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ORIGINAL PAPER

Estimating the abundance of the Southern Hudson Bay polar bear subpopulation with aerial surveys

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Abstract The Southern Hudson Bay (SH) polar bear subpopulation occurs at the southern extent of the species' range. Although capture–recapture studies indicate abundance was likely unchanged between 1986 and 2005, declines in body condition and survival occurred during the period, possibly foreshadowing a future decrease in abundance. To obtain a current estimate of abundance, we conducted a comprehensive line transect aerial survey of SH during 2011–2012. We stratified the study site by anticipated densities and flew coastal contour transects and systematically spaced inland transects in Ontario and on Akimiski Island and large offshore islands in 2011. Data were collected with double-observer and distance sampling protocols. We surveyed small islands in James Bay and eastern Hudson Bay and flew a comprehensive transect along the Québec coastline in 2012. We observed 667 bears in Ontario and on Akimiski Island and nearby islands in 2011, and we sighted 80 bears on offshore islands during 2012. Mark–recapture distance sampling and sight–resight models yielded an estimate of 860 (SE = 174) for the 2011 study area. Our estimate of abundance for the entire SH subpopulation (943; SE = 174) suggests that abundance is unlikely to have changed significantly since 1986. However, this result should be interpreted cautiously because of the methodological differences between historical studies (physical capture–recapture) and this survey. A conservative management approach is warranted given previous increases in duration of the ice-free season, which are predicted to continue in the future, and previously documented declines in body condition and vital rates.

Keywords Abundance estimation · Aerial survey · Line transect · Mark–recapture distance sampling · Polar bear · Southern Hudson Bay · *Ursus maritimus*

Introduction

Accelerating loss of sea ice (Stroeve et al. 2007, 2012; Comiso et al. 2008) spells an increasingly tenuous future for Arctic wildlife species that rely upon it. For ice-obligate polar bears (*Ursus maritimus*), the impacts of the changing Arctic environment are not projected to be spatially or temporally uniform: bears inhabiting the higher latitudes of the Canadian archipelago and portions of the polar basin may be buffered against the initial effects as the system changes from multi-year ice to seasonal ice, whereas those in Hudson Bay likely will be among the first to demonstrate climate-associated physiological and demographic changes (Derocher et al. 2004; Amstrup et al. 2008; Stirling and Derocher 2012). In the Hudson Bay ecosystem, polar bears are forced ashore in summer and fall because the ice melts

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completely each year (Markham 1986; Etkin 1991; Wang et al. 1994a, b; Stirling and Parkinson 2006). Consequently, the bears spend 4–5 months on land without access to sea ice hunting platforms from which they capture their preferred prey, ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977).

Extension of the ice-free season via earlier sea ice break-up and later freeze-up may result in additional reductions in prey accessibility, diminished fat stores, greater physiological stress, and ultimately negative demographic effects (Derocher et al. 2004; Molnár et al. 2010, 2011; Stirling and Derocher 2012). Evidence of such deleterious changes already exists for the Western Hudson Bay (WH) subpopulation, one of five management units (hereafter termed subpopulations) located within the seasonal ice ecoregion (Amstrup et al. 2008). In WH, increases in the duration of the ice-free season have been linked to reductions in body condition and natality (Stirling et al. 1999; Stirling and Parkinson 2006). Survival rates of cubs, subadults, and senescent bears in WH have declined and are correlated with earlier sea ice break-up (Regehr et al. 2007). Regehr et al. (2007) further reported that total abundance decreased by about 22 % between the mid-1980s and mid-2000s. Though a recent aerial survey suggests that current abundance is greater than initially projected by simulations from capture–recapture studies, these new findings do not indicate that the WH subpopulation is increasing (Stapleton et al. 2014).

The Southern Hudson Bay (SH) subpopulation, which is located at the southern extent of polar bear range and shares its western border with WH, presents a somewhat different narrative. Aerial survey indices conducted from 1963 to 1996 and intensive mark–recapture efforts completed during the 1980s and mid-2000s provide a historical perspective. There is some evidence of an increase in abundance from the 1960s to 1980s (Kolenosky and Prevett 1983; Leafloor 1990, 1991), but more robust and recent studies suggest a period of relative stability from the mid-1980s to the mid-2000s (Obbard et al. 2007). As of 2005, abundance was estimated at ~900–1000 bears, a figure that combined results from studies on the Ontario mainland and in James Bay (Akimiski Island and on North and South Twin Islands; Obbard 2008). This estimate reflects some upward adjustment to account for unsurveyed areas and the potential for capture heterogeneity in inland areas (and thus negative bias; Obbard 2008).

Despite the apparent stability in abundance, capture studies have documented significant declines in body condition of all sex and age classes (Obbard et al. 2006). They also have provided some indication of decreases in survival rates between the 1980s and 2000s (Obbard et al. 2007). Combined, these lines of evidence indicate that although polar bears in SH are exhibiting poorer body condition and perhaps diminished survival rates, significant changes in abundance and other demographic parameters have not yet been observed. These findings are consistent with predictions regarding the differing impacts of climate change on polar bear subpopulations (e.g., Stirling and Derocher 2012) and may foreshadow future declines in population size in SH.

Sea ice dynamics in Hudson Bay may explain why some demographic impacts reported from WH have not yet been documented in SH. In Hudson Bay, currents flow counterclockwise and prevailing winds are often northwesterly, such that the last sea ice usually remains off the northern Ontario coast, within or near the bounds of SH, in summer (Etkin 1991; Saucier et al. 2004). Hence, polar bears that summer in SH (most reside on land in Ontario and on nearby islands) may have access to remnant ice floes and prey for longer than bears in WH (Markham 1988; Etkin 1991; Hochheim et al. 2011; Hochheim and Barber 2014), such that physiological and demographic effects may lag behind those exhibited by bears in WH. However, regional sea ice break-up dates are occurring earlier (Scott and Marshall 2010) and this trend is predicted to continue in the future (Castro de la Guardia et al. 2013). Thus, more conclusive declines in survival rates as well as changes in population size may now be apparent in SH.

