



# Demographic response of a high-Arctic polar bear (*Ursus maritimus*) subpopulation to changes in sea ice and subsistence harvest

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**ABSTRACT:** Climate change is a long-term threat to polar bears. However, sea-ice loss is hypothesized to provide transient benefits in high latitudes, where thick multiyear ice historically limited biological productivity and seal abundance. We used joint live-recapture and dead-recovery mark-recapture models to analyze data for one of the most northerly polar bear subpopulations, Kane Basin. The data consisted of 277 initial live captures and genetic identifications (1992–1997 = 150, 2012–2014 = 127), 89 recaptures or re-identifications (1992–1997 = 53, 2012–2014 = 36), and 24 harvest returns of research-marked bears during 1992–2014. We estimated mean annual abundance of 357 bears (95 % CI: 221–493) for 2013–2014. This suggests a likely increase relative to our estimate of 224 (95 % CI: 145–303) bears in the mid-1990s and relative to a previously published estimate of 164 (95 % CI: 94–234) bears in the mid-1990s that used some of the same data. This is also supported by an apparent increase in the density of bears in eastern Kane Basin during 2012–2014. Estimates of total survival for females  $\geq 3$  yr old (mean  $\pm$  SE:  $0.95 \pm 0.04$ ) and their dependent offspring were similar to previous estimates from the 1990s, and estimates of unharvested survival for females  $\geq 3$  yr ( $0.96 \pm 0.04$ ) appear sufficient for positive population growth. Estimates of total survival were lower for males  $\geq 3$  yr ( $0.87 \pm 0.06$ ). We documented a reduction in mortality associated with subsistence harvest, likely attributable to implementation of a harvest quota by Greenland in 2006. Our findings, together with evidence for increased range sizes, improved body condition for all sex and age classes, and stable reproductive metrics, show that this small high-Arctic polar bear subpopulation remains productive and healthy. These benefits are likely temporary given predictions for continued climate change.

**KEY WORDS:** Genetic mark-recapture-recovery · Polar bear · Kane Basin · Abundance · Sea ice · *Ursus maritimus*

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## 1. INTRODUCTION

The Kane Basin (KB) subpopulation of polar bears is one of the most northerly subpopulations in the world (PBSG 2018). Historically, KB has been characterized by a mix of annual and multiyear sea ice (Hamilton et al. 2014, Moore et al. 2019). Multiyear sea ice is thicker and less biologically productive than annual ice but has the benefit of providing a year-round platform from which polar bears can hunt seals. The KB subpopulation is part of the archipelago ecoregion (Amstrup et al. 2008), where bears have access to sea ice year round and can avoid the prolonged fasting period associated with ice-free conditions in other polar bear ecoregions.

KB polar bears inhabit the southern part of the Last Ice Area (LIA), an area of thick multiyear sea ice along the margin of the North American and Greenlandic Arctic basins. This area is expected to be a climate refuge for many ice-dependent species, including polar bears (Moore et al. 2019), because sea-ice cover in the region is forecasted to persist through the 21<sup>st</sup> century. However, the LIA is losing ice mass at twice the rate of the Arctic Ocean (Moore et al. 2019), and both ecosystem productivity and seal densities in the area are unknown.

Laidre et al. (2020b) reported that polar bears in KB appear to be experiencing transient benefits from climate change, as loss of multiyear sea ice over the past 20 yr was associated with increased range sizes, improved body condition for all sex and age classes, and stable reproductive metrics. This appears consistent with predictions that areas previously covered in multiyear ice may exhibit increased primary and secondary productivity because the thinner annual ice can be penetrated by solar radiation (Mundy et al. 2009, 2014, Arrigo et al. 2012, 2014, Assmy et al. 2017). Annual ice is expected to provide more productive and suitable habitat for ice seals (i.e. ringed seals *Pusa hispida* and bearded seals *Erignathus barbatus*), the primary prey of polar bears (Derocher et al. 2004). Such changes have been hypothesized to lead to shifts in polar bear movement patterns (Ferguson et al. 2000) and possibly confer energetic benefits to bears due to improved foraging conditions (Derocher et al. 2004, Hamilton et al. 2014).

Abundance of the KB subpopulation was last estimated using a physical (i.e. involving live capture and release) mark–recapture study completed during 1992–1997 (Taylor et al. 2008). At that time, abundance was estimated to be 164 bears (SE: 34.6), and the estimate of population growth rate ( $\lambda$ ) including harvest was 0.919, suggesting that abundance

was declining due to overexploitation. The estimated unharvested growth rate also was low ( $\lambda = 1.009$ ; Taylor et al. 2008), suggesting limited capacity for the KB subpopulation to increase even in the absence of human-caused removals. The small subpopulation size, low growth rates, and long-term exploitation led Taylor et al. (2008) to suggest that KB may act as a sink for neighboring polar bear subpopulations such as Baffin Bay (BB). Wiig et al. (2022) used an aerial survey to estimate abundance of 190 bears (95% lognormal CI: 87–411; coefficient of variation [CV]: 39%) in KB in 2014, though they reported that the estimate was likely negatively biased because not all areas could be surveyed.

Under the direction of the Canada-Greenland Joint Commission on Polar Bear, we conducted a physical and genetic (i.e. via biopsy darting) live-capture and dead-recovery mark–recapture study of the KB subpopulation during 2012–2014. We followed a survey plan developed by Atkinson et al. (2011) as part of an interjurisdictional initiative to develop less invasive methods to monitor polar bears when logistical, financial, or societal constraints preclude physical handling. Here, we estimate reproduction, survival, and abundance for the KB polar bear subpopulation during a period when it experienced a physical and ecological shift from multiyear to annual sea-ice conditions. This study presents the first mark–recapture estimate for this subpopulation since the 1990s and provides insight into how other high-Arctic subpopulations inhabiting multiyear ice over biologically productive shallow waters (<300 m) may respond to climate change.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The KB subpopulation ranges over KB, Nares Strait, Smith Sound, and adjacent fjords along eastern Ellesmere Island and northwestern Greenland (the Qaanaaq areas), south of 80° 15' N and north of 76° 45' N on the Ellesmere Island side and north of 77° N on the Greenland side (PBSG 2018) (Fig. 1). The subpopulation is bounded to the north by the Arctic Basin subpopulation (via Kennedy Channel), to the south by the BB and Lancaster Sound (LS) subpopulations, and to the west by the Norwegian Bay subpopulation (PBSG 2018; Fig. 1). Previous studies have documented limited interchange between the KB and neighboring subpopulations (Taylor et al. 2001, SWG 2016).

