NRC Research Press

ARTICLE

Re-assessing abundance of Southern Hudson Bay polar bears by aerial survey: effects of climate change at the southern edge of the range

Martyn E. Obbard, Seth Stapleton, Guillaume Szor, Kevin R. Middel, Charles Jutras, and Markus Dyck

Abstract: The Southern Hudson Bay polar bear (*Ursus maritimus* Phipps, 1774) subpopulation is considered stable, but conflicting evidence lends uncertainty to that designation. Capture–recapture studies conducted in 1984–1986 and 2003–2005 and an aerial survey conducted in 2011/2012 suggested that abundance was likely unchanged since the mid-1980s. However, body condition and body size declined since then, and duration of sea ice decreased by about 30 days. Due to the conflicting information on subpopulation status and ongoing changes in sea ice, we conducted another aerial survey in 2016 to determine whether abundance had changed. We collected data via mark–recapture distance sampling and double-observer protocols. Results suggest that abundance declined 17% from 943 bears (95% CI: 658–1350) in 2011/2012 to 780 (95% CI: 590–1029) in 2016. The proportion of yearlings declined from 12% of the population in 2011 to 5% in 2016, whereas the proportion of cubs remained similar (16% in 2011 vs. 19% in 2016) suggesting low survival of the 2015 cohort. In a warming Arctic, duration of sea ice is predicted to continue to decline in Hudson Bay affecting all ice-dependent wildlife; therefore, further monitoring of this subpopulation is warranted. We recommend a conservative approach to harvest management and repeating the aerial survey in 2021.

Key words: abundance estimation, aerial survey, mark–recapture distance-sampling, polar bear, Southern Hudson Bay.

Résumé : La sous-population d'ours polaires (*Ursus maritimus* Phipps, 1774) du sud de la baie d'Hudson est considérée stable, mais des données contradictoires rendent ce postulat incertain. Des études réalisées par capture–recapture de 1984–1986 et de 2003–2005 et un levé aérien effectué en 2011/2012 suggèrent que l'abondance était probablement la même depuis le milieu des années 80. Cependant, l'état et la taille corporels ont diminué depuis, et la période de glace marine a raccourci d'environ 30 jours. En raison d'informations contradictoires sur l'état de la sous-population et des changements continuels de la glace marine, nous avons effectué un autre levé aérien en 2016 pour déterminer si l'abondance avait changé. Nous avons recueilli des données en utilisant les protocoles de l'échantillonnage à distance par marquage–recapture et de la

Received 15 March 2018. Accepted 15 May 2018.

M.E. Obbard and K.R. Middel. Wildlife Research and Monitoring Section, Ontario Ministry of Natural Resources and Forestry, DNA Building, Trent University, Peterborough, ON K9J 7B8, Canada.
S. Stapleton. Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA.
G. Szor and C. Jutras. Direction de la gestion de la faune du Nord-du-Québec, Ministère des Forêts, de la Faune et des Parcs, 951 boulevard Hamel, Chibougamau, QC G8P 2Z3, Canada.
M. Dyck. Wildlife Research Section, Department of Environment, Government of Nunavut, P.O. Box 209, Igloolik, NU X0A 0L0, Canada.
Corresponding author: Martyn Obbard (e-mail: martyn.obbard@ontario.ca).

Arctic Science **4:** 634–655 (2018) dx.doi.org/10.1139/as-2018-0004

méthode « double-observer ». Les résultats suggèrent que l'abondance a diminué de 17 %, soit de 943 ours en 2011/2012 (95 % IC 658–1350) à 780 en 2016 (95 % IC 590–1029). La proportion d'oursons a diminué de 12 % de la population en 2011 à 5 % en 2016, tandis que la proportion de nouveau-nés est restée constante (16 % en 2011 contre 19 % en 2016), indiquant un faible taux de survie pour la cohorte de 2015. Dans un Arctique en réchauffement, il est prévu que la période de glace marine continue à raccourcir dans la baie d'Hudson, affectant toute la faune dépendante de la glace; c'est pourquoi un suivi approfondi de cette sous-population est nécessaire. Nous recommandons une approche prudente pour la gestion de la récolte et de refaire le levé aérien en 2021. [Traduit par la Rédaction]

Mots-clés : estimation de l'abondance, levé aérien, échantillonnage à distance par marquage–recapture, ours polaire, sud de la baie d'Hudson.

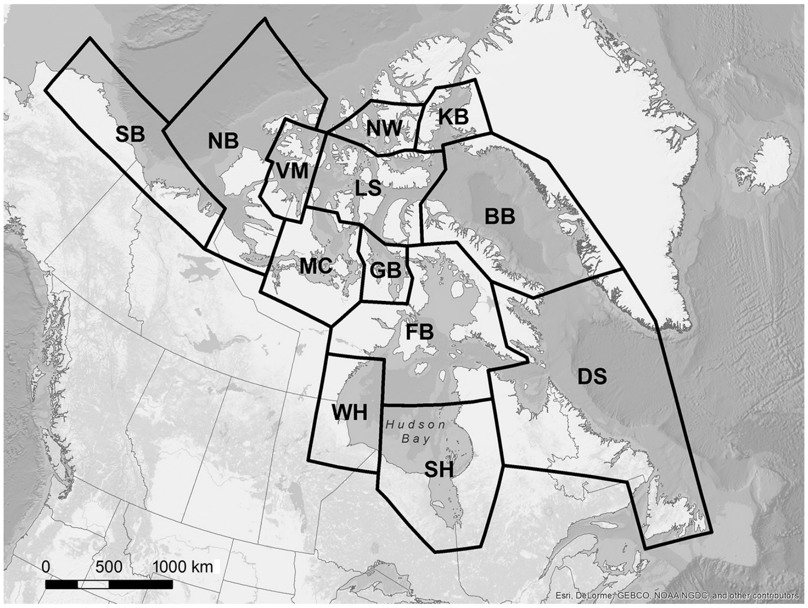
Introduction

Declines in the duration and distribution of sea ice in the Arctic have been implicated in large changes in several polar bear (*Ursus maritimus* Phipps, 1774) subpopulations. These changes include those at the level of individuals such as declines in body condition (Stirling et al. 1999; Rode et al. 2012; Obbard et al. 2016) and decreases in body size (Rode et al. 2010). Changes at the population level have also been related to declines in sea ice; these include shifts in distribution (Durner et al. 2009) and declines in survival rates and abundance (Regehr et al. 2007, 2010; Bromaghin et al. 2015; Lunn et al. 2016). The Southern Hudson Bay (SH) subpopulation occurs at the southern edge of the species' range in eastern Hudson Bay and James Bay (Fig. 1) in an area where, depending on criteria used to define break-up and freeze-up dates; break-up has advanced 3.0–5.0 days/decade, and freeze-up has been delayed by 3.6–5.0 days/decade since 1980 (Obbard et al. 2016; Stern and Laidre 2016).

Results of capture–recapture studies conducted on the Ontario mainland 1984–1986 and 2003–2005 suggested that abundance of the SH polar bear subpopulation was unchanged in that 20 year period from 634 (95% CI: 390–878) to 673 bears (95% CI: 396–950) (Obbard et al. 2007; Obbard 2008). Model-averaged survival estimates provided only weak evidence for a decline in total apparent survival of all age and sex classes between 1984–1986 and 1999–2005 (Obbard et al. 2007). Nonetheless, a decline in survival rates was consistent with the hypothesis that the SH population was under stress as suggested by declines in body condition between 1984–1986 and 2003–2005 (Obbard et al. 2006). Obbard (2008) suggested that such declines in body condition would eventually have negative demographic consequences because of the high sensitivity of polar bear population growth rates to changes in adult female survival. Because of the conflicting information indicating declines in body condition and survival but no declines in abundance, combined with the view of traditional knowledge holders that the population was stable or increasing, an aerial survey of the entire range of the SH subpopulation was conducted in 2011 and 2012 (Obbard et al. 2015). The abundance estimate for the entire SH subpopulation from that aerial survey (conducted on the Ontario mainland and Akimiski Island in 2011, and on the Québec coastline and nearshore islands and on the islands in eastern Hudson Bay and remaining islands in James Bay in 2012) was 943 bears (95% CI: 658–1350; Obbard et al. 2015).

Results from the 2011/2012 aerial survey and the two capture–recapture studies conducted 1984–1986 and 2003–2005 suggested that abundance in SH likely remained stable over about the previous 25 years. Nevertheless, both the duration of sea ice within the bounds of SH (Hochheim and Barber 2014; Stern and Laidre 2016) and body condition of

Fig. 1. Recognized boundaries of Canadian polar bear subpopulations. SB, South Beaufort; NB, North Beaufort; VM, Viscount Melville; NW, Norwegian Bay; LS, Lancaster Sound; MC, M'Clintock Channel; GB, Gulf of Boothia; BB, Baffin Bay; DS, Davis Strait; FB, Foxe Basin; WH, Western Hudson Bay; SH, Southern Hudson Bay. More information on subpopulations may be found in Lunn et al. (2010).



bears (Obbard et al. 2016) declined over the same period. In addition, duration of sea ice is expected to continue to decline in Hudson Bay in the future (Castro de la Guardia et al. 2013). Worldwide, polar bear abundance is expected to decline by 30% over the next three generations or 36 years (Regehr et al. 2016). Within the Hudson Bay region, habitat models predict major declines in distribution and abundance of polar bears in this area by mid-century (Amstrup et al. 2008). By 2012, polar bears in SH were already spending on average 30 days longer on land than bears did in 1980 (Obbard et al. 2016).

Although ecological change in the Arctic via changing duration and distribution of sea ice resulting from climate warming (Stirling and Derocher 2012) is currently considered the greatest threat to conservation of polar bears (PBSG 2010*a*, p. 85), harvest remains as an additional threat that is managed via measures such as quotas. Therefore, a current estimate of abundance is necessary to inform management and provide insight to sustainable harvest levels. In the context of ongoing declines in body condition in SH, predictions of further declines in sea ice in Hudson Bay, predictions of declines in abundance in Hudson Bay and worldwide, and ongoing legal harvest, we conducted a second aerial survey of the entire range of the SH subpopulation in September 2016 to assess whether abundance had changed since the previous aerial survey. To enable direct comparison of results of the two aerial surveys we closely followed the design of the 2011/2012 survey.