Here, our objective was to obtain a current estimate of abundance for the SH polar bear subpopulation by conducting a comprehensive aerial survey during 2011–2012. We hypothesized that the ongoing changes in Hudson Bay sea ice dynamics would have resulted in a decrease in abundance since the 1980s.

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 southern Hudson Bay and all of James Bay, 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 WH and Foxe Basin (FB) subpopulations border SH to the west and north, respectively (Fig. 1). Small nearshore and offshore islands in James Bay and eastern Hudson Bay are also included within SH. In sum, 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.

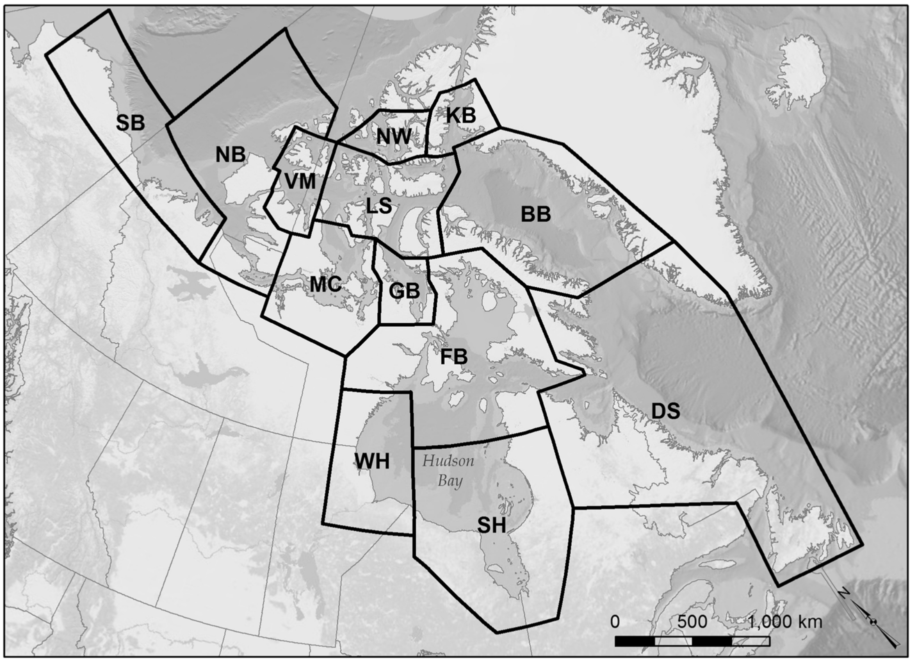

Fig. 1 Recognized boundaries of Canadian polar bear subpopulations. *SB* South Beaufort, *NB* North Beaufort, *VM* Viscount Melville, *NW* Norwegian Bay, *LS* Lancaster Sound, *MC* M'Clintock Channel, *GB* Gulf of Boothia, *BB* Baffin Bay, *DS* Davis Strait, *FB* Foxe Basin, *WH* Western Hudson Bay,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

We conducted the survey during the late summer, ice-free seasons of 2011 and 2012. During this time of year, polar bears in SH are confined to land, demonstrating strong fidelity to general geographic regions (Obbard and Walton 2004; Stirling et al. 2004) and remaining segregated from neighboring subpopulations. This study period effectively minimized the extent of the survey area. In 2011, we surveyed Ontario, Akimiski Island, and nearshore islands; our sampling in 2012 included Québec and small islands in James Bay and eastern Hudson Bay (e.g., the Twin, Ottawa and Belcher Islands).

Study design

2011

We used historical capture records (Kolenosky et al. 1992; Obbard 2008), telemetry data (Obbard and Middel 2012; Middel 2013), and local knowledge (Lemelin et al. 2010) to design and implement a systematic line transect aerial survey. We defined 2 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. 2). We also delineated a coastal zone that included land within 500 m of the shoreline, tidal flats, nearshore islands and spits.

For bears carrying 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 2013). 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 in spring, denned within 60 km of the coast ($\bar{x} = 37.1$ km); the 23rd bear denned 62.7 km inland from the coast (Obbard and Middel unpublished data). Pregnant bears in SH typically enter maternity dens between the last week of October and mid-November (Middel 2013); the earliest that a bear appeared to localize at a den location was September 17; the next earliest was October 8. Therefore, we planned to conduct our aerial survey in late September when the vast majority of bears in the subpopulation would be available to be counted.

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 (Derocher and Stirling 1990; Obbard and Walton 2004; Towns et al. 2010), arranging the overland (hereafter perpendicular) transects against 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 (see "Analyses" section). However, accurately delineating the extensive tidal flats in GIS based on satellite imagery was difficult; therefore, we measured lengths of perpendicular transects to the coast and polar bear sightings were