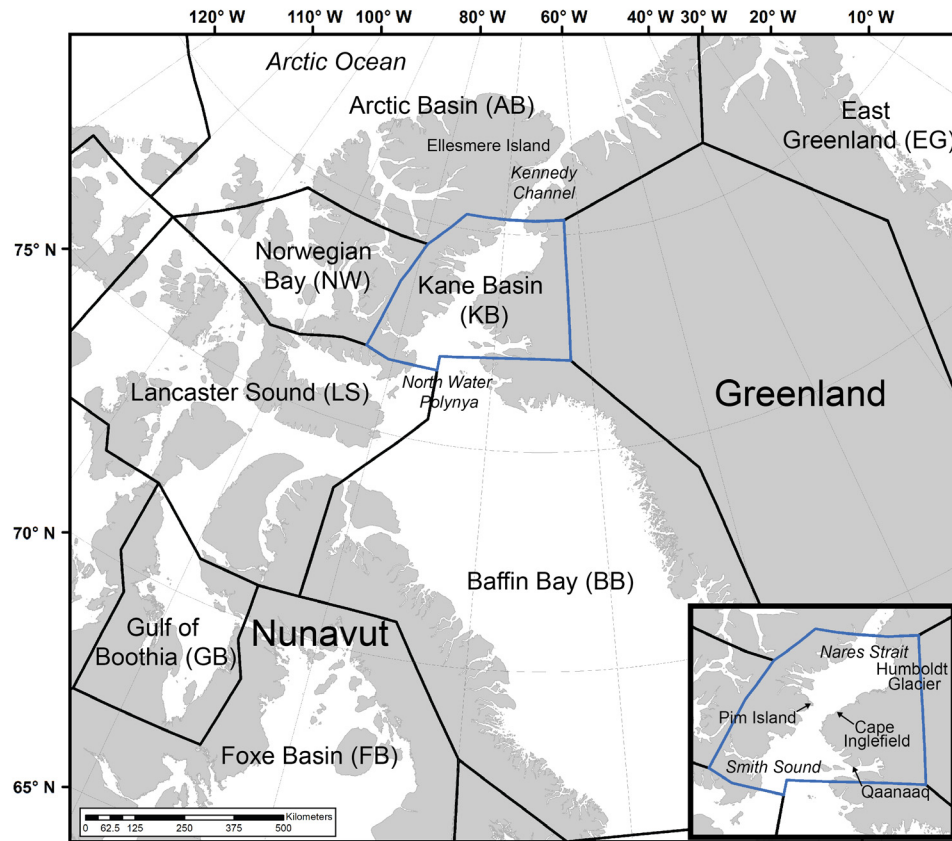


Fig. 1. Kane Basin polar bear subpopulation is located between Nunavut, Canada, and Greenland and part of the Arctic Archipelago region. Other neighboring polar bear subpopulations and places names in the text are shown on the map for reference

Sea ice persists in the northern portion of our study area (i.e. Nares Strait-KB) throughout the year, largely due to the influx of pack ice from the Arctic Basin, and reaches a minimum in late summer. However, sea-ice conditions have changed markedly in the KB region in recent decades (Born et al. 2011, Stern & Laidre 2016, Laidre et al. 2020a). Laidre et al. (2020b) showed that sea-ice habitat in KB has shifted from a year-round ice platform (~50% coverage in summer) in the 1990s to nearly complete melt-out (<5% coverage in summer) in the 2010s. The North Water Polynya (NOW), a large area of open water in northern BB and southern Smith Sound, is an important regional feature that varies in spatial extent within and among years and is thought to form a partial barrier between KB and the neighboring BB and LS subpopulations. Historically, a distinct sea-ice bridge existed north of the NOW, extending from Cape Inglefield in northwestern Greenland across to Pim Island at Ellesmere Island in the northern part of Smith Sound, Canada (Barber et al. 2001). However, due to thinning sea ice, this bridge has failed to form reliably every year, and open water of the NOW has

stretched north into the Nares Strait-KB region in some years since 2007 (Born et al. 2011, Vincent 2020, Moore et al. 2021).

## 2.2. Field sampling

Initial surveying of the KB subpopulation was conducted in the spring (April–May) from 1992 to 1997 using physical capture methods, as described in Taylor et al. (2008). Additional sampling was completed in fall 1994, but we excluded these data from the present analyses to reduce temporal heterogeneity (e.g. sampling cubs of the year [COY] in spring vs. fall yields substantial differences in estimates of survival). All sighted bears, including dependent offspring, were chemically immobilized (Stirling et al. 1989) and uniquely marked with plastic ear tags and lip tattoos (Taylor et al. 2008). Ages of independent bears were estimated by extracting vestigial premolars and counting annular rings (Calvert & Ramsay 1998), whereas COY and yearling bears could be visually aged without error. A sample of adult females

was outfitted with satellite collars as part of a separate study quantifying movements and spatial ecology (Taylor et al. 2001, Laidre et al. 2020b).

Although Taylor et al. (2008) reported a uniform search effort throughout the KB subpopulation area during 1992–1997, subsequent examination of the distribution of captures suggested increases in the size of the study area, with an apparent northward expansion in the sampling frame between 1992 and 1993 (i.e. along eastern Ellesmere Island into the Nares Strait region). In 1994–1997, survey efforts appeared to expand eastward into KB proper, off the Humboldt Glacier in northwestern Greenland (Fig. 2). Although eastern KB was surveyed each spring during 1994–1997, few bears were encountered and tagged (1994: 0; 1995: 4; 1996: 0; and 1997: 3) in comparison to the western side of KB along Ellesmere Island (Taylor et al. 2001). No live-capture sampling occurred during 1998–2011, although we obtained harvest records for research-marked bears, which allowed estimation of survival and harvest recovery

probabilities during this interval (Peacock et al. 2012).

We surveyed the KB subpopulation during 25 April–6 May 2012, 27 April–10 May 2013, and 28 April–19 May 2014. The timing of annual sampling was comparable to the 1990s, although surveying in 1992 and 1993 occurred earlier (mid-April) and for shorter periods. We sampled sea-ice habitats by helicopter (Bell 206 LongRanger) across the entirety of western and northern KB, including landfast ice in fjords and nearshore areas as well as offshore pack ice, but excluded areas with low sea-ice concentration and open water around the NOW that could not be safely sampled with a helicopter. We also excluded fjords in the human-populated Qaanaaq region in northwestern Greenland (i.e. eastern parts of the NOW) because hunting pressure for polar bears in this area is high and polar bears do not remain resident (Born et al. 2011, E. Born pers. obs.). Sampling was completed via directed searching in 2012, with searches focused in areas believed to provide the

