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# Recovery From Reduction: The M'Clintock Channel Polar Bear Subpopulation, Nunavut, Canada

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ABSTRACT. To retain viable polar bear subpopulations, scientific monitoring studies are conducted to inform adaptive management frameworks. Here we report the results of the second structured population study for polar bears in the M'Clintock Channel (MC) subpopulation. Data included biopsy samples collected during a 2014–16 subpopulation-wide survey, live mark-recapture data collected during the first subpopulation study from 1998 to 2000, and harvest recovery data from 1998 to 2016. Results of a closed capture-recapture model, implemented in a Bayesian framework for animals over 2 yr., produced a mean abundance estimate of 716 (95% Credible Interval = 545–955) for 2014–16, indicating an increase from the 1998–2000 study estimate (284; our Bayesian-calculated estimate: 325 bears). However, closed model assumptions mean our estimate represents the superpopulation. Mean litter sizes did not differ between study periods, but mean number of yearlings per adult female declined from 0.39 ± 0.10 (SE) to 0.27 ± 0.06 between 1998–2000 and 2014–16. Apparent survival estimates from observed data were biased low (0.88 ± 0.02) due to unknown immigration and emigration. However, survival calculated using the change in abundance estimates between study periods equaled 0.93, representing a population growth rate of 2%. Body condition improved between study periods. Our findings indicate the MC subpopulation recovered from overharvesting between 1979 and 1999 and may be transiently benefitting from increased biological productivity associated with local sea ice changes. Our demographic analyses were constrained by low density, low harvest, small sample sizes, low recapture probability, and lack of movement information; hence, harvest management decisions should be applied with appropriate caution.

Key words: capture-mark-recapture; demography; genetic biopsy sampling; Nunavut; polar bear; superpopulation; *Ursus maritimus*

RÉSUMÉ. Des études de surveillance scientifique sont effectuées pour éclairer les cadres de gestion adaptative visant à garder des sous-populations d'ours polaires viables. Dans cet article, nous présentons les résultats de la deuxième étude structurée sur la population d'ours polaires composée de la sous-population du détroit de M'Clintock (MC). Les données comprenaient des échantillons de biopsies prélevés dans le cadre d'un relevé de l'ensemble de la sous-population réalisé de 2014 à 2016, des données réelles de marquage-recapture recueillies pendant la première étude de la sous-population de 1998 à 2000, et les données de récupération des récoltes de 1998 à 2016. Les résultats d'un modèle fermé de capture-recapture, appliqués dans un cadre bayésien pour les animaux de plus de deux ans, ont donné une estimation de l'abondance moyenne de 716 (intervalle de crédibilité de 95 % = 545–955) pour les années 2014 à 2016, ce qui représente une hausse par rapport à l'estimation de l'étude de 1998 à 2000 (284; notre estimation calculée selon le cadre bayésien : 325 ours). Cependant, les hypothèses du modèle fermé signifient que notre estimation représente la superpopulation. Les tailles de portées moyennes n'ont pas varié d'une période d'étude à l'autre, mais le nombre moyen d'ours d'un an par femelle adulte a diminué, passant de 0,39 ± 0,10 (ET) à 0,27 ± 0,06 de 1998 à 2000 et de 2014 à 2016. Les estimations du taux de survie apparente à partir des données observées ont fait l'objet d'un faible biais (0,88 ± 0,02) en raison du manque de données sur l'immigration et l'émigration. Toutefois, le calcul du taux de survie à l'aide de la variation des estimations de l'abondance entre les périodes étudiées correspondait à 0,93, soit un taux de croissance de la population de 2 %. Par ailleurs, la condition corporelle s'est améliorée entre les périodes étudiées. Selon nos constatations, la sous-population de MC s'est remise de la surchasse qui a eu cours de 1979 à 1999. Aussi, elle bénéficie peut-être, de façon transitoire, de la productivité biologique accrue découlant des changements touchant la glace de mer locale. Nos analyses démographiques ont été contraintes par la faible densité, le faible taux de récolte, la petite taille des échantillons, la faible probabilité de recapture et le manque d'information sur les déplacements. Par conséquent, les décisions en matière de gestion des récoltes devraient être prises avec circonspection.