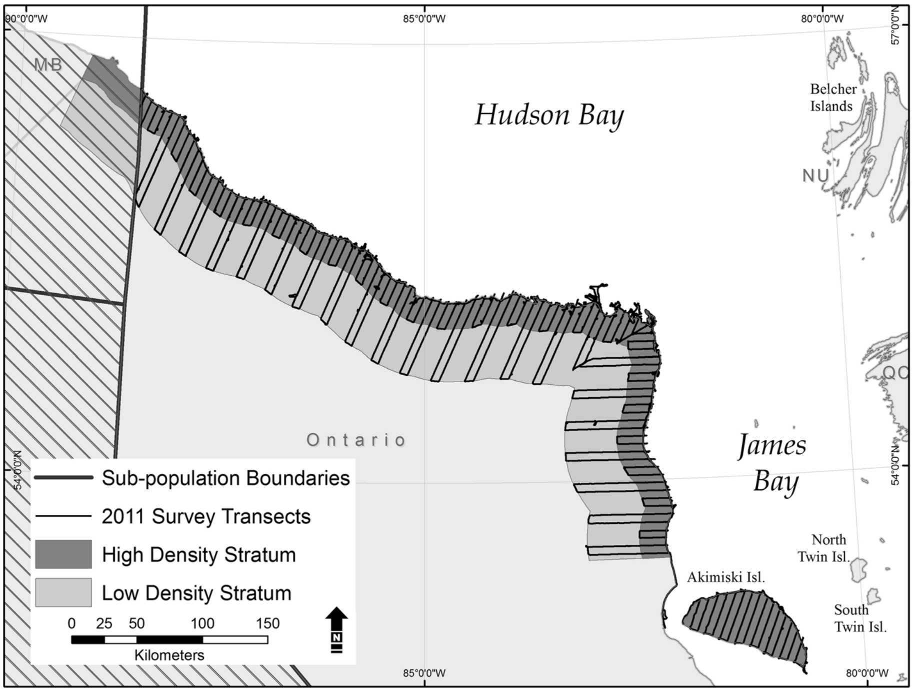

Fig. 2 Strata and survey transects completed during an aerial survey of the SH polar bear subpopulation, September 25–October 5, 2011

considered to have occurred on land for analyses. This procedure had a trivial impact on the abundance estimate because the tidal flats and high-density inland strata were sampled at the same intensity. Perpendicular transects were spaced at 6-km intervals in the high-density stratum. Every other pair of transects was extended through the low-density stratum, such that transect spacing there averaged 12 km (Fig. 2).

The coastal zone was comprehensively surveyed with contour transects flown at or slightly below the high water line from west central James Bay (ca. 225 km from the bay's northwestern corner) to the western border of SH (Fig. 2). Perpendicular transects also sampled the coastal zone; therefore, bears there could be sighted from both contour and perpendicular transects (see also Stapleton et al. 2014). Thus, we were able to estimate abundance in the coastal zone with data collected from both types of transects, enabling us to generate a more reliable abundance estimate. Including data from the coastal zone with other perpendicular transect sightings increased encounters and enabled us to better estimate detection (see "Analyses" section). Sampling from coastal contour transects enabled us to best address the highly clumped distribution of bears along the coastline in order to improve estimate reliability and reduce variance. Analytical procedures ensured that bears in the coastal zone were not double-counted in the overall abundance estimate (see "Analyses" section). We also comprehensively surveyed all small islands, spits and gravel bars offshore of northern Ontario.

2012

Historical data and traditional knowledge suggest that the 2011 study area encompassed nearly all regions polar bears inhabit in SH during the late summer. However, polar bears from SH also occupy other islands in James Bay and eastern Hudson Bay at this time (Doutt 1967; Russell 1975; Jonkel et al. 1976; Crête et al. 1991) and are occasionally found in coastal areas of Québec (McDonald et al. 1997: 89). Therefore, to increase confidence in the abundance estimate, we extended our sampling into Québec and to other offshore islands during late summer 2012. Anecdotal reports and recent research in FB (Stapleton et al. 2015) indicated that very low densities of bears occur inland in mainland Québec during late summer (McDonald et al. 1997: 89) Therefore, we surveyed Québec and nearshore islands using only comprehensive coastal contour transects, extending from northeastern James Bay to the northern border of SH. We surveyed the Belcher Islands, located in southeastern Hudson Bay and including the Nunavut community of Sanikiluaq, using a combination of overland, perpendicular transects and coastal contours, which facilitated sampling about 50 % of the shoreline. Finally, we comprehensively surveyed small offshore islands in James Bay and eastern Hudson Bay.

Field protocols

During 2011, all sampling was conducted from a Eurocopter EC-130 helicopter, flown at a target above ground level (AGL) altitude of 120 m (400 ft) and a groundspeed of 160 km/h (90 knots). We based flight parameters on experience from polar bear aerial surveys conducted earlier in Ontario (Prevett and Kolenosky 1982; Obbard and Walton 2004) and in other regions (e.g., Stapleton et al. 2014, 2015) in order to provide excellent viewing opportunities. In 2012, the coastal contour transects in Québec were surveyed from a helicopter (Eurocopter AS350-BA), maintaining the same target speed and AGL altitude. A twin-engine platform was required to access the offshore islands in Hudson Bay and James Bay, so these areas were surveyed from a Twin Otter (de Havilland DHC-6). The aircraft flew at an AGL altitude of 120–150 m (400–500 ft) and groundspeed of 160 km/h (90 knots).

We simultaneously collected data for both sight–resight (i.e., double observer; Pollock and Kendall 1987) and distance sampling (Buckland et al. 2001) during most of the survey. We implemented a double-observer platform in which 2-person teams of front and rear observers worked independently to sight bears. An opaque partition was erected 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.

For the helicopter survey, 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). With the fixed wing, which is more difficult to manoeuver to turn off transect to record locations of sighted bears, we measured angles from the flight path to sightings with an inclinometer and calculated distances. We defined a group (hereafter cluster) of bears as individuals whose sightings were non-independent (i.e., spotting one bear led to the observation of others; e.g., family groups comprised of an adult female and one or more dependent young).

For each sighting, we recorded the number of bears in a cluster, a bear's activity (e.g., running, sitting) when first spotted, field age class (adult, subadult, yearling, cub), body condition (1–5; Stirling et al. 2008), and other covariates that could affect detection probabilities. These covariates included vegetation height within 30 m (<1, 1–3, >3 m), vegetation density (sparse tundra, moderate, and dense), topographic relief (flat, hilly, and mountainous), and visibility (poor, fair, and excellent). For the 2011 survey, 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. For the 2012 surveys, data were entered into a laptop computer at the time of observation.