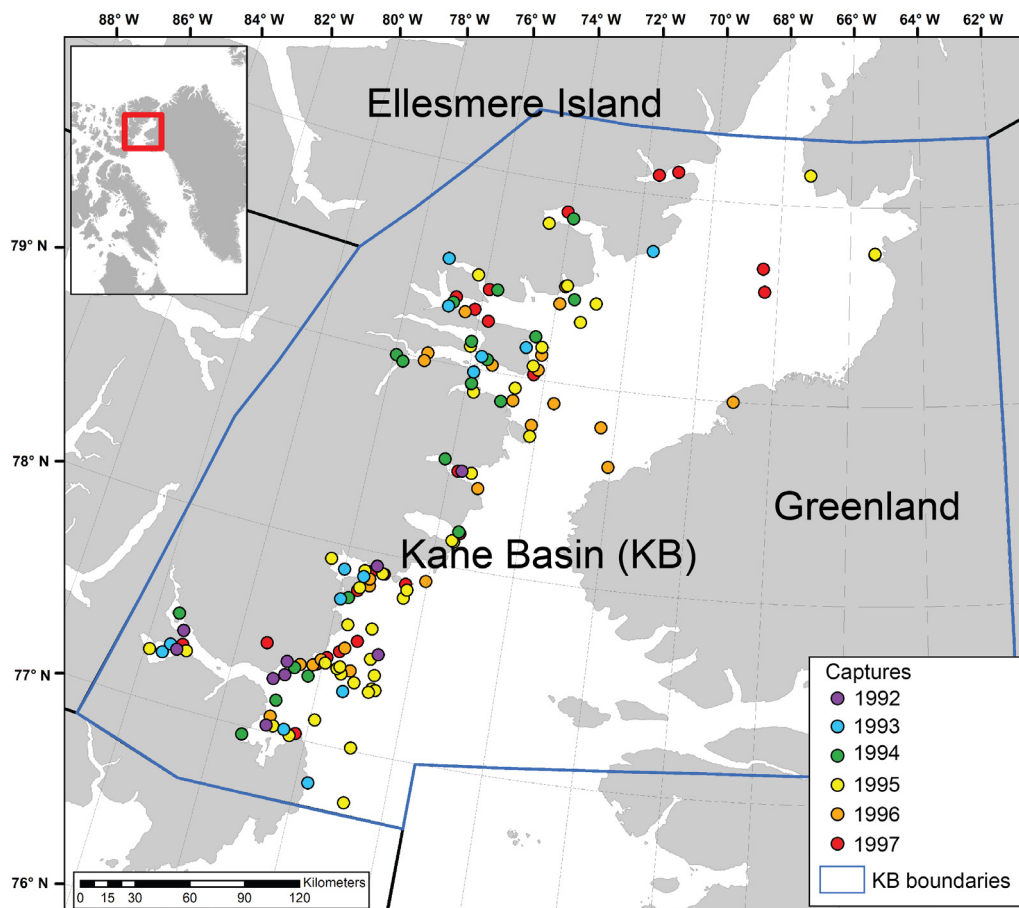


Fig. 2. Locations of polar bears physically captured in the Kane Basin subpopulation during springtime, 1992–1997. Kane Basin is highlighted in red in the inset

most suitable polar bear habitat (i.e. adaptive sampling). In 2013, we completed directed searching similar to 2012 and flew ad hoc transects oriented perpendicular to the coastline, particularly near Greenland, to ensure that effort was well distributed across the different sea-ice types (consolidated ice and moving pack ice).

In 2012 and 2013, just over half of encountered bears (54 of 99) were sampled via physical capture, including chemical immobilization and application of ear tags and lip tattoos as described above. We collected tissue samples from all physically captured bears for genotyping and recorded additional information including sex, family status, field-estimated age class (i.e. COY, yearling, 2 yr old, subadult [3–4 yr], or adult) and morphometric measurements. We deployed satellite transmitters on 20 adult female polar bears captured in 2012 and 2013 (SWG 2016, Laidre et al. 2020b). The remaining bears (45 of 99) we encountered in 2012 and 2013 were sampled via biopsy darting from the helicopter (Pagano et al. 2014) to collect tissues for genotyping (e.g. Atkinson et al. 2021). COY were too small in springtime to be biopsy darted and thus were not sampled when their mothers were biopsy darted (although COY were sampled during physical captures). For bears that were biopsy darted, sex was confirmed upon genetic analyses (see Section 2.4).

In 2014, all sampling was conducted via remote biopsy darting. Furthermore, we stratified the study area into high- and low-density areas, based on our observations of polar bears in 2012 and 2013 (i.e. presumed densities) and satellite telemetry data, and searched for bears from systematically spaced transects. This design enabled us to more efficiently allocate effort and reduced the potential for spatial heterogeneity in detection. Systematic sampling also facilitated the simultaneous completion of an aerial survey to derive an abundance estimate, based on distance sampling methodology (Wiig et al. 2022), for comparison with the mark–recapture abundance estimate. Transects were spaced at 6 and 18 km intervals in the high- and low-density strata, respectively, based on anticipated encounter rates and available resources. The 2 strata generally conformed to landscape features and ice types: the high-density stratum included landfast ice within fjords and nearshore pack ice (within ~30 km of the nearest land mass), and the low-density stratum included farther offshore pack ice (Fig. 3). We delineated the landward extent of the study area using current GIS layers for Greenland and Nunavut. We used moderate resolution imaging spectroradiometer (MODIS; [http://modis.gsfc.](http://modis.gsfc.nasa.gov/)

[nasa.gov/](http://modis.gsfc.nasa.gov/)) images with a 250 m resolution to delineate the extent of available habitat by approximating the edge of the NOW. Because the polynya's boundaries can change rapidly, we delineated the extent of the polynya adjacent to the section surveyed on a particular day using MODIS imagery from that day or as close to it as possible (i.e. if imagery was unclear on that day due to atmospheric conditions). We examined the delineated study area in relation to weekly regional sea-ice charts produced by the Canadian Ice Service (<https://www.canada.ca/en/environment-climate-change/services/ice-forecasts-observations/about-ice-service.html>) for confirmation. During sampling, we also collected GPS waypoints at the edge of the polynya to verify delineation.

### 2.3. Harvest recoveries

We used harvest records and biological samples to compile recovery data for polar bears captured in KB and subsequently harvested there or in neighboring subpopulations during 1992–2014. Harvest was monitored by the return of ear tags or lip tattoos during 1992–2010 and by genotyping samples provided by hunters during 2011–2014. Data for bears killed as part of the subsistence harvest or in defense of life and property also included date, location, sex, and estimated age. Reported harvest was higher in the 1990s (range: 10–12 bears per year, data include unmarked bears) and lower in the 2010s (5–6 bears per year; SWG 2016), likely due to changes in sea-ice conditions limiting hunter access by use of dog sleds to northeastern KB (Born et al. 2011) and implementation of a quota system in Greenland in 2006. The Greenlandic harvest from KB in the 1990s was largely based on estimates (SWG 2016). Greenland's reporting system also improved with the implementation of the quota (SWG 2016). Previous studies assumed that harvests of all marked bears were reported when natural survival was calculated; therefore, the reporting rate ( $r$ ) was interpreted as the proportion of mortality due to harvest (e.g. Taylor et al. 2005, 2008). However, more recently, genetic data suggested underreporting of marked bears in the harvest, with decreases in reporting correlated with increasing marker age.

### 2.4. Genetic analyses

DNA was extracted from ~3 mm<sup>2</sup> pieces of tissue with QIAGEN DNeasy Blood and Tissue kits ([www.qiagen.com/](http://www.qiagen.com/)). Most biopsy darting samples consisted