Mot clés : capture-marquage-recapture; démographie; échantillonnage de biopsies génétiques; Nunavut; ours polaire; superpopulation; *Ursus maritimus*

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## INTRODUCTION

Wildlife managers face complex decisions when seeking to balance conservation and human priorities, particularly for species of conservation concern. Demographic parameters of a population, such as abundance, survival, and reproductive indices, are critical pieces of information that feed into an adaptive management framework to inform decision making (Lancia et al., 1996; Johnson, 1999; Nichols and Williams, 2006; Gibbs, 2008). The utility of adaptive, or state-dependent, management depends on the ability to obtain these demographic parameters, which can be influenced by various factors including management objectives, species' biology, and the monitoring agency's available resources (Gibbs, 2008).

One species that has received significant monitoring attention is the polar bear (*Ursus maritimus* Phipps 1774), which occurs globally in 19 subpopulation units (Obbard et al., 2010). Despite this attention, reliable current abundance and demographic information are lacking for many subpopulations (Obbard et al., 2010; Vongraven et al., 2012; Durner et al., 2018), partly because polar bear research is financially and logistically challenging. Polar bears are sparsely distributed across expansive ranges, highly mobile, and cryptic, further complicating monitoring. Given ongoing habitat loss due to climate change and concurrent subsistence use by Indigenous peoples, regular monitoring is critical for managers to ensure the sustainability of polar bear subpopulations (Derocher et al., 2004; Durner et al., 2009; Atwood et al., 2016).

The M'Clintock Channel polar bear subpopulation (MC) occurs within an area that encompasses approximately 495,000 km$^2$, including 140,000 km$^2$ of marine waters that are covered by sea ice to various extents throughout the year. In addition to the geographic M'Clintock Channel proper, the MC subpopulation area also includes Dease Strait, Coronation Gulf, Queen Maud Gulf, Larsen Sound, and Franklin Strait. It is bounded by Victoria Island to the west, Prince of Wales Island to the north, Boothia Peninsula to the east, and the Nunavut mainland to the south (Barber and Iacozza, 2004; Hamilton and Derocher, 2019; Fig. 1). Initial physical mark-recapture studies from 1973 to 1978 included both MC and the adjacent Gulf of Boothia (GB) subpopulation area together as a single demographic unit (Schweinsburg et al., 1981). The total abundance estimate for both areas was 1081 but was known to be biased by non-representative sampling. Managers subsequently increased abundance to 900 for GB and 900 for MC based on local traditional ecological knowledge (TEK) and back-calculations to determine abundance levels that would sustain the existing subsistence harvest levels of 34 bears/year (Aars et al., 2006; Taylor et al., 2006). In the mid-1990s, MC and GB subpopulation area boundaries were delineated based on movements of satellite radio-collared adult female bears (Taylor et al., 2001), recoveries of research-marked bears in the harvest (Taylor and Lee, 1995; Taylor et al., 2001), and TEK about how local conditions may influence the movements of polar bears (Keith et al., 2005). Microsatellite genetic analyses also suggested some level of differentiation between the MC and GB subpopulations, although the magnitude of population structuring was higher among females than males (Campagna et al., 2013). Concurrently, the MC estimate was revised downwards to 700 based on TEK from hunters reporting reduced densities of polar bears (Aars et al., 2006; Taylor et al., 2006). A designed capture-mark-recapture study for MC in 1998–2000 estimated 284 ± 59.3 (mean ± SE) bears, supporting TEK of a declining population (Taylor et al., 2006). Harvest levels between 1970 and 2001 were considered unsustainable (approximately 32 ± 10 bears (range: 12–55; roughly 19.5 males and 12.0 females; Taylor et al., 2006; Government of Nunavut, unpubl. data), which resulted in a harvest moratorium from 2001 to 2004 and afterwards a reduced harvest of three bears annually until 2015 in order to allow population recovery. Local knowledge from Gjoa Haven and Taloyoak resident hunters, who routinely hunt in both the MC and GB subpopulation units, indicated that more bears had been seen in the 2000s during their sea ice travels. This relative increase in bear observations triggered a rise in the annual harvest beginning with the 2015–16 harvest season from three to twelve bears at a two-to-one male-to-female harvest sex ratio, though empirical abundance remained unknown.