Analyses

Perpendicular transects

We used distance sampling (Buckland et al. 2001) to derive an abundance estimate from perpendicular transects. Distance sampling is based on the premise that an individual is best at detecting nearby objects; detectability declines as the distance between the observer and the target increases. A model describing how detection changes with distance is fit to the sightings data, yielding an estimate of the animals in the surveyed area which were not observed. This, in turn, yields a density estimate and facilitates extrapolation across the study area to derive an overall abundance estimate.

Because bears along the shoreline or on tidal flats could be sighted from both coastal contour and perpendicular transects, for most of the study area we compiled two datasets that either included or excluded the coastal zone sightings from the perpendicular transect data. However, perpendicular transects of Akimiski Island did not extend through the coastal zone and fully over the extensive tidal flats due to logistical constraints; therefore, we estimated the number of bears in Akimiski Island's coastal zone using only the coastal contour transect data (see "Coastal contours and small islands" section below).

Histograms summarizing sightings distances from the flight path indicated strong support for a distance-based detection function (Fig. 3). However, preliminary double-observer analyses suggested that detection at distance zero was significantly less than one, violating a fundamental assumption of distance sampling. Therefore, we elected to use mark–recapture distance sampling for these analyses (MRDS; Laake and Borchers 2004). MRDS relaxes the assumption of perfect detection on the transect line by enabling estimation of detection at distance zero using double-observer data. Because the survey was completed in a helicopter, rear observers had a blind spot of about 60 m on either side of the aircraft in which they were unable to sight bears. To ensure that all bears were available to both sets of observers, we left-truncated the sightings data at 60 m (i.e., bears sighted within 60 m of the flight path were discarded, and 60 m was subtracted from all other observations; Borchers et al. 2006; Stapleton et al. 2014).

We completed distance sampling analyses in program DISTANCE (version 6.0, Release 2; Thomas et al. 2010). We pooled observations from the high- and low-density strata to fit a global detection function. 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). These preliminary analyses enabled us to evaluate general model fit and examine potential cluster size bias in detection.

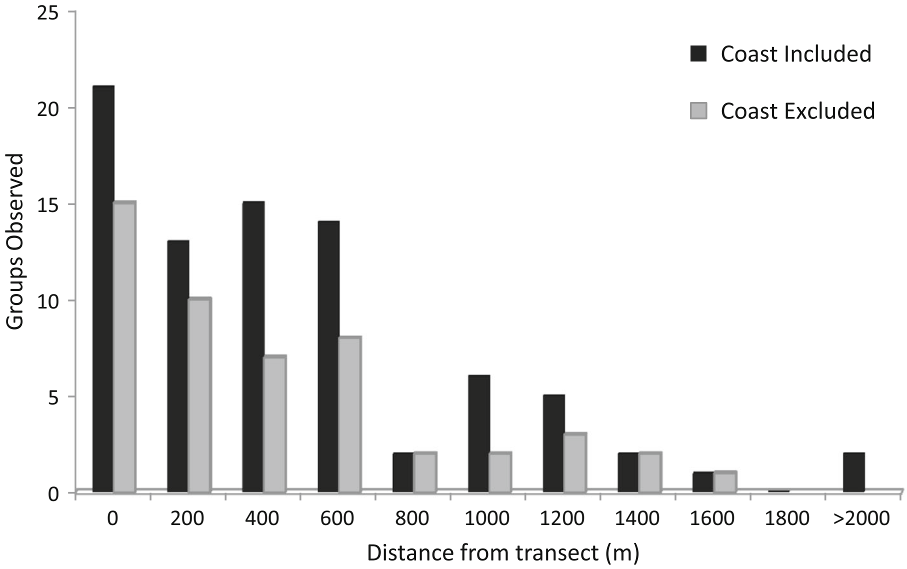

Fig. 3 Distances of polar bear sightings from the transect line, SH, September 25–October 5, 2011. Observations were *left*-truncated at 60 m (i.e., 60 m was subtracted from the original measurements) to compensate for the rear observers' blind spot directly beneath the helicopter. These data were used in the distance sampling analyses. The histogram excludes one observation that was *right*-truncated in the analysis that excluded the coastal observations, and two observations that were *right*-truncated in the analysis that included the coastal sightings

For both datasets, we right-truncated data at about 2 % (i.e., the most distant 2 % of observations were discarded). Although right-truncating at 5 % is typically recommended to improve model fit (Buckland et al. 2001), our data did not exhibit spurious bumps in the "tails" of the histograms that would require additional truncation (Fig. 3).

We conducted all additional modeling in the MRDS engine of program Distance. We specified the point independence model (independence assumed at adjusted distance 0; i.e., after left-truncation). The point independence model requires that observations are statistically independent only at a single point rather than across all distances; thus, it is a more robust means to include double-observer data in distance sampling than assuming full independence (Laake and Borchers 2004; Borchers et al. 2006). This model enables separate estimation of the mark–recapture model (i.e., the conditional detection function, in which detection by an observer is conditional on being sighted by the other observer as well as the sighting-specific covariates) and the distance sampling model (i.e., the unconditional detection function; Laake and Borchers 2004).

We examined three covariates potentially influencing detectability with both mark–recapture and distance sampling models, including visibility and cluster size. We collected two sighting-specific habitat variables, vegetation height and density, but because they were highly correlated (Pearson's $r = 0.89$), we only considered vegetation height in modeling. We also examined observer (i.e., front or rear, enabling detection probabilities to vary between observer teams) and distance as covariates with the mark–recapture models.