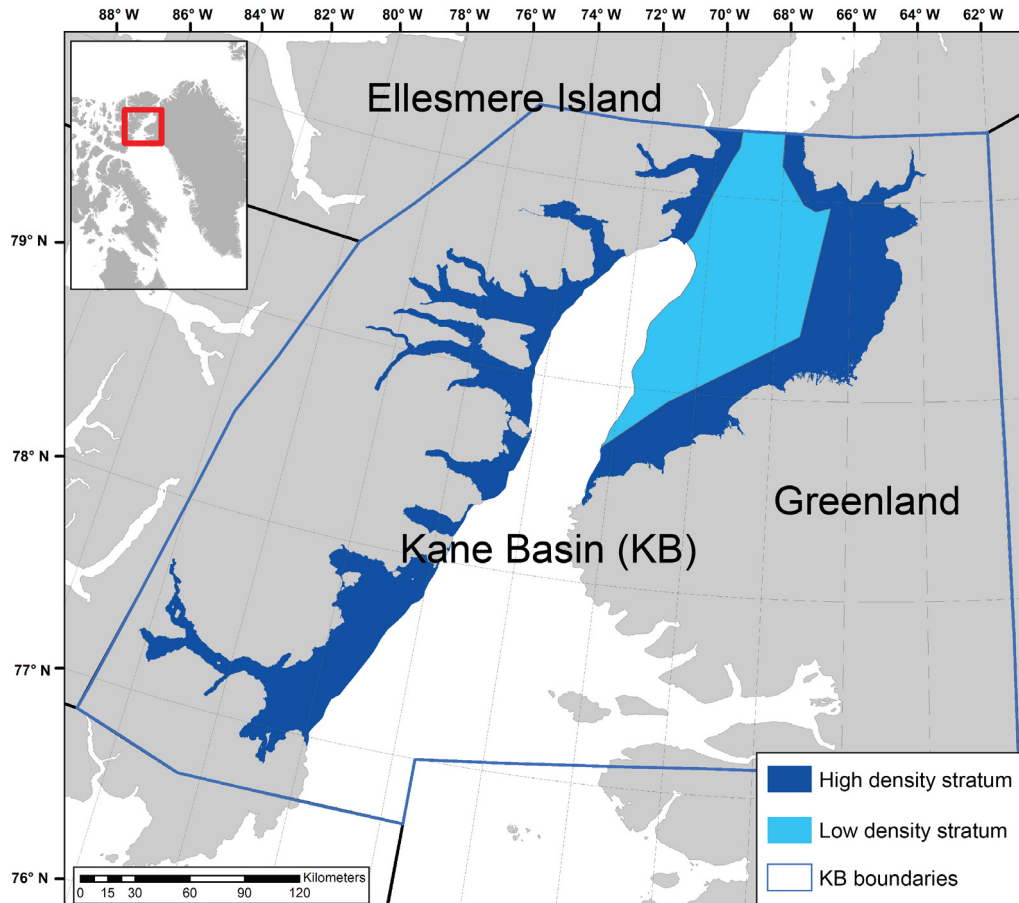


Fig. 3. Sampling strata for genetic mark-recapture and aerial survey of the Kane Basin polar bear subpopulation, April and May 2012–2014. The aerial survey is reported in Wiig et al. (2022)

of a plug of skin and subcutaneous tissue. This provided ample material for DNA extraction and residual tissue for future analyses. In one case, the available sample consisted of a tuft of hair stuck to a dart, so we soaked the biopsy dart in the lysis mix (QIAGEN buffer ATL + proteinase K) and added the hairs to the solution.

Genotyping to identify individuals and their sexes used the same 9 markers (microsatellites *G10B*, *CXX20*, *G10H*, *G10P*, *REN145P07*, *UARMU50*, *UARMU59*, and *G10X* plus a ZFX/ZFY length polymorphism) and protocols as previously used for these purposes in the adjacent BB subpopulation (Atkinson et al. 2021). Multiple attempts were made to produce genotypes for every marker that satisfied a series of objective and subjective criteria (Paetkau 2003).

## 2.5. Statistical analyses

We jointly analyzed live-capture and dead-recovery data from the KB subpopulation with the Burnham

(1993) model, which combines the Cormack-Jolly-Seber live-recapture model with the Seber dead-recovery model to estimate survival ( $S$ ), recapture ( $p$ ), reporting ( $r$ ), and fidelity ( $F$ ) probabilities. With the Burnham model, live recaptures are assumed to occur instantaneously within the study area, whereas dead recoveries can occur year round between live-capture periods and may take place within or outside the live-encounter study area. We assumed that harvests prior to (and including) 15 April occurred before the live-encounter period in year  $t$  (i.e. in year  $t - 1$ ) and that harvest after 15 April occurred after the live-encounter period (i.e. in year  $t$ ). This approach resulted in no instances in which a bear was recovered before being captured alive. Although there was some temporal overlap of live-recapture and dead-recovery periods, the exact timing of harvest relative to the live-capture sampling period is less important for long-lived species like polar bears.

We analyzed data and constructed models using the program MARK (White & Burnham 1999). We assembled capture histories from the live-capture

and dead-recovery data, including harvest recoveries through 2013. Although numeric ages were estimated from cementum annuli for physical captures, there was uncertainty in visual estimates of age class for bears that were biopsy darted during 2012–2014. Hence, we simplified our model structure to recognize 4 age classes (cf. Taylor et al. 2008, Peacock et al. 2013), including COY, yearlings (yrl), 2 yr olds (2yr), and individuals age 3 yr and above (3<sup>+</sup>).

Because KB is a small subpopulation and capture and recovery data were sparse, we evaluated a limited number of simple candidate models representing alternative biological assumptions and hypotheses. Based on previous analyses for polar bears (e.g. Regehr et al. 2007), we hypothesized that survival would differ among age classes and therefore included age structure in all candidate models, although we constrained yrl and 2yr (referred to as 1&2 in model terminology) survival to be equal due to small sample sizes. Because COY are fully dependent on their mothers, we assumed that survival would not vary between male and female COY. However, we expected that survival would differ between sexes for adults and possibly also yrl and 2yr due to a 2:1 male:female sex ratio in the harvest (SWG 2016). Therefore, we examined structures in which (1)  $S$  differed between sexes for age 3<sup>+</sup> bears only (denoted  $S_{\text{COY},1\&2,[3^+],\text{sex}}$ ) or (2)  $S$  differed between sexes for the combined yrl and 2yr age class (1&2) and for age 3<sup>+</sup> bears, with a single logit link parameter to estimate the effect size of sex for both age classes ( $S_{\text{COY},[1\&2,3^+],\text{sex}}$ ). Given small sample sizes and the relatively short periods of intensive sampling, we did not consider year-to-year variability in  $S$  or relationships between  $S$  and time-varying environmental covariates in our *a priori* model set (but see Section 4, Discussion).

Estimates of  $p$  in the Burnham model reflect both the probability of an animal being in the sampling area and thus available for recapture and the probability of the animal being recaptured conditional on its presence in the sampling area (i.e. temporary emigration is incorporated in  $p$ ; Burnham 1993). We examined 7 submodel structures for recapture probability ( $p$ ) of previously marked bears, as follows. (1) We hypothesized that female bears (plus their dependent COY and yrl offspring, regardless of sex) may have a different  $p$  than independent male bears due to potential differences in temporary emigration and habitat use ( $p_{(\text{sex})}$ ). (2) Because search effort and sampling protocols differed between the 2 sampling epochs (1992–1997 vs. 2012–2014), we considered structures with a different  $p$  for each epoch ( $p_{(\text{epoch})}$ ).

(3) Although data were scant, we hypothesized that interannual variability in weather and sea-ice conditions may have caused  $p$  to vary among years, so we considered a fully time-varying structure ( $p_{(\text{year})}$ ). We also considered structures with (4) additive effects between sex and epoch ( $p_{(\text{sex}+\text{epoch})}$ ), (5) additive effects between sex and year ( $p_{(\text{sex}+\text{year})}$ ), and (6) interactive effects between sex and epoch ( $p_{(\text{sex}\times\text{epoch})}$ ). Finally, we evaluated (7) a null submodel with a constant recapture probability over all individuals and time periods ( $p_{(\text{constant})}$ ).

Because some adult females in our 1990s sample were outfitted with satellite collars with very high frequency beacons ( $n = 12$ ) that may have assisted capture teams in locating them, we created a binary radio covariate indicating whether a bear was available for recapture with the assistance of radio telemetry. We applied the covariate for 2 yr post-collaring during the 1990s sampling period, unless there was evidence that the collar was physically removed from the bear. We included the radio covariate in all model structures and coded dependent offspring to have the same covariate structure as their mother. Satellite collars were not used to locate bears during the 2012–2014 period. Some captured individuals were not genotyped ( $n = 25$ ) because tissue samples were either missing or inadequate for genotyping. These individuals had a reduced  $p$  during 2012 and 2013 when physical capture and biopsy darting both occurred, and no probability of detection during 2014 when bears were only sampled via biopsy darting. To reflect this, we included a binary genotyped covariate (0 = successfully genotyped; 1 = not genotyped) in all model structures for 2012 and 2013. Furthermore, in 2014, we fixed  $p = 0$  for non-genotyped individuals and fixed  $p = 0$  for all animals in 1998–2011 because there was no live-encounter sampling.