To evaluate the extent to which the subpopulation recovery strategy was successful, as well as to update demographic parameters for MC, we carried out a genetic biopsy mark-recapture study from 2014 to 2016. Our primary objectives were to compare updated abundance and demography with the 1998–2000 study results and to assess the status of the MC subpopulation.

## METHODS

### *Study Area*

Our study area included the extent of the MC subpopulation (Fig. 1). Like much of the Arctic, the MC study area has experienced a change in sea ice quantity and composition in which multiyear sea ice has declined and been replaced by annual ice (Rothrock et al., 1999; Barber and Iacozza, 2004; Keith et al., 2005; Howell et al., 2009; Comiso, 2012; Kwok, 2018). Annual ice in the MC study area is generally flat and interspersed by long pressure ridges, and rougher multiyear ice is largely limited to localized areas (e.g., M'Clintock Channel proper; M. Dyck, pers. observ.). For most of the year, the area is completely ice-covered except for a few small polynyas that attract seals, polar bears, and other species (Stirling, 1980; Hannah et al., 2009). From approximately mid-June to July, wide cracks form and extend for many kilometers, providing haul-out habitat for ringed (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) and thus, good foraging habitat for polar bears. From August to early October, much of the

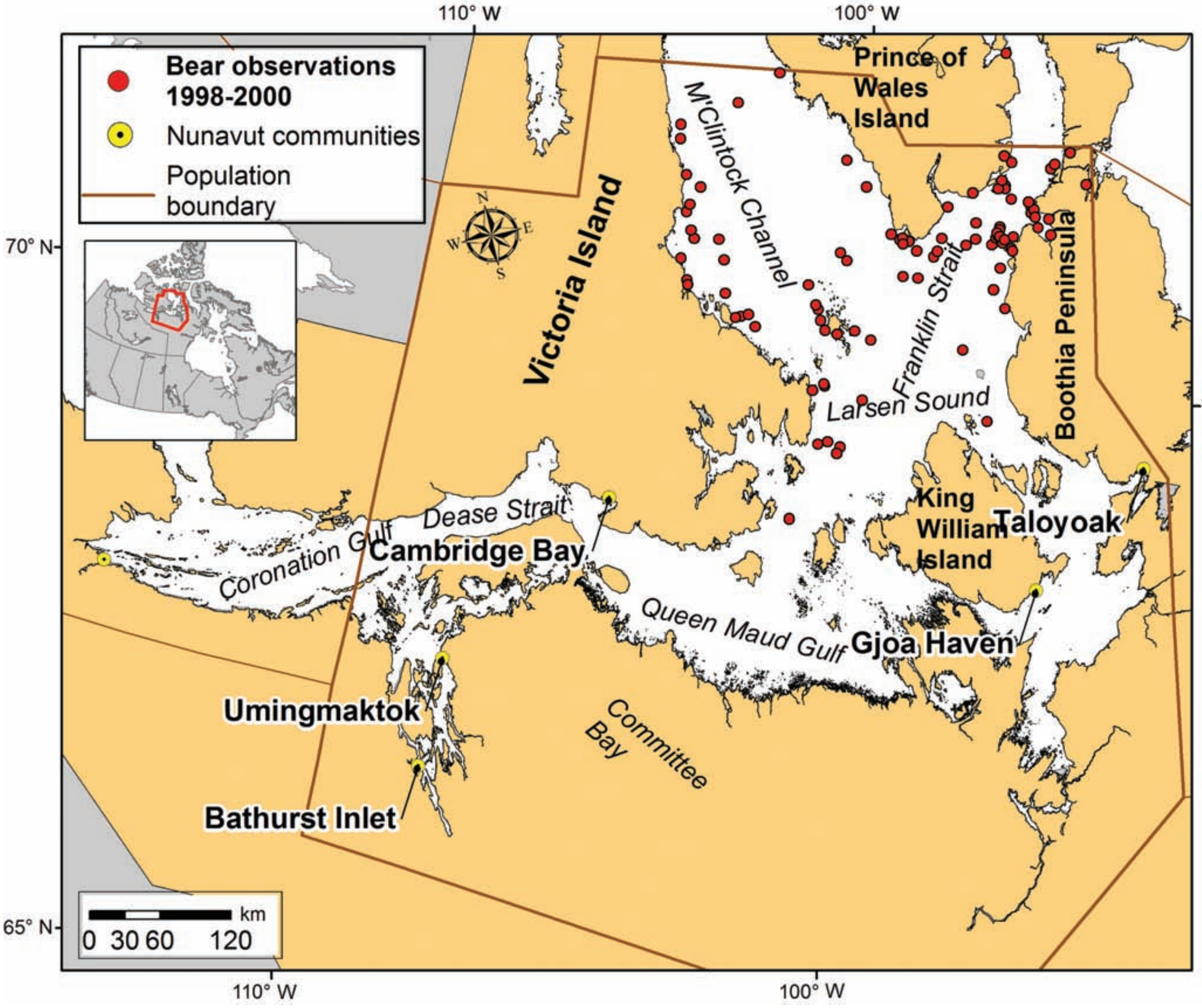

FIG. 1. Overview of the M'Clintock Channel polar bear subpopulation study area in Nunavut, Canada, with capture locations of bears from the 1998–2000 study (GH = Gateshead Island; JL = Jenny Lind Island).

sea ice disappears in the southern and eastern portion of the study area (Stewart et al., 2007; Howell et al., 2008, 2009). In recent years, southward ice drift from the Queen Elizabeth Islands and M'Clure Strait (Howell et al., 2008, 2009) has resulted in multiyear ice remaining in M'Clintock Channel proper year-round.