In distance sampling, the hazard rate detection function requires estimation of both shape and scale parameters, whereas only an intercept and covariates must be estimated with mark–recapture models. Because our data were sparse, we permitted a maximum of one and two covariates for the distance sampling and mark–recapture models, respectively, with the dataset excluding the coastal sightings (Giudice et al. 2012). Our constraints meant that a maximum of three parameters would be estimated for each of the mark–recapture and distance sampling models. The number of observations was significantly greater with the dataset including the coastal zone sampling from perpendicular transects, so we restricted the maximum covariates to two and three for the mark–recapture and distance sampling models, respectively. We modeled all effects as additive.

We first evaluated mark–recapture models by holding constant the distance sampling model and incorporating covariates through forward stepwise selection. We then evaluated the full MRDS models by parameterizing the most supported mark–recapture models and fitting distance sampling models, again incorporating covariates with a forward stepwise process. We selected the most highly supported models with Akaike's Information Criteria (AIC) for both the initial mark–recapture modeling and the full MRDS modeling (Burnham and Anderson 2002). We used encounter rates and cluster sizes from each stratum to estimate densities and abundance by stratum. To obtain an overall abundance estimate for the portion of the study area sampled by distance sampling, we summed stratum estimates and estimated variance by the Innes et al. (2002)

method within DISTANCE (Stapleton et al. 2014). 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 small islands

2011 We used double-observer data collected along coastal contour transects to generate an independent estimate of abundance for the coastal zone. Coastal contour data were unsuitable for MRDS analysis because bears were concentrated along the coastline, such that distance data might reflect this spatial distribution as well as detection (Stapleton et al. 2014). 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. We comprehensively surveyed offshore islands. Data from offshore islands and the coastal zone were pooled for analyses. We compiled two datasets: (1) including all offshore islands and the entire coastline, and (2) including all offshore islands and only the coastline of Akimiski Island.

We completed all double-observer modeling in Program MARK (White and Burnham 1999) and employed AIC 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 three covariates: visibility (as scored above), activity (moving or stationary), and group size. There was insufficient variability in vegetation height or density to warrant their inclusion as covariates. 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 inflated and multiplied variances via the Delta method (Powell 2007).

A few spits and offshore islands were small enough to be effectively censused. These bears were incorporated in the overall abundance estimate as raw counts (Aars et al. 2009).

2012 For the small, offshore islands in eastern Hudson Bay surveyed by Twin Otter, we used double-observer modeling, estimated detection probabilities, and generated an abundance estimate as outlined for 2011. The islands in James Bay, however, were surveyed without a double-observer platform because they were small enough to be censused. Very sparse observations in other areas (i.e., the Belcher Islands, surveyed via perpendicular transects and coastal contours; coastline of Québec) precluded modeling, so observations were added to the final estimate.

Total abundance

Double sampling the coastal zone enabled us to obtain two abundance estimates in 2011. First, we added estimates and summed variances from offshore islands (including total counts), the Akimiski Island coastline, and the perpendicular transect analysis that included the coastal zone. We also summed the abundance estimates and variances from the offshore islands, the complete coastal contour transects, and the perpendicular transects analysis that excluded the coastal zone. We assigned equal weights and averaged the two estimates in a model-averaging framework (Burnham and Anderson 2002) to generate a final abundance estimate for the 2011 study area and to estimate unconditional variance (Stapleton et al. 2014). To obtain an overall abundance estimate for SH, we summed this estimate with the estimate from the 2012 survey.

Results

Survey effort and sightings

We completed the 2011 aerial survey during an 11-day period from September 25 to October 5, 2011. Sampling progressed systematically from Akimiski Island in James Bay, 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 recorded a total of 667 individuals in SH. Because we independently sampled the coastal zone with both perpendicular and contour transects, bears near the shoreline may have been counted twice, and we were unable to calculate the number of unique individuals.

Although bears were occasionally spotted far inland (e.g., 31 bears were observed >10 km from the shoreline), observations were highly concentrated near the coastline (Fig. 4). A single individual was sighted beyond the inland extent of the defined study area while we flew between two adjacent, far inland perpendicular transects.

We surveyed the Québec coast of Hudson Bay and nearshore islands in eastern Hudson Bay on September 5–10, 2012, small offshore islands in James Bay on September 11, 2012, and offshore islands in eastern Hudson Bay on September 18–21, 2012. We surveyed the entire Québec coastline from Long Island at the northeastern corner of James Bay to the SH–FB border without sighting a single bear (Fig. 4). Intensive surveys of small islands in James

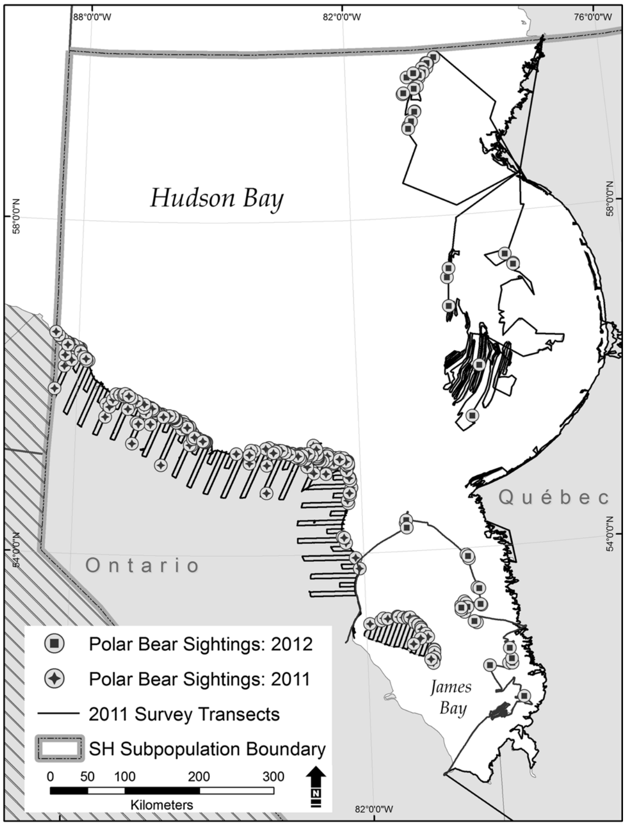

Fig. 4 Transects flown and polar bears sighted during the aerial survey of the SH polar bear subpopulation, 2011 and 2012

Bay and eastern Hudson Bay yielded sightings of 80 individuals.