Materials and methods

Study area

Polar bear subpopulations are delineated based on a combination of ice movement patterns, tag returns from harvested bears, capture–recapture studies, and conventional and satellite radio-telemetry (Lunn et al. 2010). The boundaries of SH span much of eastern and SH and all of James Bay (Fig. 2), extending from the coastlines of Ontario and Québec to inland regions where bears are known to construct maternity dens (Jonkel et al. 1976; Kolenosky and Prevett 1983; Obbard and Walton 2004; Obbard and Middel 2012). The inland portion of the management unit includes areas up to 200 km inland, though documented use of sites >120 km inland is rare (Kolenosky and Prevett 1983; Obbard and Walton 2004; Obbard and Middel 2012). The Western Hudson Bay (WH) and Foxe Basin (FB) subpopulations border SH to the west and north, respectively (Fig. 2). Small nearshore and offshore islands in James Bay and eastern Hudson Bay are also included within SH. In total, the subpopulation covers about 465 000 km^2 of the surface area of Hudson Bay and James Bay and about 1270 and 1731 km of the coastlines of Ontario and Québec, respectively (Fig. 2).

Study design

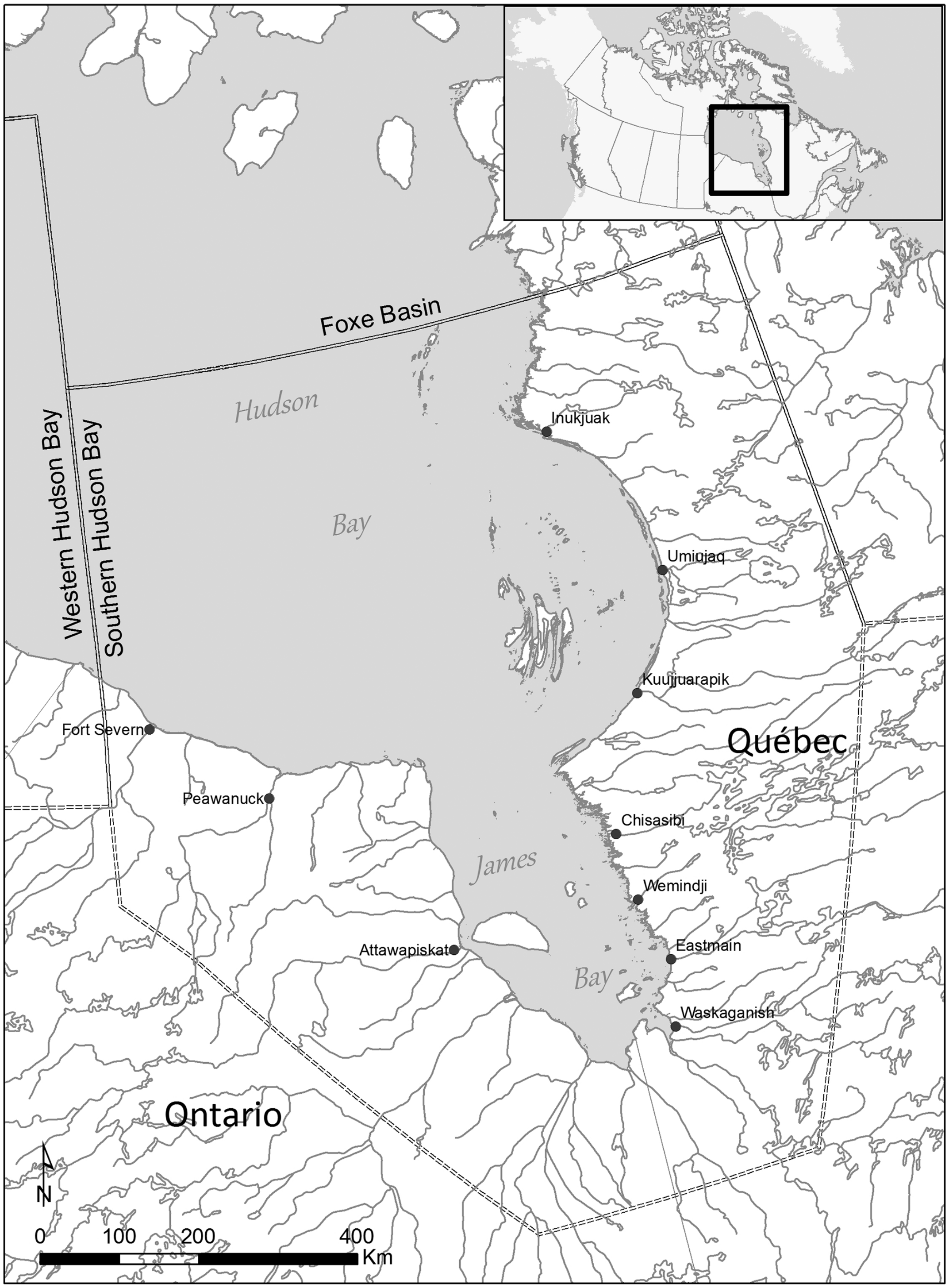
During the late summer and fall ice-free season in Hudson Bay (Markham 1988; Wang et al. 1994*a*, 1994*b*) polar bears in SH are confined to land, demonstrating strong fidelity to particular geographic regions (Obbard and Walton 2004; Stirling et al. 2004; Obbard and Middel 2012) and remaining segregated from neighbouring subpopulations in FB and WH. Pregnant bears in SH typically enter maternity dens between the last week of October and mid-November (Middel 2014); the earliest that a bear appeared to localize at a den location was 17 September; the next earliest was 8 October. Therefore, following Obbard et al. (2015), we conducted our aerial survey in September when most bears in the subpopulation would be available to be counted.

Except for total counts of bears on very small islands, we simultaneously collected data for both sight–resight (i.e., double-observer; Pollock and Kendall 1987) and distance sampling (Buckland et al. 2001). We implemented a double-observer platform in which two-person teams of front and rear observers worked independently to sight bears. We erected an opaque partition between front and rear observers to ensure that sightings by the front team did not cue rear observers, and sightings were only announced after both teams were afforded a full opportunity to spot a bear. We defined a group (hereafter cluster) of bears as individuals whose sightings were nonindependent (i.e., spotting one bear led to the observation of others; e.g., family groups comprised an adult female and one or more dependent young or a group of male bears). For each sighting, we recorded the number of bears in a cluster, and the bear's activity (e.g., running and sitting) when first spotted; we also estimated field age class (adult, subadult, yearling, and cub-of-the-year), body condition (1–5; Stirling et al. 2008), and other covariates that could affect detection probabilities. These latter covariates included vegetation height within a 30 m radius (<1, 1–3, and >3 m), vegetation density at the same spatial scale (1 = sparse tundra, 2 = moderate, and 3 = dense), visibility [1 = poor (e.g., dense fog or rain), 2 = fair (e.g., light fog, light rain, overcast, and excessive glare), and 3 = excellent (e.g., clear and sunny, partly cloudy)]. We used GPSs to record flight paths and bear locations.

Survey of Québec coast and coastal inland transects

Following Obbard et al. (2015), we designed and implemented a systematic helicopter-based line transect aerial survey of the Québec coast and nearshore islands. We used an A Star 350 BA helicopter, flown at a target altitude of 150 m above ground level (AGL) and a ground speed of approximately 150 km/h. We modified the methodology of this portion of the survey slightly from Obbard et al. (2015) based on additional input from traditional knowledge holders in Inukjuak, Umiujaq, and Kuujjuarapik collected by the Nunavik Marine Region Wildlife Board in 2016 (NMRWB 2018). Coverage of the coastline and nearshore islands was the same as in 2012, but we added coverage to include inland habitats believed to be occasionally used by polar bears in late summer. To achieve this, we flew a

Fig. 2. Boundaries and extent of the Southern Hudson Bay polar bear subpopulation in Ontario and Québec, including islands in James Bay and eastern Hudson Bay. Inset shows location in Canada.



series of 20 km inland transects, oriented perpendicular to the coastline and spaced 6 km apart (for comparability with the Ontario mainland and Akimiski Island portion of the overall survey), from Pointe Louis XIV/Long Island at the junction of James Bay and Hudson Bay to north of Inukjuak, except for the Lake Tasiujaq area (Lac Guillaume-Delisle) where the lake shoreline was surveyed instead of flying over extensive areas of open water. We surveyed all nearshore islands (i.e., those within 5 km of the coast) as well as the Québec coastline (Fig. 3).

Offshore islands in James Bay and eastern Hudson Bay

For safety reasons, a twin-engine platform was required to access the offshore islands in Hudson Bay and James Bay (Fig. 3); therefore, these areas were surveyed using a de Havilland DHC-6 Twin Otter with two pilots and four observers in the rear of the aircraft. Pilots did not contribute to the count, nor did they alert observers to bears seen by them. When bears were sighted, we recorded the covariates mentioned above, and data were entered immediately onto a field computer. The aircraft flew at a planned height of 150 m AGL and at a planned speed of 150 km/h.