### *Sampling – Field Collections*

The 2014–16 MC study design was similar to the previous physical mark-recapture study conducted between 1998 and 2000 (Taylor et al., 2006; Fig. 1), however, our study did not involve the immobilization and physical handling of bears. Nunavut Inuit co-management partners expressed their concern over wildlife capture and handling (Lunn et al., 2010; Government of Nunavut, Department of Environment, 2013); as a result, we employed a feasible alternative technique (i.e., genetic capture-mark-recapture) that is minimally invasive (Garshelis, 2006) and has been successfully applied on various species, including polar bears (Brown et al., 1991; Palsbøll et al., 1997; Boulanger et al., 2004; Pagano et al., 2014; SWG, 2016). We spent approximately 88 hr in each field season searching and sampling bears via helicopter, flying approximately 100–120 m above sea level, at an average speed of 120–150 km per hr (Fig. 2). To minimize potential sampling bias and to allow replication of this study, we used a semi-structured sampling approach of transect lines across the sea ice and small islands with search intensity proportional to apparent bear activity (or bear presence). Further, we discussed search areas with hunters and local hunters and trappers' associations during pre-study consultations to gain insight about sea ice conditions, bear distribution, and where to prioritize effort should time or resources become constrained. Finally, we attempted to take past capture locations (Fig. 1) into account when searching the sea ice, adjacent coastal areas, and small islands of our study area. Approximately 80% of the entire MC area