Abundance estimation

Perpendicular transects

Following left- and right-truncation, we included 79 polar bear clusters in the distance sampling analysis that included the coastal zone data (right-truncation at 1753 m) and 49 clusters in the analysis that excluded coastal sightings (right-truncation at 1518 m). Analyses incorporated 163 transects for variance estimation, with 116 and 47 transects sampled in the high- and low-density strata, respectively.

All highly supported models specified a half-normal key function for the distance sampling detection function. The best models also included covariates for both the mark–recapture and distance sampling components (Table 1). Whereas cluster size and observer were included in virtually all of the most supported mark–recapture models, distance from the flight path was not. Vegetation height was included as a covariate in all distance sampling models within ΔAIC of 3 for both datasets. All highly supported MRDS models yielded adequate overall Chi-square goodness-of-fit statistics ($P > 0.05$; Table 1), and distance sampling models showed suitable fit with additional metrics (Kolmogorov–Smirnov and Cramér-von Mises tests: all $P > 0.75$). Because density estimates were consistent among the most highly supported models, we selected the top models in each dataset to derive estimates of abundance. We estimated 667 bears [SE = 141.6; 95 % log-normal confidence interval (CI) 441–1009] with the dataset including the coastal region, and 520 bears (SE = 149.7; 95 % CI 298–907) with the dataset excluding the coastal zone.

Coastal contours and small islands

2011 We included 42 clusters in the double-observer analysis with sightings from only offshore islands and the Akimiski Island coastline. The most highly supported model included no covariates and estimated separate detection probabilities for front and rear observers (p_{front}: 0.86, SE = 0.07; p_{rear}: 0.63, SE = 0.08), yielding an overall inclusion probability of ~0.95. We included 204 clusters for the analysis with sightings from the entire coastal zone and small offshore islands. The best model in this second analysis also estimated separate detection probabilities for the two teams of observers and included covariates for visibility and bear activity at first sighting ($\bar{p}_{\text{front}}$: 0.80, SE = 0.03; $\bar{p}_{\text{rear}}$: 0.67, SE = 0.04). We estimated a total of 44 and 221 clusters with the two datasets. After multiplying by mean cluster sizes ($\bar{x}_{\text{Akimiski Island}}$: 1.67; SE = 0.07; $\bar{x}_{\text{complete}}$: 1.75; SE = 0.08) and combining variances, we estimated 74 bears (SE = 4.6) on offshore islands and the Akimiski coastline, and 385 bears (SE = 21.5) when the entire coastline was included. An additional 23 bears were sighted at total count sites on offshore islands and along the Akimiski Island coastline; 48 bears were spotted at total count sites on offshore islands and along the entire coastal zone.

2012 We spotted 37 bears on the small islands in James Bay that were comprehensively surveyed (i.e., without a double-observer platform). We sighted 32 clusters while surveying small islands in eastern Hudson Bay. Double-observer modeling yielded an estimate of 34 clusters and, after multiplying by mean group size (1.31; SE = 0.11), produced an abundance estimate of 44 bears (SE = 4.5). A single bear was sighted from a coastal contour transect on the Belcher Islands. Because we sampled about 50 % of the coastline, we doubled this value and added it to our overall 2012 figure. No bears were observed in Québec or on perpendicular transects on the Belcher Islands. In summary, we estimated 83 bears (SE = 4.5) in the 2012 study area.

Table 1 Summary of modeling results from mark–recapture distance sampling analyses of an aerial survey of the SH polar bear subpopulation, September 2011

Dataset	Model: mark–recapture/ distance sampling	ΔAIC	Param (Total)	Density: bears/1000 km^2 (95 % CI)			GOF: overall Chi-square (*P*)
				High-density stratum[a]	Low-density stratum	Global[a]	
Including coastal sightings	Clust + Obs/VegHt + Vis	0.00	6	35.8 (23.7–54.1)	4.3 (1.5–12.8)	17.3 (11.4–26.2)	0.11
	Clust + Obs + VegHt/ VegHt + Vis	0.89	7	37.0 (24.1–56.8)	5.6 (1.7–17.9)	18.5 (11.7–29.2)	0.08
	Clust + Obs + Vis/ VegHt + Vis	1.35	7	35.6 (23.7–53.6)	4.6 (1.5–13.6)	17.3 (11.5–26.2)	0.09
	Clust + Obs + Dist/ VegHt + Vis	1.85	7	36.6 (24.0–55.9)	4.5 (1.5–13.5)	17.7 (11.6–27.2)	0.08
Excluding coastal sightings	Obs + Vis/VegHt	0.00	5	25.5 (14.4–45.3)	5.6 (1.9–15.9)	13.6 (7.8–23.8)	0.58
	Obs + Clust/VegHt	2.75	5	22.7 (13.5–38.1)	5.0 (1.7–14.6)	12.2 (7.2–20.4)	0.38

Models with ΔAIC < 3 are presented. All highly supported distance sampling models include a half-normal key function. In the column *Model*, covariates are cluster size (Clust), left-truncated distance from the transect (Dist), observer (Obs; front or rear), vegetation height (VegHt), and visibility (Vis). Goodness-of-fit metrics for the distance sampling detection function also included Kolmogorov–Smirnov and Cramer-von Mises tests (all $P > 0.75$ 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