The reporting ( $r$ ) parameter represents the probability that a dead bear is identified and reported to authorities. Assuming complete reporting of harvest and no recoveries from bears dying of natural causes,  $r$  reflects the proportion of mortality that can be attributed to harvest (including bears killed to protect life or property). We hypothesized that  $r$  would vary among age classes (1&2 vs. age 3<sup>+</sup>) because harvesting family groups or dependent young is illegal. We also allowed  $r$  to vary by sex for age 3<sup>+</sup> individuals ( $r_{(1\&2,[3^+],\text{sex})}$ ) due to sex-selective harvest (i.e. 2:1 male:female ratio). Because recovery data were sparse (Table 1;  $\bar{x} = 1.04$  recoveries per year; range: 0–5), we did not consider models with annual variation in  $r$ , but we created an alternative structure which included an additive effect for time period

Table 1. Summary of live captures and dead recoveries during the mark–recapture study of the Kane Basin polar bear subpopulation in Nunavut, Canada, and Greenland, 1992–2014. Dashes (–) indicate that data are not available due to an absence of marking or recapture. COY: cubs of the year; 1&2: 1 and 2 yr olds; 3+: bears age 3 yr and older

	Initial capture						Live recapture				Dead recovery					
	Female			Male			Female		Male		Female			Male		
	COY	1&2	3+	COY	1&2	3+	1&2	3+	1&2	3+	COY	1&2	3+	COY	1&2	3+
1992	4	0	7	2	0	3	–	–	–	–	0	0	1	0	0	0
1993	1	3	6	3	1	8	0	2	0	0	0	0	0	0	0	0
1994	2	0	9	3	0	4	1	3	2	2	0	0	0	0	0	0
1995	12	3	21	5	2	13	0	7	0	6	0	0	1	0	0	1
1996	5	2	8	2	2	4	1	7	0	5	0	0	0	0	0	1
1997	0	4	4	3	1	3	1	8	0	8	0	1	1	0	0	2
1998	–	–	–	–	–	–	–	–	–	–	–	0	3	–	0	2
1999	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	2
2000	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	0
2001	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	0
2002	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	1
2003	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	0
2004	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	0
2005	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	0
2006	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	0
2007	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	0
2008	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	0
2009	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	0
2010	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	1
2011	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	0
2012	2	3	19	1	4	11	–	2	–	0	0	0	1	0	0	0
2013	6	4	20	2	2	19	0	9	1	3	0	0	0	0	0	0
2014	0	2	21	0	1	10	2	12	0	7	–	–	–	–	–	–
Total	32	21	115	21	13	75	5	50	3	31	0	1	13	0	0	10

(pre-2006; 2006–2013) for age 3+ individuals to reflect the changes in harvest and improvements in the Greenlandic reporting system over the past decade ( $r_{(1\&2[3^+]_{\text{sex+period}})}$ ). There were no records of COY in the KB harvest during the first year after marking, so we fixed  $r_{\text{COY}}$  to 0 in all models. Because harvest data were only available through 2013, we fixed  $r$  to 0 for all age classes in 2014.

We hypothesized that polar bears may permanently emigrate from KB, based on the semi-discreteness of subpopulation boundaries (Taylor et al. 2001) and the spatial distribution of historical recapture and recovery data. Thus, we chose to estimate the  $F$  parameter, rather than assume that there was no permanent emigration and fix  $F$  to 1, as done in some previous studies (e.g. Taylor et al. 2005, 2008, 2009). We considered structures in which (1)  $F$  was constant across sex and age classes ( $F_{(\text{constant})}$ ) and (2)  $F$  differed between females (plus dependent young) and males ( $F_{(\text{sex})}$ ).

We used the most general model that excluded individual covariates ( $S_{(\text{COY}[1\&2,3^+]_{\text{sex}})}$ ,  $P_{(\text{sex+year})}$ ,  $I_{(1\&2[3^+]_{\text{sex+period}})}$ ,  $F_{(\text{sex})}$ ) to estimate overdispersion using the median  $\hat{c}$  method, as implemented in

program MARK (Cooch & White 2019). Because results indicated the data were not significantly overdispersed, we proceeded with model selection using Akaike's information criterion adjusted for small sample size but not for overdispersion (i.e. AICc; Burnham & Anderson 2002). We constructed all possible combinations of parameter-specific submodels, as described above, resulting in 56 candidate models.

We evaluated models via AICc and derived model-averaged parameter estimates using models with  $\Delta\text{AICc} < 4$  (Burnham & Anderson 2002). Because estimates of survival reflected harvest mortality, we estimated natural survival as  $S + r \times (1 - S)$  and estimated variance via the delta method (Taylor et al. 2008).

We estimated annual abundance using a generalized Horvitz-Thompson (H-T) estimator:

$$\hat{N}_t = \sum_{i=1}^{k_t} n_{i,t} / \hat{p}_{i,t} \quad (1)$$

where  $n_{i,t}$  is the number of bears captured in group  $i$  and year  $t$  (e.g. 3 for a female with 2 COY, 1 for an adult male),  $\hat{p}_{i,t}$  is the estimated recapture probability for that group, and  $k_t$  is the number of groups cap-



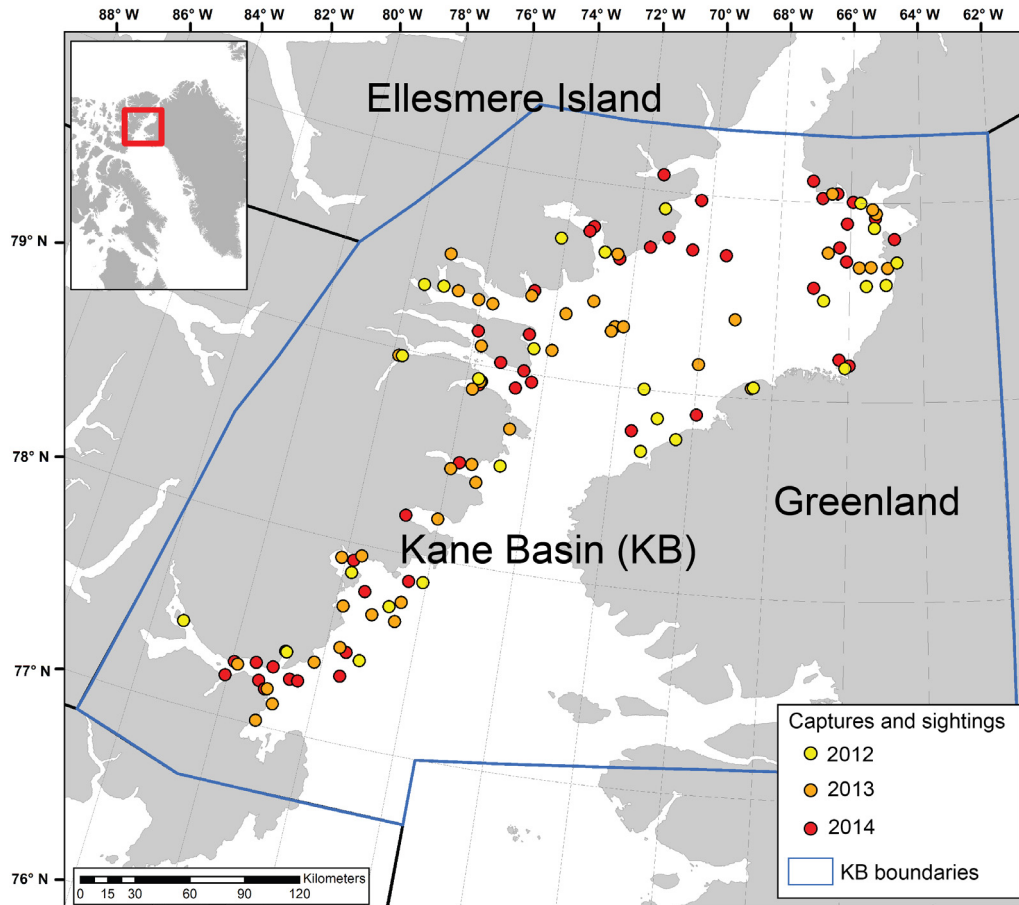


Fig. 4. Locations of polar bears biopsy darted, captured, and sighted in Kane Basin during April and May 2012–2014. The North Water Polynya varied among years but, in general, included the south-central portion of the subpopulation in all years. We did not sample sea ice in southeastern Kane Basin due to logistical constraints presented by the polynya and anticipated low densities