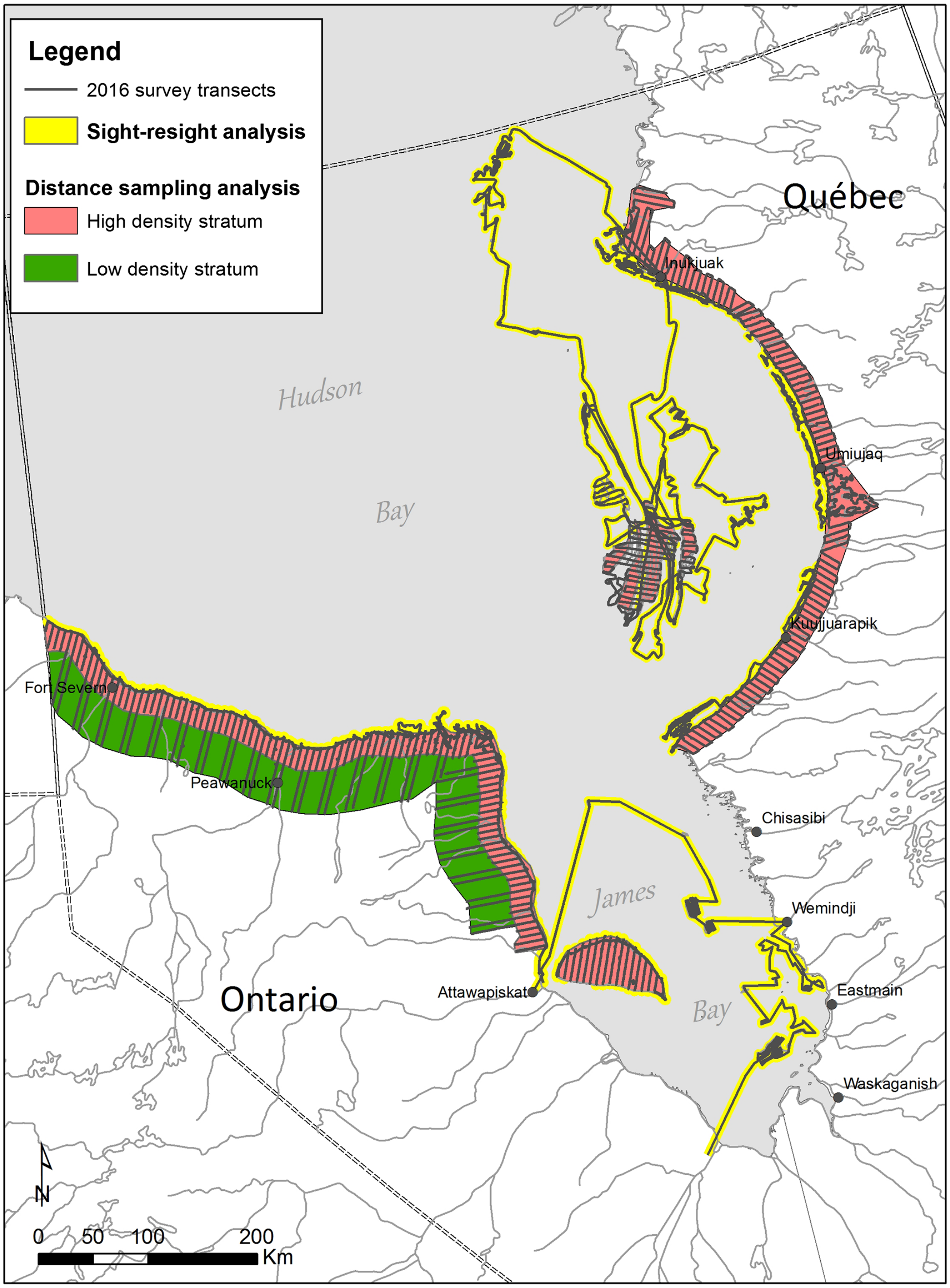
We surveyed the Belcher Islands, located in southeastern Hudson Bay, using a combination of overland, perpendicular transects and coastal contours, which facilitated sampling about 50% of the shoreline. Surveys of other islands in eastern Hudson Bay such as the Ottawa, Sleeper, and King George island complexes were spatially comprehensive. The coverage and methodology for the eastern Hudson Bay offshore islands were identical to that in Obbard et al. (2015) except for a small area added in the coverage of the Belcher Islands region following input from the Hunters and Trappers Organisation of Sanikiluaq. Protocols enabled the simultaneous collection of data for both sight–resight (double-observer) and distance sampling analyses as above. However, for the distance sampling analysis, we used a clinometer to measure the angle from the aircraft to the bear, once the aircraft was perpendicular to the bear, to estimate its distance because the exact position of the bears when sighted could not be recorded with the fixed-wing aircraft. We recorded the same covariates as in other portions of the survey.

Coverage of the James Bay islands was similar to the 2012 survey except for a few small nearshore islands that were added (Paint Hills Islands, Moar Bay, and Old Factory Bay) based on input from traditional and local knowledge holders collected by the Eeyou Marine Region Wildlife Board in 2016. We surveyed larger islands in James Bay (Charlton, South Twin, and North Twin) using transects spaced 3 km apart. Finally, we comprehensively surveyed small offshore islands in James Bay and eastern Hudson Bay (Fig. 3).

Survey of Ontario mainland and Akimiski Island

Following methods of Obbard et al. (2015), we designed and implemented a systematic helicopter-based line transect aerial survey of the Ontario mainland and Akimiski Island in James Bay. Our survey area extended from the boundary of SH near the Ontario/Manitoba border to the Ekwan River on James Bay (Fig. 3). Polar bears occur rarely south of the Ekwan River during the ice-free season (Obbard and Walton 2004), so we did not survey this area. For bears outfitted with GPS collars between 2007 and 2011 during August–October, the maximum distance from the coast for any bear was 49.8 km ($\bar{x} = 5.9$ km, $n = 13\,132$ locations; Middel 2014). A few maternity dens have been recorded >100 km inland in Ontario (Kolenosky and Prevett 1983), but most denning occurs within our defined study area. For example, based on winter aerial surveys, Kolenosky and Prevett (1983) documented 12 of 19 dens <60 km from the coast. More recently, data from satellite or GPS-collared bears indicated that from 2002 to 2011, 22 of 23 bears, whose den locations were checked by site visits after they were abandoned the following spring,

Fig. 3. Strata and survey transects completed during an aerial survey of the Southern Hudson Bay polar bear subpopulation, September 2016. Mainland areas and nearshore islands in Ontario and Québec plus Akimiski Island in James Bay were surveyed by helicopter. Offshore islands in James Bay and eastern Hudson Bay were surveyed by twin-engine fixed-wing aircraft.



denned within 60 km of the coast ($\bar{x} = 37.1$ km); the 23rd bear denned 62.7 km inland from the coast (M.E. Obbard and K.R. Middel, unpublished data). Therefore, consistent with Obbard et al. (2015), we defined two inland strata in Ontario, including a high-density zone extending from the coastline to 20 km inland, and a low-density stratum extending 20–60 km inland (Fig. 3). We also delineated a coastal zone that included land within 500 m of the shoreline, tidal flats, nearshore islands, and spits. We used both overland transects, oriented perpendicular to the coastline, and coastal contour transects. Because polar bears congregate near the shore during the ice-free season and are less frequent farther inland (Derocher and Stirling 1990*a*, 1990*b*; Obbard and Walton 2004; Towns et al. 2010), arranging the overland (hereafter perpendicular) transects along this density gradient minimized estimate bias and improved precision (Buckland et al. 2001; Stapleton et al. 2014). We extended perpendicular transects over exposed tidal flats so that we could estimate abundance without the coastal contours. We spaced perpendicular transects at 6 km intervals in the high-density stratum. Every other pair of transects was extended through the low-density stratum (i.e., to 60 km inland), such that transect spacing there averaged 12 km (Fig. 3).

We used a Eurocopter EC-130 helicopter and flew at a planned altitude of 150 m AGL and a speed of 150 km/h. Data were recorded using a double-observer protocol for the coastal transects, and following a distance sampling protocol for inland transects perpendicular to the coast. We erected an opaque screen between front and rear observers. The helicopter pilot was one of the front observers. When we sighted bears, we recorded covariates as described above, and data were recorded immediately on a field computer. We used a GPS to record flight paths and bear locations and adapted procedures from Marques et al. (2006) to measure distances from the transect lines to sightings in a GIS (ArcMap 9.3; Environmental Systems Research Institute, Redlands, CA, USA). All data were entered at the time of the observation into a Panasonic Toughbook running ESRI ArcPad version 8.0; the Toughbook had a built-in GPS that recorded all track files. Because fuel caches were located close to the coast; operationally, we divided the area to be surveyed into approximately 2 h legs, in part based on fuel capacity of the helicopter. We started a leg at a fuel cache and flew the coastal contour transect first, then we flew all perpendicular transects back to the fuel cache. In this way, we minimized the possibility that bears might move large distances between when the coastal transect was flown and when perpendicular transects were flown, thereby minimizing the possibility that bears might be counted more than once.

Analyses

Perpendicular transects

To ensure comparability between the previous aerial survey (2011/2012) and this study, the design, sampling protocols, and analytical methods were followed Obbard et al. (2015) as closely as possible. We used distance sampling (Buckland et al. 2001) to derive an abundance estimate from perpendicular transects in mainland Ontario, Akimiski Island, and the large islands around Sanikiluaq. Perpendicular transects used to sample smaller islands in southeastern Hudson Bay were tightly spaced (<3 km intervals between transects), such that sampling was essentially spatially comprehensive. In addition, because these islands were very small, transects often included large portions of the coastline, at times running approximately parallel to the shore. Because bears congregate on or near the coastline during the late summer ice-free season, they may partially reflect this density gradient rather than the actual detection function (Stapleton et al. 2014; Obbard et al. 2015). Hence, these data were inappropriate for distance sampling and were analyzed via double observer analyses (see below). We also note that extensive sampling of mainland Québec yielded no sightings from perpendicular transects, so these transect data and the associated study area were not included in distance sampling analyses.

Fig. 4. Distances of polar bear sightings from the transect line of the Ontario mainland and Akimiski Island, 15–25 September 2016. Data include bears sighted from perpendicular transects in the coastal zone.

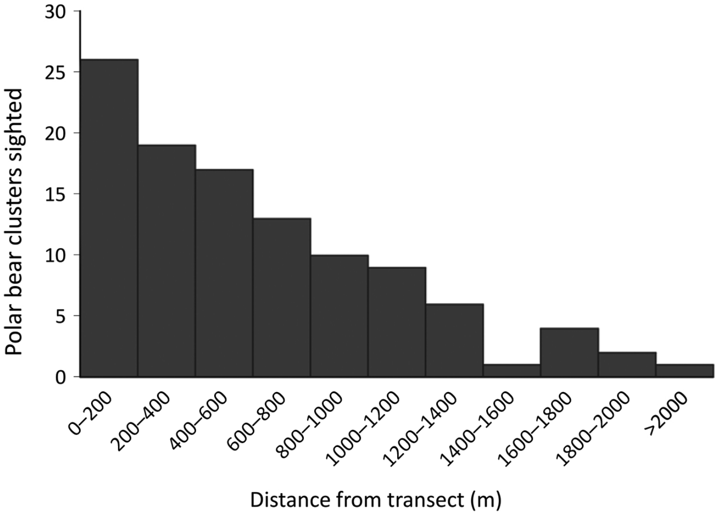
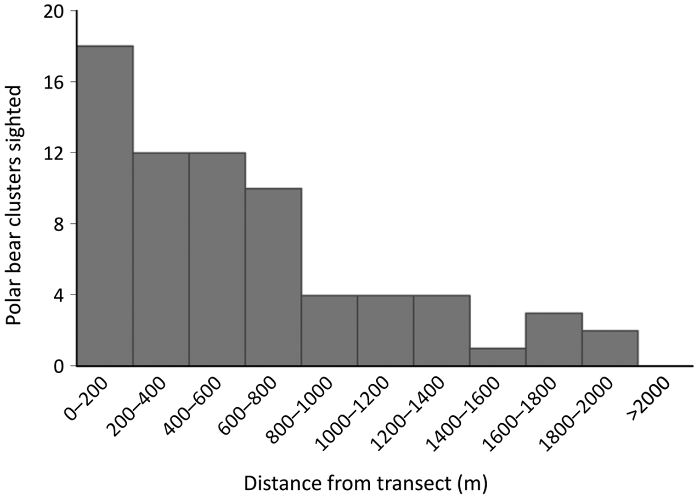


Fig. 5. Distances of polar bear sightings from the transect line of the Ontario mainland and Akimiski Island, 15–25 September 2016. Data exclude bears sighted from perpendicular transects in the coastal zone.



