.
- Wang, M., and J. E. Overland. 2009. A sea ice free summer Arctic within 30 years? *Geophysical Research Letters*. <http://dx.doi.org/10.1029/2009GL037820>
- Weber, D. S., et al. 2013. Low MHC variation in the polar bear—implications in the face of Arctic warming? *Animal Conservation* 16:671–683.
- Wielgus, J., M. Gonzalez-Suarez, D. Aurioles-Gamboa, and L. R. Gerber. 2008. A noninvasive demographic assessment of sea lions based on stage-specific abundances. *Ecological Applications* 18:1287–1296.

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