tured in year  $t$ . Because some COY were not marked during the 2012–2014 sampling period, we incorporated COY in estimates of  $N$  by estimating the number of age 3+ females with COY litters via an H-T estimator and multiplying by the mean observed COY litter size. Following previous work (e.g. Taylor et al. 2005, 2008, Peacock et al. 2013), we estimated variances for total abundance, which incorporated parameter variances and covariances (calculated in MARK) as well as variance of mean litter sizes, via the delta method (Seber 1982, Powell 2007) using the R (R Development Core Team 2015) package emdbook (Bolker 2016). We derived model-averaged estimates of total abundance using model weights for  $p$  and variances obtained with the delta method. When calculating mean estimates of abundance by sampling epoch, we excluded annual estimates of  $N$  from 1993 to 1994 and 2012 because of the apparent expansion of the sampling frame between 1992 and 1995 and the long interval without live recaptures

preceding 2012, respectively (i.e. estimation of subpopulation size in 2012 was based on the estimated recapture probability of 2 recaptured bears that had been marked during the 1990s, applied to all newly encountered bears in 2012; Table 1).

### 3. RESULTS

We obtained 277 initial captures, 89 recaptures, and 24 dead recoveries over the 23 yr study period (Table 1). More bears were captured in the eastern regions of KB (i.e. off Humboldt Glacier in northwestern Greenland) during 2012–2014 than during the 1990s (Figs. 2 & 4). Capture data were particularly sparse during the 1990s, except for 1995 (Table 1). Similarly, few bears were recovered via the harvest during the 2000s (Table 1). No males initially marked in KB during the 1990s were recaptured during 2012–2014, and only 1 male marked in the 1990s was

reported in the harvest after 2002. Mean observed litter sizes during 2012–2014 were 1.6 (SD: 0.5; 15 twin litters, 10 singletons) for COY, 1.3 (SD: 0.5; 3 twin litters, 9 singletons) for yr1, and 1.0 (3 singletons) for 2 yr that still accompanied their mother during the spring sampling period.

All capture and biopsy samples from the 2012–2014 sampling period produced genotypes for every locus that satisfied our criteria for high-confidence scoring. Using the 134 unique 9-locus genotypes (i.e. individuals) observed among these 174 samples, the mean observed and expected heterozygosity across the 8 microsatellite loci was 0.78. Among these 134 unique genotypes, the most similar pair differed at 3 loci, demonstrating both that the marker system had ample power to generate a unique genotype for each sampled individual and that genotyping errors at 1 or 2 loci had not caused pairs of samples from the same individual to receive different genotypes (Paetkau 2003). One of the KB captures was a recapture from BB (where 1410 BB bears were genetically identified between 2011 and 2013, Atkinson et al. 2021).

The most supported mark–recapture–recovery model included an additive effect of sex on  $S$  for the 1&2 and 3<sup>+</sup> age classes; a sex effect on  $p$ ; and age, sex, and period effects (i.e. pre- vs. post-2006) on  $r$  (Table 2). Individual covariates were highly supported and indicated that radio-collared females in 1993–1995 had recapture probabilities of 0.58 (SE: 0.11) vs. 0.17 (SE: 0.03) for females that did not provide telemetry data. Non-genotyped females and males in 2012–2013 had recapture probabilities that were 0.07 to 0.11 lower, respectively, than estimates of  $p$  for genotyped individuals. Estimates of  $p$  were higher for males (0.28, SE: 0.05) than for females

(0.17, SE: 0.03) and did not vary by sampling epoch. Reporting probability was constant for the 1&2 age classes and varied by sex and epoch for the 3<sup>+</sup> age class. The estimate of  $F$  was 0.98 (SE: 0.04) and did not vary by sex, age, or epoch.

Eleven models were within 4 AICc units of the most supported model (Table 2). These models included parameterizations like the most supported model as well as combinations of the following modifications: (1) sex effects on  $S$  for 3<sup>+</sup> adults only, (2) a single average value of  $p$ , (3) an epoch effect on  $p$  (i.e. 1992–1997 vs. 2012–2014), and (4) separate values of  $F$  for males vs. females. The top 12 models had a cumulative AICc weight of 0.76.

Model-averaged estimates of total survival for males were lower than those for females in both the 1&2 and 3<sup>+</sup> age classes, although we note that the additive effect in  $S$  was shared across age classes (Table 3). This pattern was also evident in estimates of unharvested  $S$  (1&2 females: 0.74, SE: 0.15; 1&2 males: 0.54, SE: 0.17; age 3<sup>+</sup> females, 2006–2013: 0.96, SE: 0.04; and 3<sup>+</sup> males, 2006–2013: 0.88, SE: 0.05). Reporting probabilities in 1992–2005 were 4- to 5-fold greater than those in 2006–2013 and were higher for adult males than for adult females and lowest for young bears (Table 3). Model-averaged estimates of  $F$  indicated strong fidelity to the spring-time study area for females and dependent bears ( $F$ : 0.98, SE: 0.04), with slightly lower fidelity for age 3<sup>+</sup> males ( $F$ : 0.96, SE: 0.07).

Given the lack of temporal variation in capture probabilities in top supported models, interannual variation in estimates of abundance largely reflected variability in sample sizes among years (Table 4). Using model-averaged estimates of  $p$  in the H-T esti-

Table 2. Model selection results ( $\Delta\text{AIC}_c < 4$ ) from analysis of mark–recapture–recovery data from the Kane Basin polar bear subpopulation, 1992–2014. For  $p$  and  $F$ , dependent males (COY and yearlings) were treated as females, and epoch = sampling period (1992–1997; 2012–2014). For dead reporting probability, all models had the same parameter structure:  $r_{1\&2, 3^+ \times \text{sex} \times \text{period}}$ , where period = 1992–2005 or 2006–2013. AICc: corrected Akaike's information criterion; COY: cub of the year; 1&2: 1 and 2 yr olds; 3<sup>+</sup>: bears age 3 yr and older