Because bears along the shoreline or on tidal flats could be sighted from both coastal contour and perpendicular transects, we compiled two datasets that included and excluded the coastal zone sightings from the perpendicular transect data. Histograms summarizing sighting distances from the flight path suggested support for a distance-based detection function (Figs. 4 and 5). In addition, preliminary double observer analyses suggested that detection at distance zero approximated unity (i.e., the probability that at least one observer sighted a cluster bear at near the transect line was >0.95), a fundamental assumption of distance sampling. As such, we proceeded with multiple covariate distance sampling analyses, allowing us to incorporate environmental covariates that could explain variability in detection probabilities.

We completed distance sampling analyses in program Distance (version 7.0, release 1; Thomas et al. 2010). We first fit conventional distance sampling models with uniform, half-normal, and hazard rate key functions and associated series expansion terms (cosine, simple polynomial, and Hermite polynomial), enabling us to evaluate general model fit and examine potential cluster size bias in detection. For both datasets, we right-truncated data at ~5% (i.e., the most distant 5% of observations were discarded), as recommended to improve model fit (Buckland et al. 2001).

We conducted all additional modeling in the MRDS engine of program Distance and specified the single observer analysis. This protocol enabled us to derive an empirical estimate of variance via the Innes et al. (2002) method (facilitated by the MRDS engine), rather than estimate variance via bootstrapping simulations.

Because initial analyses indicated that cluster size did not significantly impact detection, we used mean cluster size for estimating abundance. We examined three covariates potentially influencing detection, including visibility and vegetation height and density within 30 m of the sighting. Although the latter two covariates were highly correlated, we considered both independently in modeling to evaluate which best explained variation in detection.

We incorporated covariates via forward stepwise selection and selected the most highly supported models using Akaike's information criterion (Burnham and Anderson 2002). The two datasets yielded estimates of abundance that reflected the entire region surveyed with perpendicular transects (i.e., including the coastal data) and the region inland of the coastal zone (i.e., excluding the coastal data).

Coastal contours and nearshore islands

We used double-observer data collected along coastal contour transects to generate an independent estimate of abundance for the coastal zone. As in Obbard et al. (2015), the Huggins model (Huggins 1989, 1991), a capture–recapture model, enabled us to include covariates in modeling and to estimate individual detection probabilities. We surveyed the region 500 m inland of the shoreline, as well as the exposed tidal flats, small nearshore islands, and spits across Ontario and Québec.

We completed all double-observer modeling in Program MARK (White and Burnham 1999) and employed AIC$_c$ for model selection. We defined polar bear clusters as the sampling unit and specified that detection probabilities either remained constant or varied between observer teams. We used forward stepwise selection to evaluate four covariates: visibility, cluster size, vegetation height, and vegetation density. Because of under-representation of some values, we condensed visibility, vegetation height, and vegetation density to binary parameters. To estimate the number of clusters present in the study area, the parameter estimates from the most supported models in each dataset were input with a generalized Horvitz–Thompson estimator. We estimated the number of individuals by incorporating the mean observed group size for each dataset, calculated group size sampling variance following Buckland et al. (2001), and propagated and multiplied variances via the Delta method (Powell 2007).

Offshore islands

Small, offshore islands in James Bay and Hudson Bay were analyzed separately using double observer modeling as outlined above. We examined visibility and cluster size covariates to explain variability in detection on the James Bay islands and those off the coasts of Ontario and Québec. In eastern Hudson Bay, we incorporated covariates for cluster size and whether the cluster was observed on land or in the sea. Other covariates were not explored due to a lack of variability. Some very small islands were comprehensively surveyed; these total counts were added to the final abundance estimate (without an estimate of variance).

Total abundance

Double sampling the coastal zone enabled us to obtain two partially independent abundance estimates. First, we added estimates from offshore islands across Ontario, Québec, and Nunavut, the perpendicular transect analysis that included the coastal zone, and small islands that were comprehensively surveyed. Second, we summed the abundance estimates from the offshore islands, the complete coastal contour transects, the perpendicular transects analysis that excluded the coastal zone, and the small, comprehensively surveyed islands. We then averaged the two point estimates (equal weights) and used a model-averaging framework (Burnham and Anderson 2002) to estimate unconditional variance, yielding a final abundance estimate and associated error estimates for SH.

Results

Survey effort and sightings

We completed the survey of the Québec coast and coastal inland transects from 6 to 13 September 2016. We surveyed progressively northward from Pointe Louis XIV to north of Inukjuak except for a small section north of Umiujaq that was skipped due to bad weather conditions and completed on the last surveying day. We flew a total of 32 h on transect and surveyed a total of 5126 km, including about 3181 km on inland transects, 1452 km on nearshore islands, and 574 km of coastline. Though many sections of the coastline were covered several times during ferrying flights, only the first surveying occasion was included in the survey effort calculation. We observed a total of four polar bears in this section of the survey, including two single adults and one adult female accompanied by a yearling, all of them on nearshore islands.

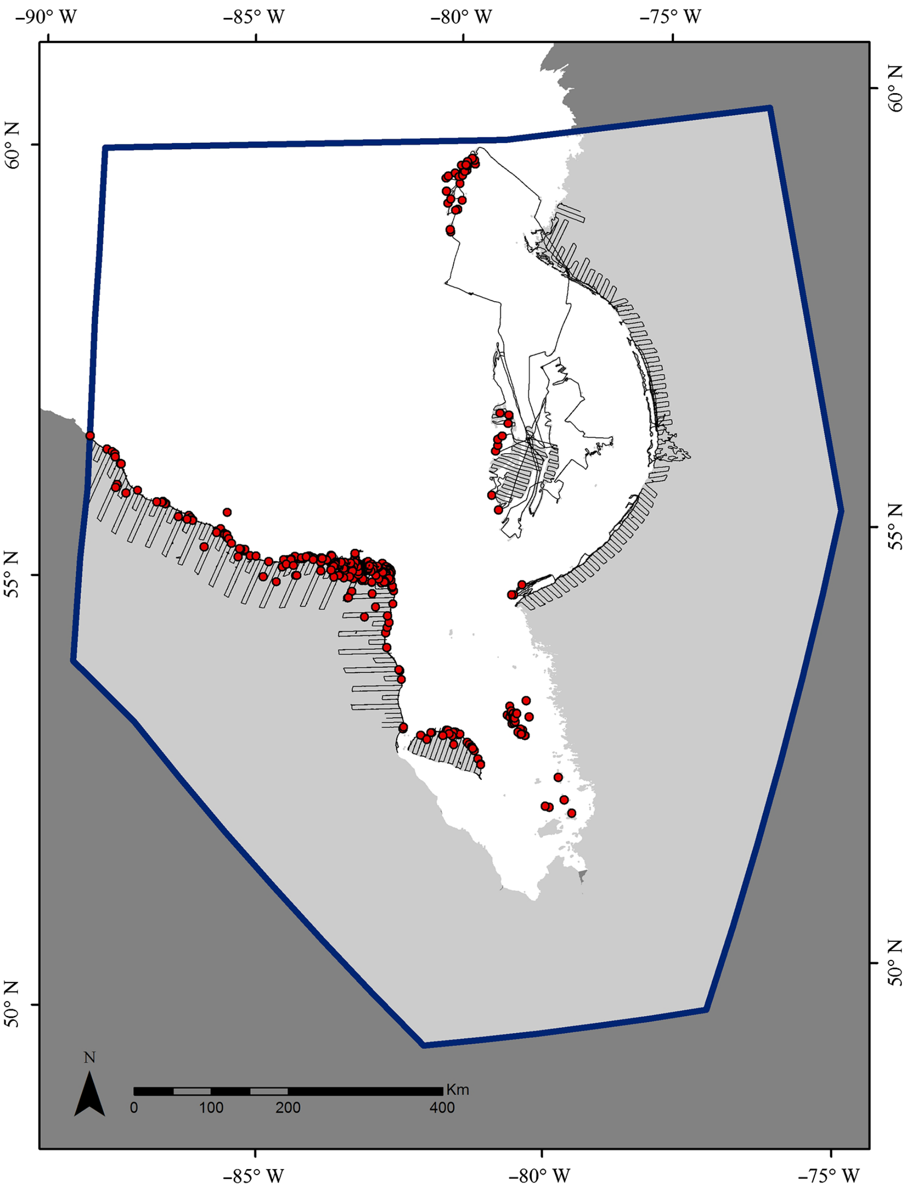
We surveyed the islands in James Bay (except for Akimiski Island; see below) on 13 September 2016. We flew a total of 7.4 h on transect. Raw counts were a total of 44 bears, including cubs and yearlings.

We surveyed islands in eastern Hudson Bay from 15 to 18 September. We flew a total of 20.3 h on transect and surveyed a total of 4236 km over the Belcher Islands and surrounding offshore islands including the Ottawa, Sleeper, and King George island complexes. Raw counts were 38 bears on the Ottawa Islands and 11 bears in the vicinity of the Belcher Islands.

We flew the Ontario mainland and Akimiski Island portions from 15 to 25 September. Sampling progressed systematically from Akimiski Island in James Bay, northwards along the James Bay coast of Ontario to Cape Henrietta Maria, thence westward to the SH boundary with WH. The survey occurred over 81 total flight hours and covered 4527 km along perpendicular transects, including sampling 2631 and 1896 km in the high-density and low-density strata, respectively.