Total abundance

The single bear sighted just outside the defined inland extent of the 2011 study area was tallied with the other estimate components, since there was no other means to incorporate it. In 2011, summing the results of the perpendicular transect analysis including the coastal zone with the estimate of bears on small islands and along the Akimiski Island coastline yielded 765 bears (SE = 141.6; 95 % lognormal CI 534–1096). We obtained an estimate of 954 bears (SE = 151.2; 95 % CI 701–1299) by adding the estimates from the coastal contour transects, the perpendicular transects excluding the coastal region, and small islands. Averaging these estimates yielded 860 bears (unconditional S = 174.0; 95 % CI 580–1274) in the mainland Ontario, neighboring islands, and Akimiski Island portions of the SH population during the 2011 ice-free season. We added this estimate to our 2012 results and obtained an overall estimate of 943 (SE = 174, 95 % CI 658–1350) for SH.

Reproduction

For the area surveyed in 2011, litter sizes averaged 1.56 (SD = 0.50; $n = 70$) and 1.49 (SD = 0.50; $n = 53$) for cubs and yearlings, respectively (Table 2). Cubs made up 16 % of the total number of bears observed and yearlings comprised 12 % of the total number of bears observed.

Discussion

Abundance estimation

We used multiple sampling and analytical techniques to obtain an aerial survey-based estimate of abundance for the SH subpopulation. Our protocols enabled us to generate two partially independent estimates for the 2011 study area. We elected, a priori, to incorporate process and model uncertainty in our final estimate by averaging. Some variation was expected between the two estimates given inherent errors with sampling and modeling. Although the estimate based nearly exclusively on perpendicular transects yielded a result that was about 20 % less than the estimate including coastal contour transects, there was significant overlap of confidence intervals. Averaging the estimates reduced precision, but we believe that the step was important to obtain a result that incorporated uncertainty and best reflected actual abundance in SH.

We were compelled to conduct the survey over 2 years due to logistical and financial constraints. However, Ontario and Akimiski Island, where the vast majority of polar bears summer (ca. 90 % of our total 2011–2012 estimate), were surveyed over a short timeframe (11 days), minimizing the possibility that a large distributional shift affected our results in 2011. Additionally, regional sea ice dynamics were generally consistent between 2011 and 2012 (Canadian Ice Service 2013), suggesting that polar bear distribution was unlikely to have significantly shifted

Table 2 Polar bear litter sizes and number of dependent young observed as proportion of all observations during the ice-free season in the SH, WH and FB subpopulations

Subpopulation	Litter size (SD) Cubs of year	Litter size (SD) Yearlings	Proportion Cubs of year	Proportion Yearling	Source
Southern Hudson Bay, aerial survey (2011)	1.56 (0.50) $n = 70$	1.49 (0.50) $n = 53$	0.16	0.12	This study
Western Hudson Bay, aerial survey (2011)	1.43 (0.50) $n = 35$	1.22 (0.43) $n = 18$	0.07	0.03	Stapleton et al. (2014)
Foxe Basin, aerial survey (2009–2010)	1.55 (0.56) $n = 155$	1.48 (0.52) $n = 118$	0.13	0.10	Stapleton et al. (2015)

within SH between years. Therefore, sampling across portions of two consecutive ice-free seasons probably had a negligible impact on our overall estimate of abundance.

Our study design and field protocols ensured that we met all fundamental assumptions of distance sampling surveys. Similarly, the definition of a narrow strip width and implementation of appropriate survey protocols enabled us to meet most assumptions of closed population (double observer) models. Nevertheless, we acknowledge that sighting periods were not entirely independent. Thus, although we attempted to account for sources of variability with modeling, double-observer estimates may have been susceptible to heterogeneity in detection and underestimated abundance. However, we believe that unmodeled heterogeneity arising from distance of sightings from the flight path was likely minimal. Examining a histogram of sighting distances for bears observed from coastal contour transects is uninformative given the spatial distribution of bears (i.e., their concentration along the shore), so we compiled histograms of sightings from perpendicular transects within 2 km of the coastline, a slightly larger area than the coastal zone but comprised of very similar habitat. This histogram suggested that detection was relatively constant to a distance 600–800 m from the flight path (the coastal zone extended 500 m inland of the high water mark), which differs from a histogram summarizing all sightings from perpendicular transects (Fig. 3). We hypothesize that the lack of vegetation along the coastline contributed to this difference. Vegetation is more widespread, taller, and denser farther from the shore; only about 1 % of sightings from coastal contour transects were recorded with vegetation >1 m in height. Moreover, vegetation was an important covariate in MRDS modeling (Table 1).

We were surprised that our detection at distance zero was significantly less than one. Polar bears are a conspicuous target species, and because our study was conducted on land (i.e., against a darker background), we anticipated that detection would approximate unity (see Stapleton et al. 2015). Although our detection at and near the flight path was ~80 % or less, the integration of MRDS protocols and modeling enabled us to adjust for incomplete detection and reduce potential bias in the abundance estimate. However, this finding highlights that perfect detection on the line should not be assumed, regardless of study species or environment; rather, it must be explicitly tested and accommodated by appropriate design and analytical treatment. Other key assumptions met through study design and sampling protocols included (1) random sampling (i.e., allocation of transects) with respect to the distribution of bears; (2) bears sighted at their initial locations before any significant, responsive movements to the approaching aircraft; (3) accurate measurement of bear distances from the flight path (Buckland et al. 2001); and (4) the implicit assumption that the distribution of bears was statistically uniform [Fewster et al. 2008; see Stapleton et al. (2014) for a thorough review of assumptions and associated design specifications with polar bear aerial surveys].