Survival ( $S$ )	Recapture ( $p$ )	Fidelity ( $F$ )	Parameters	$\Delta\text{AIC}_c$	AICc weight	Deviance
COY, [1&2, 3 <sup>+</sup> ] + sex	Sex	Constant	13	0	0.23	723.71
COY, [1&2, 3 <sup>+</sup> ] + sex	Sex	Sex	14	1.22	0.13	722.76
COY, [1&2, 3 <sup>+</sup> ] + sex	Sex + epoch	Constant	14	1.23	0.13	722.77
COY, [1&2, 3 <sup>+</sup> ] + sex	Constant	Constant	12	1.88	0.09	727.74
COY, 1&2, 3 <sup>+</sup> + sex	Sex	Constant	13	2.19	0.08	725.90
COY, [1&2, 3 <sup>+</sup> ] + sex	Sex + epoch	Sex	15	2.57	0.06	721.94
COY, [1&2, 3 <sup>+</sup> ] + sex	Sex $\times$ epoch	Constant	15	2.62	0.06	721.99
COY, 1&2, 3 <sup>+</sup> + sex	Sex	Sex	14	2.83	0.06	724.38
COY, 1&2, 3 <sup>+</sup> + sex	Constant	Constant	12	3.06	0.05	728.92
COY, [1&2, 3 <sup>+</sup> ] + sex	Epoch	Constant	13	3.37	0.04	727.08
COY, 1&2, 3 <sup>+</sup> + sex	Sex + epoch	Constant	14	3.45	0.04	724.99
COY, [1&2, 3 <sup>+</sup> ] + sex	Constant	Sex	13	3.90	0.03	727.61

Table 3. Model-averaged ( $\Delta\text{AICc} < 4$ ) parameter estimates for the Kane Basin polar bear subpopulation obtained from mark–recapture study, 1992–2014. Abbreviations as in Table 2

Parameter	Class	Estimate (SE)
Total survival ( <i>S</i> )	COY	0.45 (0.15)
	1&2 females	0.73 (0.13)
	1&2 males	0.52 (0.17)
	3 <sup>+</sup> females	0.95 (0.04)
	3 <sup>+</sup> males	0.87 (0.06)
Reporting ( <i>r</i> )	1&2	0.04 (0.04)
	3 <sup>+</sup> females, 1992–2005	0.42 (0.26)
	3 <sup>+</sup> females, 2006–2013	0.09 (0.08)
	3 <sup>+</sup> males, 1992–2005	0.32 (0.12)
	3 <sup>+</sup> males, 2006–2013	0.06 (0.05)
Fidelity ( <i>F</i> )	3 <sup>+</sup> females (+ dependent young)	0.98 (0.04)
	3 <sup>+</sup> males	0.96 (0.07)

mator, the mean total abundance of the KB subpopulation was 224 (SE: 40; 95 % CI: 145–303) during 1995–1997 and 357 (SE: 92; 95 % CI: 221–493) during 2013–2014. Based on a randomization procedure that assumed normal distributions for abundance estimates, this corresponds to a probability of 0.95 that abundance increased by at least 1 bear and a probability of 0.86 that abundance increased by at least 50 bears, between the 1990s and 2010s.

#### 4. DISCUSSION

Our objective was to estimate the current abundance and vital rates of polar bears in the KB subpopulation. We used a combination of physical and genetic mark–recapture techniques (e.g. Palsbøll et al. 1997, Boersen et al. 2003, Boulanger et al. 2004, Atkinson et al. 2021), including live recaptures and dead recoveries, to estimate demographic parameters over a 23 yr study period. Our findings suggest that the KB population increased in abundance between 1995–1997 and 2013–2014 and currently has a positive demographic status. In conjunction with

information on sea-ice dynamics, habitat use, and nutritional ecology (Laidre et al. 2020b), this suggests that the KB subpopulation has benefited in recent decades from thinner sea ice and reduced harvest pressure. This is consistent with scientific predictions that climate warming may provide transient benefits for high-latitude polar bear subpopulations that were historically limited by thick multiyear sea ice and low biological productivity (Laidre et al. 2020b).

##### 4.1. Abundance of KB bears

Our estimates of abundance suggest that the KB polar bear subpopulation grew approximately 1.6-fold from 1995–1997 to 2013–2014 (i.e. 224 to 357), which would indicate a finite annual growth rate of  $\lambda = 1.027$  between survey periods. We encourage caution in interpreting population growth due to small sample sizes, potential expansion of the sampling frame, and differences in sampling protocols between the 1990s and 2010s. We note that the H-T estimator used to estimate abundance yielded biologically implausible rates of population growth from 1994 to 1995 (119 to 318 bears), 1995 to 1996 (318 to 189 bears), and 2012 to 2013 (221 to 328 bears; Table 4). Although these changes might be partly attributable to an increased sampling frame in 1995 and a paucity of previously marked bears in 2012, it is also a consequence of the estimator itself. Specifically, if recapture probabilities are estimated as temporal constants across groups and time periods, only variation in numbers of captures contributes to interannual variation in estimates of abundance. Because data for this analysis were sparse and models with interannual variation in *p* were not supported, our H-T estimates of abundance are influenced primarily by variation in annual sample size of captured bears. Given this limitation, we suggest focusing on mean

Table 4. Numbers of captures of older males (3<sup>+</sup> M), older females (3<sup>+</sup> F), dependent young of both sexes (age 0, 1, or 2), and model-averaged ( $\Delta\text{AICc} < 4$ ) estimates of abundance ( $\hat{N} \pm \text{SE}$  with 95 % CI) of the Kane Basin polar bear subpopulation from mark–recapture study, 1992–1997 and 2012–2014. Abbreviations as in Table 2

	1993	1994	1995	1996	1997	2012	2013	2014
3 <sup>+</sup> M	8	6	19	9	11	11	22	17
3 <sup>+</sup> F	8	12	28	15	12	21	29	37
Young	8	8	22	12	9	10	15	5
$\hat{N} \pm \text{SE}$	120 $\pm$ 19	119 $\pm$ 21	318 $\pm$ 53	189 $\pm$ 36	164 $\pm$ 28	221 $\pm$ 41	328 $\pm$ 60	385 $\pm$ 78
95 % CI	(83–156)	(77–160)	(214–429)	(119–259)	(110–218)	(141–301)	(211–445)	(233–537)

estimates of abundance for the 2 sampling epochs. Furthermore, our data were insufficient to quantify immigration or to differentiate potential immigration from *in situ* population growth. Integrated population models that include abundance as a latent parameter and link changes in abundance to estimates of survival, reproduction, and movement (e.g. Regehr et al. 2018) might help to resolve these issues in future analyses, if sample sizes are sufficient to fit more highly parameterized models.

Wiig et al. (2022) estimated abundance in KB (190 bears, 95 % lognormal CI: 87–411; CV: 39 %) from an aerial survey conducted in 2014. They noted this was likely an underestimate because large portions of the KB subpopulation's distribution were not sampled, although bear densities in those regions were expected to be low. Furthermore, aerial surveys provide an estimate of the number of bears in a specific region at a specific time, whereas our analyses produced estimates of the superpopulation, defined as all animals with a non-negligible probability of using the sampling area over the course of the study. Because there is likely some temporary emigration from the KB subpopulation (i.e. not all animals with fidelity to the area are available for sampling each year), it is expected that our estimates of superpopulation size are larger than estimates of abundance from the aerial survey.