We documented a total of 540 sightings in SH that were incorporated in analyses, including 487 sightings in Ontario and the James Bay islands, and 49 on and near islands in eastern Hudson Bay (Fig. 6). Extensive sampling of the coastline and interior of Québec yielded sightings of four bears comprising three clusters, all observed on islands near the junction of James Bay and Hudson Bay (Fig. 6). As in the 2011/2012 aerial survey, most sightings were concentrated on mainland Ontario near the shoreline, although bears were occasionally spotted >10 km from the coastline. Because we independently sampled the coastline of Ontario with both perpendicular and contour transects, despite our operational protocol to minimize double counting, bears near the coast may have been sighted twice, and we were unable to calculate the number of unique sightings.

Fig. 6. Locations of observations of polar bears during an aerial survey of the Southern Hudson Bay subpopulation, September 2016.



Abundance estimation

Perpendicular transects

We surveyed about 5100 km of perpendicular transects during the 2016 aerial survey, including ~2632 km in the high-density stratum, ~1896 km in the low-density strata, and ~570 km of islands in James Bay and eastern Hudson Bay. Although sampling from perpendicular transects occurred on mainland Québec, no bears were observed from those transects; therefore, these data were not included in analyses. After right-truncating the data at 1750 m (i.e., the distance at which the farthest ~5% of observations were censored), we incorporated 104 polar bear clusters in the distance sampling analysis that included the coastal zone data and 67 clusters in the analysis that excluded coastal sightings. We included 204 transects for variance estimation.

For both datasets, the most highly supported models included vegetation density as a covariate; both hazard rate and half-normal key functions were supported in model selection (Table 1). All highly supported models yielded adequate overall χ^2 goodness-of-fit statistics ($P > 0.05$; Table 1) and showed suitable fit with additional metrics (Kolmogorov–Smirnov and Cramér–von Mises tests: all $P > 0.65$). Because there was some variability in density estimation depending on key function, we model averaged the two most highly supported models in each dataset (representing both hazard rate and half-normal key functions) to derive an estimate of abundance, which allowed us to exclude those models with uninformative parameters (i.e., models that did not appreciably improve AIC_c scores with an additional parameter; Arnold 2010). We estimated 599 bears (standard error: 124.7; 95% lognormal confidence interval: 400–897) and 411 bears (SE: 90.6; 95% CI: 268–630) with the datasets including and excluding the coastal zone, respectively.

Coastal contours and small islands

Ontario

We included 137 clusters in the double observer analysis with sightings from the coastal zone and small nearshore islands. The most highly supported model included no covariates and estimated a constant detection probability for front and rear observers (P: 0.74, SE: 0.03), with an overall inclusion probability of ~0.93. After multiplying by mean cluster size ($\bar{x}$: 1.51) and inflating variances, we estimated 221 bears (SE: 12.8) in Ontario's coastal zone.

Offshore islands

We incorporated 51 and 36 clusters for modeling detection on the islands of James Bay and along the Québec coast of Hudson Bay, and on the islands in eastern Hudson Bay, respectively. In the James Bay–Québec analysis, the most highly supported model included a covariate for cluster size and estimated constant detection between front and rear observers (P: 0.83, SE: 0.05). Before inflating the raw counts with the estimates of detection via the Horvitz–Thompson estimator, we added two clusters that were not used to estimate detection because the location of observers who sighted the bear (i.e., front, rear, or both) was not recorded. We multiplied by mean cluster size ($\bar{x}$: 1.58), and inflated variances, yielding an estimate of 89 bears (SE: 8.0) in the James Bay–Québec offshore islands. For the eastern Hudson Bay islands, the best model also incorporated constant detection for front and rear observers, but included covariates for cluster size and sighting location (i.e., in the water or on land; P: 0.81, SE: 0.07). Multiplying by mean cluster size ($\bar{x}$: 1.33) yielded an estimate of 53 bears (SE: 6.4) on the islands in eastern Hudson Bay. We also spotted 22 bears on spits and small islands offshore of Ontario that were comprehensively surveyed; these areas were considered total counts (i.e., no estimate of variance).

Total abundance

We summed the results of the perpendicular transect analysis including the coastal zone with the estimates of bears on small islands, yielding 763 bears (SE: 125.1). We obtained an estimate of 796 bears (SE: 92.1) by adding the estimates from the coastal contour transects, the perpendicular transects excluding the coastal region, and small islands. Averaging these figures yielded an estimate of 780 bears (SE: 111.1; 95% CI: 590–1029) in SH during the 2016 ice-free season.

Comparison to 2011/2012 survey

The estimate from the current survey is not significantly different from the abundance estimate for the 2011/2012 survey of 943 bears (95% CI: 658–1350; Obbard et al. 2015) based

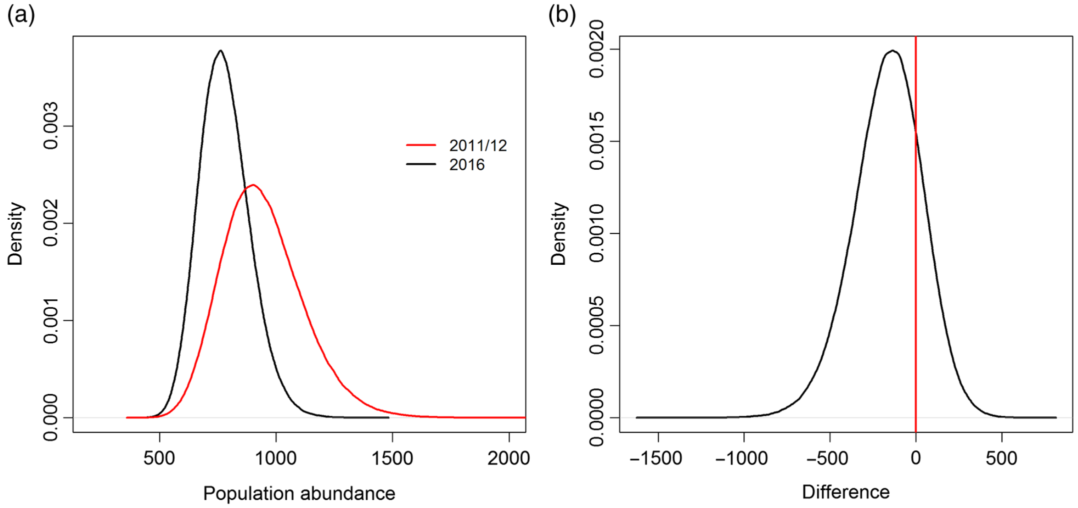
Table 1. Summary of modeling results from distance sampling analyses of an aerial survey of the Southern Hudson Bay polar bear subpopulation, September 2016.

				Density: Bears/1000 km^2 (95% CI)				
Dataset	Model (key function/ covariates)	ΔAIC	No. of parameters	High-density stratum[a]	Low-density stratum	Nunavut stratum	Global[a]	GOF: Overall χ^2 (P)
Including coastal sightings	Hazard/VegDens	0.00	3	31.1 (20.5–47.1)	2.2 (0.9–5.5)	0.7 (0.1–4.1)	13.4 (9.0–19.8)	0.35
	Half-Normal/VegDens	0.40	2	35.2 (23.5–52.7)	2.6 (1.0–6.5)	0.9 (0.2–4.9)	15.2 (10.4–22.2)	0.54
	Hazard/VegDens + Vis	2.00	4	31.1 (20.5–47.2)	2.2 (0.9–5.5)	0.7 (0.1–4.1)	13.4 (9.0–19.8)	0.24
	Half-Normal/VegDens + Vis	2.34	3	35.2 (23.4–53.0)	2.6 (1.0–6.6)	0.9 (0.2–4.8)	15.2 (10.3–22.4)	0.42
Excluding coastal sightings	Hazard/VegDens	0.00	3	21.1 (13.3–33.5)	2.4 (0.9–6.0)	0.8 (0.1–4.5)	9.4 (6.1–14.5)	0.10
	Half-Normal/VegDens	0.22	2	23.1 (14.9–35.8)	2.7 (1.0–6.8)	0.9 (0.2–5.2)	10.4 (6.9–15.6)	0.18
	Half-Normal/VegDens + Vis	1.47	3	23.2 (14.9–36.1)	2.8 (1.1–7.2)	0.9 (0.2–4.8)	10.4 (6.9–15.9)	0.10
	Half-Normal	1.60	1	22.5 (14.3–35.3)	2.8 (1.1–7.3)	1.0 (0.2–5.7)	10.2 (6.7–15.5)	0.28
	Hazard/VegDens + Vis	1.87	4	20.9 (13.3–33.1)	2.4 (0.9–6.0)	0.8 (0.1–4.3)	9.4 (6.1–14.3)	0.05
	Half-Normal/VegHt	1.97	2	22.7 (14.6–35.4)	2.7 (1.0–6.9)	0.9 (02–5.3)	10.2 (6.8–15.4)	0.18

Note: Models with ΔAIC < 3 are presented. In the column *Model*, covariates are vegetation density (VegDens), visibility (Vis), and vegetation height (VegHt). Goodness of fit metrics for the distance sampling detection function also included Kolmogorov–Smirnov and Cramér–von Mises tests (all $P > 0.65$ for all highly supported models).

[a] Density estimates refer to density within the region estimated by distance sampling. The dataset excluding coastal sightings does not incorporate those bears in the high-density stratum and global density estimates.

Fig. 7. Results of Monte Carlo simulations to explore the difference between the estimates of abundance from the 2011/2012 and 2016 surveys. Figure 7*a* (left panel) shows the overlap of distributions from the Monte Carlo simulations, and Fig. 7*b* (right panel) shows the distribution of differences.



on the confidence intervals overlapping the means. However, because polar bears are listed as Threatened in Ontario under the Endangered Species Act, we wished to better inform managers about the status of the subpopulation. To do this, we used Monte Carlo simulations to explore the difference between the two estimates. We specified a lognormal distribution defined by the point estimates and SEs of the two surveys and randomly sampled from each of these distributions to represent potential population sizes for the two surveys ($n = 1\,000\,000$ iterations). Sixty-one percent of iterations yielded a difference (i.e., a decline) of >100 between the estimates for 2011/2012 and 2016 (Figs. 7*a*, 7*b*). In terms of proportional differences, 63% of the runs showed a decline of >10% between 2011/2012 and 2016, 43% showed >20% decline and 32% showed >25% decline.