Delineation of the study area to 60 km inland was based on available scientific and traditional knowledge. A few bears have denned farther inland (Kolenosky and Prevett 1983), though evidence from recently collared bears suggests most den within 60 km of the coast. A single adult female was sighted >60 km from the coast while we flew between adjacent inland transects. 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 significant proportion of the subpopulation. Estimated densities in the far inland stratum were very low (Table 1). Applying the approximate density from this stratum (~5 bears/1000 km^2) to the region 60–70 km inland in Ontario (5080 km^2), for example, would result in roughly 25 additional bears, <3 % of the total estimate. We further note that the density estimate for the region 20–60 km inland almost certainly overestimates densities in regions >60 km inland, because polar bear density declined greatly as distance from the coast increased.

All three subpopulations in Hudson Bay have been inventoried by aerial survey from 2009 to 2012: FB (2009–2010; Stapleton et al. 2015), WH (2011; Stapleton et al. 2014), and SH (2011–2012; this study). These comprise three of the five subpopulations in the seasonal sea ice ecoregion [BB, DS, FB, SH, WH (Fig. 1); Amstrup et al. 2008]. Combined, these aerial surveys suggest that there are about 2000 bears in the southern and central portions of Hudson Bay, and roughly 4500 bears across the entire complex which comprises about 55 % of the total number of polar bears in the seasonal sea ice ecoregion (PBSG 2015).

Trends in abundance

The model averaged estimate of abundance from the 2011 aerial survey of mainland Ontario, offshore islands, and Akimiski Island in James Bay (860, 95 % CI 580–1274) did not differ from the combined capture–recapture estimates from mainland Ontario (2003–2005) and Akimiski Island and the Twin Islands (1997–1998) [681, (95 % CI 401–961) plus 110, (95 % CI 75–195); Obbard 2008]. The inclusion of 2012 survey data from the Belcher Islands, the Québec coastline, and other small islands only slightly increased the SH estimate of abundance. Therefore, our results suggest that abundance in SH has remained relatively unchanged since the mid-1980s.

Documented traditional knowledge on polar bear abundance in SH is limited. McDonald et al. (1997: 91) reported that participants stated that polar bears had increased since the 1960s in the Inukjuak and Belcher Islands area, and that Inuit from the Belcher Islands saw few polar bears on the offshore islands of eastern Hudson Bay "40 or 50 years ago" (i.e., in the 1940s and 1950s). Study participants also indicated that polar bears had increased in eastern Hudson Bay since the 1930s and more quickly since the 1960s, and suggested that polar bears were relocating to the area in response to an abundance of ringed seals, the extended floe edge, and hunting quotas in effect since the 1970s (McDonald et al. 1997: 42).

Combined, the available traditional knowledge and scientific information suggest that, although abundance in SH may have increased during the 1960s, numbers have remained relatively stable since the mid-1980s. However, the implementation of multiple inventory techniques makes the interpretation of long-term trends challenging. Negative bias can affect both capture–recapture studies (e.g., via unmodeled capture heterogeneity) and aerial surveys. Nevertheless, significant declines in body condition have been demonstrated (Obbard et al. 2006), such declines continue (Obbard unpublished data), and apparent decreases in survival rates were documented between the mid-1980s and mid-2000s (Obbard et al. 2007). As such, a cautious management approach is warranted.

Reproduction

The aerial survey results suggest that reproductive output in SH was greater than in WH in 2011 (Table 2). Mean litter sizes (cubs: 1.56; yearlings: 1.49) and proportions of cubs (0.16) and yearlings (0.12) in the SH survey were higher than those reported from the similarly timed WH survey (cub litter size: 1.43 and proportion: 0.07; yearling litter size 1.22 and proportion: 0.03; Stapleton et al. 2014), and similar to the values observed during the FB aerial surveys in 2009 and 2010 (cub litter size: 1.54 and proportion: 0.13; yearling litter size: 1.48 and proportion: 0.10; Stapleton et al. 2015).

Although a single year of data is not necessarily indicative of long-term trends in reproduction and cannot reflect inter-annual variability, the litter sizes and proportions of cubs and yearlings observed in SH were much greater than WH. Because no data on litter sizes are available from 2010 for SH, it is difficult to interpret the similar litter sizes for cubs and yearlings observed during the aerial survey. One explanation may be that much of the mortality of cubs was due to loss of entire litters, perhaps by young inexperienced females or by those that were in marginal body condition to produce sufficient milk to ensure cub survival. Alternatively, cub survival may have been higher in SH than in WH during the same period.

The future

Sea ice characteristics and dynamics differ between broad regions of the Arctic, resulting in regional differences in polar bear ecology. In their forecast of future status of polar bears worldwide, Amstrup et al. (2008) recognized four ecoregions based upon differences in historic and projected sea ice conditions. Predicted impacts of climatic warming may occur first for areas near the southern edge of the range in James Bay and Hudson Bay (Stirling and Derocher 1993; Arctic Climate Impact Assessment 2004; Derocher et al. 2004), located in the seasonal ice ecoregion (Amstrup et al. 2008). In particular, earlier break-up of sea ice likely reduces opportunities for polar bears to feed and acquire stored reserves needed to sustain them during prolonged fasting during the long ice-free season (Stirling et al. 1999). In recent decades, both the extent (Smith 1998; Parkinson et al. 1999) and duration of the sea ice cover in Hudson Bay have decreased (Etkin 1991; Stirling et al. 1999; Gough et al. 2004; Gagnon and Gough 2005). Recent analysis (Hochheim and Barber 2014) suggests that the open water season has increased by 3.1 (±0.6) weeks in Hudson Bay since 1996. Consequently, polar bears are spending longer periods ashore and the trend is likely to continue—a major ecological problem for bears of SH that will likely cause continued declines in body condition and survival rates, and ultimately in abundance.

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