#### 4.2. Sampling in KB

We documented more bears in the eastern regions of the KB subpopulation during 2012–2014 than during the 1990s. The difference in distribution between the 1990s and 2010s may reflect differences in spatial distribution of bears, possibly influenced by reduced hunting pressure by Greenland in eastern KB or differences in sampling protocols. When the eastern parts of KB (i.e. the areas east of the mid-sector line in the Nares Strait-KB area off the Humboldt Glacier) were surveyed in 1994 and 1997, few signs of polar bear activity (e.g. tracks) were observed, and only a few bears were tagged (Taylor et al. 2001). At the time, the apparent low densities of polar bears in eastern KB were assumed to reflect avoidance due to harvest pressure in the Qaanaaq region, particularly after Greenlanders were barred from hunting polar bears in Canadian territory in the late 1960s. The presence of ringed seals in eastern KB was noted during the surveys in the 1990s, suggesting that these areas comprised good habitat despite the apparent paucity of bears (Taylor et al. 2001, E. Born pers.

obs.). We could not directly evaluate the potential effects of different sampling protocols in the 1990s and 2010s because GPS tracklogs from the search helicopter were not available to quantify 1990s sampling effort. Finally, sea-ice dynamics in KB have changed since the 1990s (Laidre et al. 2020b), with less stable sea ice and more open water limiting access of hunters from Greenland to the eastern parts of the region (Born et al. 2011). Hence, we hypothesize that together with implementation of a harvest quota in Greenland in 2006, changes in hunting pressure due to changing sea-ice dynamics led to an apparent expansion of bears into the eastern parts of the Nares Strait-KB region.

#### 4.3. Survival of KB bears ( $S$ , $r$ , and $F$ )

Time-constant estimates of total survival for age 3<sup>+</sup> females (0.95; SE: 0.04) and dependent offspring were similar to estimates for the 1990s in Taylor et al. (2008). In the current analysis, we did not fit models that allowed for temporal variation in total survival due to concerns about bias resulting from small sample sizes and unmodeled heterogeneity in  $p$  (e.g. due to temporary emigration), which can occur toward the end of mark-recapture studies for mobile species (e.g. Devineau et al. 2006, Regehr et al. 2009). Estimates of unharvested survival for 3<sup>+</sup> females appear sufficiently high for positive population growth assuming sufficient reproduction. Time-constant estimates of age 3<sup>+</sup> male total survival (0.87, SE: 0.06) were lower than previous estimates for the 1990s (Taylor et al. 2008: age 5<sup>+</sup> males, 0.96, SE: 0.05) but broadly similar to estimates of adult male total survival from some other studies (e.g. Stirling et al. 2011, Peacock et al. 2012). We note that data on males were particularly scant in this study (Table 1): No male bears initially marked in the 1990s were recaptured in the 2000s, and very few individuals were reported in the harvest over the past 15 yr. We are uncertain if the disparity in estimates of male survival between our study and Taylor et al. (2008) reflects differences in modeling approaches, such as fewer age class designations in the present study and consideration of different model structures (e.g. unlike Taylor et al. 2008, we did not consider a structure in which total survival was estimated as constant between the sexes for age 3<sup>+</sup> individuals), inclusion of longer-term data in the current analysis, an impact of the changing environment on male survival, reduced fidelity of males to the study area that was not reflected in estimates of  $F$  due to sparse recovery

data, underreporting of male bears in the harvest, or some combination thereof.

We calculated post hoc estimates of unharvested survival, using methods similar to previous polar bear studies (e.g. Taylor et al. 2005), because unharvested survival reflects the subpopulation's capacity for growth and can be used in subsequent demographic analyses (e.g. matrix projection models; Regehr et al. 2021). We note that the formula used to estimate unharvested survival makes simplifying assumptions that can lead to bias under some conditions, although such concerns are small for KB polar bears due to high estimates of  $S$  and low estimates of  $r$ . The documented underreporting of marked bears in the harvest (Government of Nunavut unpubl. data) leads to an underestimation of unharvested survival, although this may be offset by a likely violation of the assumption that harvest mortality is completely additive. For example, Taylor et al. (2008) estimated unharvested survival for adult (age  $\geq 5$  yr) females and males to be 0.997, meaning that virtually all mortality during 1992–1998 resulted from harvest, and less than 1 in 300 adult bears would die annually in the absence of harvest. Although Taylor et al. (2008) did not report their estimates of  $r$ , back-calculating from survival rates in their Table 3 yields the unrealistically high values of  $r = 0.91$  for adult females and  $r = 0.93$  for adult males. Therefore, we suggest that estimates of unharvested survival and harvest mortality in Taylor et al. (2008) should be treated cautiously.

Changing sea-ice conditions, a reduction in accessibility of KB to hunters from Canada and Greenland (in the Humboldt Glacier region), and implementation of a quota in Greenland have contributed to an assumed net reduction in harvest since the 1990s (SWG 2016). This decline is reflected in lower estimates of  $r$  for the period 2006–2014 compared to 1992–2005 (Table 3). Underreporting of harvest, which anecdotally appears to increase with time as research marks are lost or become unreadable (SWG 2016), also may contribute to lower estimates of  $r$  during 2006–2013, especially given the 14 yr interval without live recaptures.

We evaluated a post hoc model to better understand mechanisms for the likely increase in subpopulation abundance between the 1990s and 2010s. Specifically, we modified the most supported *a priori* model to allow survival of adult males and females to differ between 1992–2005 and 2006–2014, concurrent with reductions in harvest in western Greenland ( $S_{\text{COY}[\text{1\&2,3}_{1992-2005}, \text{3}_{2006-2014}] + \text{sex}}$ ). This model produced nearly identical estimates of subpopulation size (changes were  $<3$  bears per year), but estimates of total survival increased over time (adult females,

1992–2005:  $S = 0.954$ , SE: 0.035 vs. 2006–2014:  $S = 0.974$ , SE: 0.024; adult males, 1992–2005:  $S = 0.837$ , SE: 0.058 vs. 2006–2014:  $S = 0.903$ , SE: 0.055). These increases are consistent with enhanced protection of female bears under harvest regulations implemented in 2006 and with apparent population growth between 1992 and 2014.

Despite the sparseness of the data and the unusual study design (i.e. 6 and 3 yr live-capture sessions connected by a 14 yr period with dead recoveries only), our estimates of  $F$  seemed biologically realistic (age 3<sup>+</sup> males: 0.96; females and dependent bears: 0.98). Polar bears showed strong seasonal fidelity to the region in which they were captured; only a small proportion of individuals emigrate to other subpopulations. This interpretation appears consistent with findings from satellite telemetry data and capture and harvest records (Taylor et al. 2001, SWG 2016, Laidre et al. 2020b).

#### 4.4. Subpopulation status

Our study indicates that the size of the KB subpopulation likely increased between the 1990s and 2010s, which is consistent with traditional ecological knowledge among polar bear hunters during the same period (Born et al. 2011). Climate change is hypothesized to provide transient benefits to polar bears in some areas where multiyear sea ice historically limited biological productivity and seal abundance (Kingsley et al. 1985, Derocher et al. 2004). Laidre et al. (2020b) provided the first empirical evidence for this phenomenon in the KB polar bear subpopulation, showing that pronounced sea-ice loss over the past 20 yr was associated with increased range sizes, improved body condition for all sex and age classes, and stable reproductive metrics. Here, we build on that work to demonstrate that these ecological changes are coupled to a likely increase in subpopulation abundance from ca. 224 bears in the 1990s (Taylor et al. 2008) to 357 bears in the 2010s.

Our data suggest that this small high-Arctic polar bear subpopulation (i.e.  $<2\%$  of the global polar bear abundance, Regehr et al. 2016) is productive and healthy, although any benefits incurred by lighter sea-ice conditions are likely temporary given predictions of continued ice loss under unmitigated climate change (Fox-Kemper et al. 2021). For polar bears in most areas, long-term sea-ice loss is expected to have negative demographic effects given the species' fundamental dependence on ice as a platform to access their seal prey (Atwood et al. 2016). Models that fore-



cast polar bear population declines in several decades or a century (e.g. Amstrup et al. 2008, Regehr et al. 2016) may inform long-term conservation status, but understanding near-term variability is necessary for effective conservation and state-dependent management (Regehr et al. 2017) as climate change progresses.

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