Reproduction

Litter sizes averaged 1.46 (SD: 0.50; $n = 72$) for cubs, and 1.32 (SD: 0.48; $n = 22$) for yearlings, based on all sightings included in analyses. Cubs comprised 19% of all observations and yearlings comprised 5% of all observations (Table 2).

Discussion

Abundance estimation

In order for us to evaluate status of the SH subpopulation, it was important for us to be able to assess trend in abundance. To ensure that results would be directly comparable with the 2011/2012 survey, we replicated its design and effort with the exception of inland transects along the Québec coast, a small area adjacent to the Belcher Islands, and a small number of nearshore islands in James Bay that were added to the study design based on input from traditional knowledge holders. Our study design incorporated coastal contour transects, which recognized that the clumped distribution of polar bears along the coast of Hudson Bay in Ontario and Manitoba during the ice-free season (Prevett and Kolenosky 1982; Derocher and Stirling 1990*a*, 1990*b*; Obbard and Walton 2004; Towns et al. 2010) could bias results. Further, our study design also incorporated transects perpendicular to the coastline and following the density of bears, which decreases with distance away from the

Table 2. Polar bear litter sizes and number of dependent young observed as proportion of all observations during the ice-free season in the Southern Hudson Bay (SH), Western Hudson Bay (WH), and Foxe Basin (FB) subpopulations.

Subpopulation	Litter size cubs of year (SD, *n*)	Litter size yearlings (SD, *n*)	Proportion cubs of year	Proportion yearlings	Source
SH aerial survey, 2016	1.46 (SD = 0.50, *n* = 72)	1.32 (SD = 0.48, *n* = 22)	0.19	0.05	This study
SH aerial survey, 2011	1.56 (SD = 0.50, *n* = 70)	1.49 (SD = 0.50, *n* = 53)	0.16	0.12	Obbard et al. 2015
WH aerial survey, 2016	1.63 (SD = 0.49, *n* = 24)	1.25 (SD = 0.46, *n* = 8)	0.12	0.03	Dyck et al. 2017
WH aerial survey, 2011	1.43 (SD = 0.50, *n* = 35)	1.22 (SD = 0.43, *n* = 18)	0.07	0.03	Stapleton et al. 2014
FB aerial survey, 2011	1.53 (SD = 0.57, *n* = 80)	1.4 (SD = 0.50, *n* = 65)	0.13	0.10	Stapleton et al. 2016

coast. Arranging the overland transects along this density gradient minimized estimate bias and improved precision (Buckland et al. 2001). Both features of our study design account for the known distribution of bears during the ice-free season and are important to minimize bias and thereby improve accuracy and precision.

Modest analytical and design differences between the two studies did not significantly influence the results or our ability to evaluate population trend and status. In the previous survey, Obbard et al. (2015) used mark–recapture distance sampling (MRDS; Laake and Borchers 2004) rather than conventional or multiple covariate distance sampling (Marques and Buckland 2003) analyses because preliminary analyses indicated that detection at distance 0 was significantly <1, thereby violating a fundamental assumption of distance sampling (Buckland et al. 2001). MRDS integrates distance sampling and double-observer analytical methods, allowing for estimation of detection at distance 0 and subsequent correction of the abundance estimate. In this study, our detection of bears on and near the transect line approximated unity, meaning that we were able to generate an accurate estimate of abundance with simpler multiple covariate distance sampling models. Although right-truncation distance differed between the two studies (Obbard et al. 2015: ~2%; here: ~5%), there was a negligible impact on results. The shoulders of the detection function (i.e., the sightings near the transect line) are most important for generating estimates of density and abundance (Buckland et al. 2001). Truncating the farthest sightings improves model fit by eliminating the need to estimate spurious bumps in this sightings "tail", with only modest impacts on estimate precision and negligible impacts on the point estimate (Buckland et al. 2001). Small differences elsewhere, including more widespread sampling in Quebec in 2016 and the incorporation of techniques to estimate abundance for the James Bay islands in 2016 (rather than relying on raw counts) similarly had trivial impacts on the results. Both the previous and current surveys met the core assumptions of distance sampling including detection on the transect line; therefore, despite the small variations in the sampling and analytical methodology, the results from the two surveys are comparable thereby enabling us to assess trend and status.

Delineation of the study area to 60 km inland along the Ontario coast of Hudson Bay and James Bay as in the previous survey was based on available scientific and traditional knowledge of the distribution of bears during the ice-free season and of denning habitat. Although we did not survey the entire inland area of SH in Ontario, extending transects farther inland would have been very expensive for minimal returns. Truncating our transects at 60 km may have resulted in some slight negative bias in the abundance estimate, but all the evidence suggests that few bears are found that far inland in September, and if any were there, they would not comprise a large proportion of the subpopulation.

Traditional knowledge holders indicated that bears were occasionally observed inland in the Québec portion of the study area north of Pointe Louis XIV/Long Island at the junction of James Bay and Hudson Bay (e.g., Laforest et al. 2018; NMRWB 2018). Based on this information, we adapted our study design slightly from the 2012 survey to provide better coverage of this region. However, despite our intensive survey (transects spaced at 6 km intervals), we observed no bears in the area. No doubt, bears occasionally occur here but their density must be very low, and their number would make only a small difference to the total abundance estimate.

Our results suggest that abundance in the SH subpopulation declined by 17% between 2011/2012 and 2016. It has been hypothesized that distribution of bears during the ice-free season along the shores of Ontario and Manitoba varies depending on where the last ice of the season persists resulting in an inverse correlation between counts from coastal strip surveys conducted at the same time in Ontario and Manitoba (Prevett and Kolenosky 1982). This argument suggests that polar bears, especially males, may choose to remain on the ice until late in the season, and as a result, they may simply occupy coastal areas closest to the location of residual ice once the ice melts completely. Location of residual ice in any year would then influence distribution of bears. Hence, one explanation for the decline in abundance that we noted for SH may be that the distribution of bears shifted due to ice conditions in 2016 such that more bears came ashore within the boundary of WH. However, using a longer dataset, Stirling et al. (2004) found no significant correlations (negative or positive) between annual counts in Ontario and those in Manitoba bringing this explanation into doubt. Furthermore, results of an aerial survey conducted in WH in 2016 at about the same time as our survey provided no evidence for an unusual number of bears in the eastern portion of the range of WH, in fact that survey suggested that subpopulation had also likely declined in abundance (Dyck et al. 2017). Lastly, the pattern of ice ablation in Hudson Bay is affected by prevailing northwesterly winds and counter-clockwise ocean currents resulting in residual ice moving south and east and gathering north of the Ontario coast (Hochheim et al. 2011). Bears remain on the ice as it drifts south and east during the melt season and eventually come to shore in Manitoba or Ontario (Parks et al. 2006; Middel 2014); there is no evidence of bears moving north as ice melts. Therefore, the decline in abundance in SH suggested by our results is unlikely to be due to a shift in distribution into WH or FB.

There are interesting parallels in trends between WH and SH. In both subpopulations changes in individual-level traits (e.g., declines in body condition; WH: Stirling et al. 1999, SH: Obbard et al. 2016) preceded changes in population-level traits (e.g., declines in survival and in abundance; WH: Regehr et al. 2007; Lunn et al. 2016, SH: Obbard et al. 2007; this study). However, these changes in morphometry and demography appear to have started sooner in WH than in SH. Because of the pattern of ice ablation and formation in Hudson Bay, on an annual basis bears from the two subpopulations are faced with a similar pattern of ice duration, but it is out of synchrony by a few weeks. That is because the last sea ice usually remains off the northern Ontario coast in summer (Etkin 1991; Saucier et al. 2004); therefore, bears in SH leave the ice later in spring than bears in WH, but return to the ice later in the fall because ice forms off the Ontario coast later (Hochheim and Barber 2010). On a long-term basis, changes in the duration of ice cover appear to have started sooner in the western portions of Hudson Bay where bears from WH mainly occur during the ice-covered season compared to the eastern portions of Hudson Bay where bears from SH mainly occur (Gagnon and Gough 2005; Hochheim et al. 2010; Hochheim and Barber 2014). Thus, the two subpopulations appear to have followed similar trajectories in response to changes in duration of sea ice, though starting later in SH, and it seems likely that these trends will continue in the future.

Reproduction

The proportion of cubs in all observations was similar in the 2011 and 2016 surveys, but the proportion of yearlings dropped from 12% to 5% (sample size from the 2012 portion of the original survey is too small for comparison). We are not aware of any evidence of reproductive synchrony in polar bear populations that would infer large variation in size of the year class of cubs born. Therefore, the low proportion of yearlings in the 2016 survey suggests low survival of cubs born in 2015. Whether this represents an ongoing trend, or was the result of unusual conditions in spring and summer of 2015 is undetermined. However, breakup in eastern Hudson Bay was about two weeks later in 2015 than in 2010–2014 (Andrews et al. 2018) suggesting that ice conditions should not have had a negative influence on cub survival in 2015. The proportion of yearlings in the 2016 SH survey was similar to that observed in the WH surveys of 2011 and 2016 (3%). In contrast, subpopulations with robust vital rates have proportions of yearlings in the 10%–12% range, such as FB and SH in 2011 (Obbard et al. 2015).

Long-lived animals should maximize their reproductive output, but should not do so at a risk to their own survival. Because the proportion of cubs remained high in 2016, many adult females in SH are still producing litters, but they may be less successful in raising cubs to yearling age. Obbard et al. (2016) suggested that because the rate of decline in body condition was less for cubs of the year in SH than for their mothers, by the late 2000s adult females were allocating a greater proportion of their reserves to lactation than females did in the mid-1980s. If this is true, but cub survival is still dropping, then adult females may be putting themselves at increased risk, especially in the context of ongoing declines in duration of sea ice that can be expected to have further negative effects on body condition. A more adaptive strategy for a long-lived species with delayed implantation such as polar bears (Wimsatt 1974; Ferguson et al. 1996) would be for females to forego reproductive bouts entirely when a reproductive bout is unlikely to be successful. Because the number of litters of cubs observed in 2016 in Ontario and Akimiski Island was similar to the number observed in 2011, females may not yet be adopting that life history strategy. Furthermore, the number of litters observed in SH in both 2011 and 2016 was about double the number observed in WH at the same time suggesting that a higher proportion of SH females continue to attempt to raise cubs successfully (given that population abundance in WH is similar to that of SH) (Lunn et al. 2016; Dyck et al. 2017). The low number of litters of yearlings observed in 2016 compared to the number of litters of cubs suggests that much cub mortality may be via loss of entire litters. If females lose litters due to high neonatal mortality, in the absence of lactational suppression of estrus (Knott et al. 2017), they may become receptive again shortly after returning to the sea ice in spring, resulting in them having litters in consecutive years. This may be happening in SH and, in itself, would put additional energetic demands on adult females in this subpopulation for no increase in fitness. If such energetic costs are additive, they could ultimately have negative consequences for survival of adult females.

Conclusions

Though the point estimates obtained from the 2011/2012 and 2016 surveys were not significantly different, point estimates of abundance are typically used to assess status (PBSG 2010*b*). The suggestion of a decline in abundance is supported by the Monte Carlo simulations where about one-third showed a >25% decline between the two estimates. Further monitoring of this subpopulation is required to determine whether the decline in abundance was a short-term response to environmental conditions or a longer-term trend. Therefore, we recommend repeating the intensive aerial survey in 2021 with additional recruitment surveys in the interim, though managers should consider whether the cost of surveying the Québec coastline can be justified in future surveys.

Derocher et al. (2013) discussed several options that might be achievable for management agencies where polar bears are forced to spend longer on land due to climate warming. These options included diversionary feeding to reduce human-bear conflict, supplemental feeding to help individual bears survive periods of food deprivation, and intentional population reduction to achieve a smaller but viable population at the lowered carrying capacity brought about by loss of habitat (Derocher et al. 2013). Careful consideration of all possible management options in consultation with all communities that are harvesting this population or could be affected by an increasing presence of nutritionally stressed bears on land will be necessary to identify the best management approach in the future. In a period of rapid environmental change and barring major mitigation of greenhouse gas emissions in the near future (Amstrup et al. 2010), managers should invoke the precautionary principle and consider conservative harvest levels for this subpopulation.

Acknowledgements

We thank pilot C. Blondin and observer B. Ford for assistance during the helicopter-based survey of the coast of Québec. We thank pilots R. Seguin and E. Bergman, and observers L. Walton and D. Holtby for assistance during the fixed-wing survey of islands in James Bay. We thank pilots R. Seguin and E. Bergman, and observers B. Ford, B. Nowkawalk, C. Takatak, A. Puasi Ippak, and D. Qavvik for assistance during the fixed-wing survey of islands in eastern Hudson Bay. We thank pilot D. Holtby and observers L. Walton and P. Burke for assistance during the helicopter survey of the Ontario mainland and Akimiski Island. J. Northrup and R. Watt provided helpful comments on earlier drafts of the manuscript. We thank J. Northrup for advice on the Monte Carlo simulations. Comments from A. Derocher and two anonymous reviewers helped us to improve the manuscript.

Major funding was provided by the Ontario Ministry of Natural Resources and Forestry, Québec Ministère des Forêts, de la Faune et des Parcs, Makivik Corporation, and Environment and Climate Change Canada. Additional funding was provided by the Cree Outfitters and Trappers Association, Nunavik Marine Region Wildlife Board, Nunavut Department of Environment, Nunavut Wildlife Management Board, Polar Bears International, and World Wildlife Fund Canada.

References

Amstrup, S.C., Marcot, B.G., and Douglas, D.C. 2008. A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. *In* Arctic sea ice decline: observations, projections, mechanisms, and implications. *Edited by* E.T. De Weaver, C.M. Bitz, and L.-B. Tremblay. American Geophysical Union, Washington, D.C., USA. pp. 213–268.

Amstrup, S.C., DeWeaver, E.T., Douglas, D.C., Marcot, B.G., Durner, G.M., Bitz, C.M., and Bailey, D.A. 2010. Greenhouse gas mitigation can reduce sea-ice loss and increase polar bear persistence. Nature, **468**: 955–958. doi: 10.1038/nature09653. PMID: 21164484.

Andrews, J., Babb, D., and Barber, D.G. 2018. Climate change and sea ice: shipping in Hudson Bay, Hudson Strait, and Foxe Basin (1980–2016). Elem. Sci. Anth. **6**: 19. doi: 10.1525/elementa.281.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J. Wildl. Manage. **74**: 1175–1178. doi: 10.1111/j.1937-2817.2010.tb01236.x.

Bromaghin, J.F., McDonald, T.L., Stirling, I., Derocher, A.E., Richardson, E.S., Regehr, E.V., Douglas, D.C., Durner, G.M., Atwood, T., and Amstrup, S.C. 2015. Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. Ecol. Appl. **25**: 634–651. doi: 10.1890/14-1129.1. PMID: 26214910.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, UK.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, N.Y., USA.

Castro de la Guardia, L., Derocher, A.E., Myers, P.G., Terwisscha van Scheltinga, A.D., and Lunn, N.J. 2013. Future sea ice conditions in Western Hudson Bay and consequences for polar bears in the 21st century. Glob. Chang. Biol. **19**: 2675–2687. doi: 10.1111/gcb.12272. PMID: 23716301.

Derocher, A.E., and Stirling, I. 1990*a*. Observations of aggregating behaviour in adult male polar bears (*Ursus maritimus*). Can. J. Zool. **68**: 1390–1394. doi: 10.1139/z90-207.

Derocher, A.E., and Stirling, I. 1990*b*. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Can. J. Zool. **68**: 1395–1403. doi: 10.1139/z90-208.

Derocher, A.E., Aars, J., Amstrup, S.C., Cutting, A., Lunn, N.J., Molnár, P.K., Obbard, M.E., Stirling, I., Thiemann, G.W., Vongraven, D., Wiig, Ø., and York, G. 2013. Rapid ecosystem change and polar bear conservation. Conserv. Lett. **6**: 368–375. doi: 10.1111/conl.12009.

Durner, G.M., Douglas, D.C., Nielson, R.M., Amstrup, S.C., McDonald, T.L., Stirling, I., Mauritzen, M., Born, E.W., Wiig, Ø., DeWeaver, E., Serreze, M.C., Belikov, S.E., Holland, M.M., Maslanik, J., Aars, J., Bailey, D.A., and Derocher, A.E. 2009. Predicting 21st-century polar bear habitat distribution from global climate models. Ecol. Monogr. **79**: 25–58. doi: 10.1890/07-2089.1.

Dyck, M., Campbell, M., Lee, D.S., Boulanger, J., and Hedman, D. 2017. 2016 aerial survey of the Western Hudson Bay polar bear subpopulation: final report. Status report 2017-xx. Nunavut Department of Environment, Wildlife Research Section, Igloolik, Nun., Canada. 82 pp.

Etkin, D.A. 1991. Break-up in Hudson Bay: its sensitivity to air temperatures and implications for climate warming. Climatol. Bull. **25**: 21–34.

Ferguson, S.H., Virgl, J.A., and Larivière, S. 1996. Evolution of delayed implantation and associated grade shifts in life history traits of North American carnivores. Écoscience, **3**: 7–17.

Gagnon, A.S., and Gough, W.A. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. Arctic, **58**: 370–382.

Hochheim, K.P., and Barber, D.G. 2010. Atmospheric forcing of sea ice in Hudson Bay during the fall period, 1980–2005. J. Geophys. Res.: Oceans, **115**: C05009. doi: 10.1029/2009JC005334.

Hochheim, K.P., and Barber, D.G. 2014. An update on the ice climatology of the Hudson Bay system. Arct. Antarct. Alp. Res. **46**: 66–83. doi: 10.1657/1938-4246-46.1.66.

Hochheim, K.P., Barber, D.G., and Lukovich, J.V. 2010. Changing sea ice conditions in Hudson Bay, 1980–2005. *In* A little less Arctic. *Edited by* S.H. Ferguson, L.L. Loseto, and M.L. Mallory. Springer Netherlands. pp. 39–52.

Hochheim, K.P., Lukovich, J.V., and Barber, D.G. 2011. Atmospheric forcing of sea ice in Hudson Bay during the spring period, 1980–2005. J. Mar. Syst. **88**: 476–487. doi: 10.1016/j.jmarsys.2011.05.003.

Huggins, R. 1989. On the statistical analysis of capture experiments. Biometrika, **76**: 133–140. doi: 10.1093/biomet/76.1.133.

Huggins, R. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics, **47**: 725–732. doi: 10.2307/2532158.

Innes, S., Heide-Jørgensen, M.P., Laake, J.L., Laidre, K.L., Cleator, H.J., Richard, P., and Stewart, R.E.A. 2002. Surveys of belugas and narwhals in the Canadian High Arctic in 1996. NAMMCO Sci. Publ. **4**: 169–190. doi: 10.7557/3.2843.

Jonkel, C., Smith, P., Stirling, I., and Kolenosky, G.B. 1976. Notes on the present status of the polar bear in James Bay and the Belcher Islands. Canadian Wildlife Service Occasional Paper No. 26. Canadian Wildlife Service, Ottawa, Ont., Canada.

Knott, K.K., Mastromonaco, G.F., Owen, M.A., and Kouba, A.J. 2017. Urinary profiles of progestin and androgen metabolites in female polar bears during parturient and non-parturient cycles. Conserv. Physiol. **5**: cox023. doi: 10.1093/conphys/cox023. PMID: 28458884.

Kolenosky, G.B., and Prevett, J.P. 1983. Productivity and maternity denning of polar bears in Ontario. Int. Conf. Bear Res. Manage. **5**: 238–245. doi: 10.2307/3872543.

Laake, J.L., and Borchers, D. 2004. Methods for incomplete detection at distance zero. *In* Advanced distance sampling. *Edited by* S. Buckland, D. Anderson, K. Burnham, J. Laake, D. Borchers, and L. Thomas. Oxford University Press, Oxford, UK. pp. 108–189.

Laforest, B.J., Hébert, J.S., Obbard, M.E., and Thiemann, G.W. 2018. Traditional ecological knowledge of polar bears in the northern Eeyou Marine Region, Québec, Canada. Arctic, **71**: 40–58. doi: 10.14430/arctic4696.

Lunn, N.J., Branigan, M., Carpenter, L., Justus, J., Hedman, D., Larsen, D., Lefort, S., Maraj, R., Obbard, M.E., Peacock, L., and Pokiak, F. 2010. Polar bear management in Canada, 2005–2008. *In* Polar bears: Proceedings of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, Copenhagen, Denmark, 29 June–3 July 2009. *Edited by* M.E. Obbard, G.W. Thiemann, E. Peacock, and T.D. DeBruyn. Occasional Paper of the IUCN Species Survival Commission No. 43. IUCN, Gland, Switzerland. pp. 87–113.

Lunn, N.J., Servanty, S., Regehr, E.V., Converse, S.J., Richardson, E., and Stirling, I. 2016. Demography of an apex predator at the edge of its range: impacts of changing sea ice on polar bears in Hudson Bay. Ecol. Appl. **26**: 1302–1320. doi: 10.1890/15-1256. PMID: 27755745.

Markham, W.E. 1988. Ice atlas: Hudson Bay and approaches. Environment Canada, Atmospheric Environment Service, Downsview, Ont., Canada.

Marques, F.F.C., and Buckland, S.T. 2003. Incorporating covariates into standard line transect analyses. Biometrics, **59**: 924–935. doi: 10.1111/j.0006-341X.2003.00107.x. PMID: 14969471.

Marques, T.A., Andersen, M., Christensen-Dalsgaard, S., Belikov, S., Boltunov, A., Wiig, Ø., Buckland, S.T., and Aars, J. 2006. The use of global positioning systems to record distances in a helicopter line-transect survey. Wildl. Soc. Bull. **34**: 759–763. doi: 10.2193/0091-7648(2006)34[759:TUOGPS]2.0.CO;2.

Middel, K.R. 2014. Movement parameters and space use for the Southern Hudson Bay polar bear subpopulation in the face of a changing climate. M.Sc. thesis, Trent University, Peterborough, Ont., Canada. 131 pp.

Nunavik Marine Region Wildlife Board (NMRWB). 2018. Nunavik Inuit knowledge and observations of polar bear: polar bears of the Southern Hudson Bay subpopulation. Nunavik Marine Region Wildlife Board, Inukjuak, Que., Canada. xiv + 73 pp.

Obbard, M.E. 2008. Southern Hudson Bay polar bear project 2003–2005. Final report. Ontario Ministry of Natural Resources, Peterborough, Ont., Canada. 64 pp.

Obbard, M.E., and Middel, K.R. 2012. Bounding the Southern Hudson Bay polar bear subpopulation. Ursus, **23**: 134–144. doi: 10.2192/URSUS-D-11-00030.1.

Obbard, M.E., and Walton, L.R. 2004. The importance of Polar Bear Provincial Park to the Southern Hudson Bay polar bear population in the context of future climate change. *In* Parks and protected areas research in Ontario, 2004: planning northern parks and protected areas. Proceedings of the Parks Research Forum of Ontario Annual General Meeting. *Edited by* C.K. Rehbein, J.G. Nelson, T.J. Beechey, and R.J. Payne. Parks Research Forum of Ontario, Waterloo, Ont., Canada. pp. 105–116.

Obbard, M.E., Cattet, M.R.L., Moody, T., Walton, L.R., Potter, D., Inglis, J., and Chenier, C. 2006. Temporal trends in the body condition of Southern Hudson Bay polar bears. Climate Change Research Information Note No. 3. Ontario Ministry of Natural Resources, Sault Ste. Marie, Ont., Canada. 8 pp.

Obbard, M.E., McDonald, T.L., Howe, E.J., Regehr, E.V., and Richardson, E.S. 2007. Polar bear population status in Southern Hudson Bay, Canada. Administrative Report. U.S. Geological Survey, Reston, Va., USA. 32 pp.

Obbard, M.E., Stapleton, S., Middel, K.R., Thibault, I., Brodeur, V., and Jutras, C. 2015. Estimating the abundance of the Southern Hudson Bay polar bear subpopulation with aerial surveys. Polar Biol. **38**: 1713–1725. doi: 10.1007/s00300-015-1737-5.

Obbard, M.E., Cattet, M.R.L., Howe, E.J., Middel, K.R., Newton, E.J., Kolenosky, G.B., Abraham, K.F., and Greenwood, C.J. 2016. Trends in body condition in polar bears (*Ursus maritimus*) from the Southern Hudson Bay subpopulation in relation to changes in sea ice. Arct. Sci. **2**: 15–32. doi: 10.1139/as-2015-0027.

Parks, E.K., Derocher, A.E., and Lunn, N.J. 2006. Seasonal and annual movement patterns of polar bears on the sea ice of Hudson Bay. Can. J. Zool. **84**: 1281–1294. doi: 10.1139/z06-115.

Polar Bear Specialist Group (PBSG). 2010*a*. Press release 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group. *In* Polar Bears: Proceedings of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 29 June–3 July 2009, Copenhagen, Denmark. *Edited by* M.E. Obbard, G.W. Thiemann, E. Peacock, and T.D. DeBruyn. Occasional Paper of the IUCN Species Survival Commission No. 43. IUCN, Gland, Switzerland. pp. 85–86.

Polar Bear Specialist Group (PBSG). 2010*b*. 2009 status report on the world's polar bear subpopulations. *In* Polar Bears: Proceedings of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 29 June–3 July 2009, Copenhagen, Denmark. *Edited by* M.E. Obbard, G.W. Thiemann, E. Peacock, and T.D. DeBruyn. Occasional Paper of the IUCN Species Survival Commission No. 43. IUCN, Gland, Switzerland. pp. 31–80.

Pollock, K., and Kendall, W. 1987. Visibility bias in aerial surveys: a review of estimation procedures. J. Wildl. Manage. **51**: 502–510. doi: 10.2307/3801040.

Powell, L. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor, **109**: 949–954. doi: 10.1650/0010-5422(2007)109[949:AVODPU]2.0.CO;2.

Prevett, J.P., and Kolenosky, G.B. 1982. The status of polar bears in Ontario. Nat. Can. **109**: 933–939.

Regehr, E.V., Lunn, N.J., Amstrup, S.C., and Stirling, I. 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in western Hudson Bay. J. Wildl. Manage. **71**: 2673–2683. doi: 10.2193/2006-180.

Regehr, E.V., Hunter, C.M., Caswell, H., Amstrup, S.C., and Stirling, I. 2010. Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. J. Anim. Ecol. **79**: 117–127. doi: 10.1111/j.1365-2656.2009.01603.x. PMID: 19754681.

Regehr, E.V., Laidre, K.L., Akçakaya, H.R., Amstrup, S.C., Atwood, T.C., Lunn, N.J., Obbard, M., Stern, H., Thiemann, G.W., and Wiig, Ø. 2016. Conservation status of polar bears (*Ursus maritimus*) in relation to projected sea-ice declines. Biol. Lett. **12**: 20160556. doi: 10.1098/rsbl.2016.0556. PMID: 27928000.

Rode, K.D., Amstrup, S.C., and Regehr, E.V. 2010. Reduced body size and cub recruitment in polar bears associated with sea ice decline. Ecol. Appl. **20**: 768–782. doi: 10.1890/08-1036.1. PMID: 20437962.

Rode, K.D., Peacock, E., Taylor, M., Stirling, I., Born, E.W., Laidre, K.L., and Wiig, Ø. 2012. A tale of two polar bear populations: ice habitat, harvest, and body condition. Popul. Ecol. **54**: 3–18. doi: 10.1007/s10144-011-0299-9.

Saucier, F.J., Senneville, S., Prinsenberg, F.R., Smith, G., Gachon, P., Caya, D., and Laprise, R. 2004. Modelling the sea ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson Strait, Canada. Clim. Dyn. **23**: 303–326. doi: 10.1007/s00382-004-0445-6.

Stapleton, S., Atkinson, S., Hedman, D., and Garshelis, D. 2014. Revisiting Western Hudson Bay: using aerial surveys to update polar bear abundance in a sentinel population. Biol. Conserv. **170**: 38–47. doi: 10.1016/j.biocon.2013.12.040.

Stapleton, S., Peacock, E., and Garshelis, D. 2016. Aerial surveys suggest long-term stability in the seasonally ice-free Foxe Basin (Nunavut) polar bear population. Mar. Mammal Sci. **32**: 181–201. doi: 10.1111/mms.12251.

Stern, H.L., and Laidre, K.L. 2016. Sea-ice indicators of polar bear habitat. Cryosphere, **10**: 2027–2041. doi: 10.5194/tc-10-2027-2016.

Stirling, I., and Derocher, A.E. 2012. Effects of climate warming on polar bears: a review of the evidence. Glob. Chang. Biol. **18**: 2694–2706. doi: 10.1111/j.1365-2486.2012.02753.x. PMID: 24501049.

Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climatic change. Arctic, **52**: 294–306. doi: 10.14430/arctic935.

Stirling, I., Lunn, N.J., Iacozza, J., Elliott, C., and Obbard, M. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open water season, in relation to population trends and annual ice patterns. Arctic, **57**: 15–26. doi: 10.14430/arctic479.

Stirling, I., Thiemann, G.W., and Richardson, E. 2008. Quantitative support for a subjective fatness index for immobilized polar bears. J. Wildl. Manage. **72**: 568–574. doi: 10.2193/2007-123.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, R.B., Marques, T.A., and Burnham, K.P. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. J. Appl. Ecol. **47**: 5–14. doi: 10.1111/j.1365-2664.2009.01737.x. PMID: 20383262.

Towns, L., Derocher, A.E., Stirling, I., and Lunn, N.J. 2010. Changes in land distribution of polar bears in western Hudson Bay. Arctic, **63**: 206–212. doi: 10.14430/arctic975.

Wang, J., Mysak, L.A., and Ingram, R.G. 1994*a*. Interannual variability of sea-ice cover in Hudson Bay, Baffin Bay and the Labrador Sea. Atmos.-Ocean, **32**: 421–447. doi: 10.1080/07055900.1994.9649505.

Wang, J., Mysak, L.A., and Ingram, R.G. 1994*b*. A numerical simulation of sea ice cover in Hudson Bay. J. Phys. Oceanogr. **24**: 2515–2533. doi: 10.1175/1520-0485(1994)024<2515:ANSOSI>2.0.CO;2.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study, **46**(Suppl. 1): S120–S139. doi: 10.1080/00063659909477239.

Wimsatt, W.A. 1974. Delayed implantation in the Ursidae, with particular reference to the black bear (*Ursus americanus* Pallas). *In* Delayed implantation. *Edited by* A.C. Enders. University of Chicago Press, Chicago, Ill., USA. pp. 49–86.