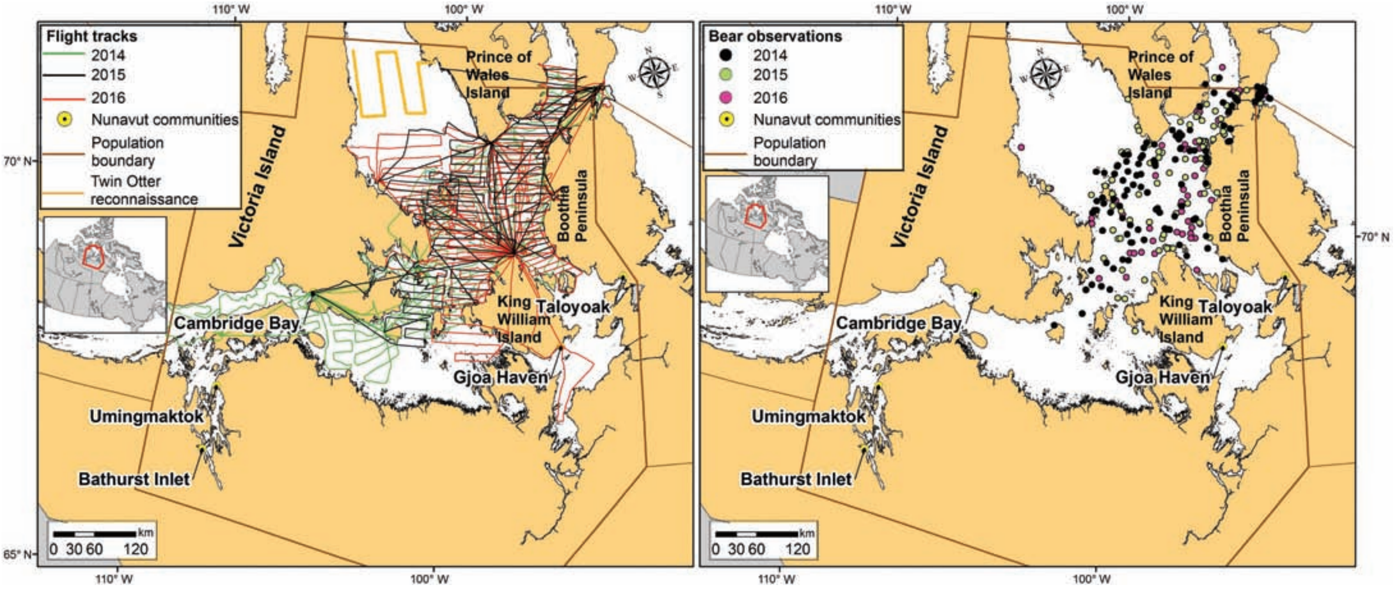

FIG. 2. Overview of field activities during the 2014–16 biopsy study in M'Clintock Channel, Nunavut, Canada, with flown search paths and locations of polar bear encounters for each year shown.

was searched every year, though poor weather and unsafe flying conditions prevented us from searching the entire study area during each field season, and we were unable to search M'Clintock Channel proper. On 10 April 2016 during a bright day with good visibility, we conducted a reconnaissance flight over M'Clintock Channel proper in a fixed-wing aircraft with five observers plus the pilots to assess bear presence and signs (Fig. 2). This survey allowed us to infer whether this portion of the study area potentially contained animals unlikely to be exposed to sampling effort unless they moved into areas searched by field crews. In 2016, we did not survey Coronation Gulf and Queen Maud Gulf areas because we observed very low bear activity and presence during our previous survey flights, and hunters confirmed that bears are rarely seen in those areas.

We obtained small tissue samples (< 5 mm diameter) of individual bears in this study via a remote biopsy dart (Pneudart Type C - Polar Bear, Williamsport, Pennsylvania) fired from a dart gun (Capchur Model 196) approximately 3–7 m above the ground and targeted at the rump (Pagano et al., 2014; SWG, 2016). All bears except cubs-of-the-year (C0s) were sampled. Cubs-of-the-year are still small and easily separated from their mothers in spring (Atkinson and Ramsay, 1995; Robbins et al., 2012) and therefore were not darted to avoid possible injury or separation from their mother. Field information including field identification number, date, time, location of each observed bear (or group of bears), body condition based on visual assessment using a standardized fat index from 1–5 with 1 being skinny, 3 average, and 5 obese (Stirling et al., 2008), specific markings or characteristics, group or litter size, the estimated field age class (e.g., C0, yearling (C1), 2 yr. old, subadult [approx. 2–4 yr.], adult [approx. ≥ 5 yr.]), and estimated field sex were recorded. Field age class and sex were both recorded with a confidence qualifier (e.g., high and low confidence). Dependent offspring were distinguished as C0s, C1s, and 2-yr.-olds based on their size relative to their mother. Cues such as body size of the individual bear in relation to its surrounding or group members, body shape and proportions, presence of scars, secondary sexual characteristics, observation of urination, and gait were all used to determine field sex and age class (SWG, 2016; Laidre et al., 2020a, b). When field age class and sex of a bear were initially assessed with low confidence, additional field notes were taken. For example, notes may suggest an alternative field age class and sex if observers were unsure, particularly for difficult to discern solitary young subadult male bears and younger adult females. These field observations together with genetic microsatellite results allowed us to confirm field-estimated sex and age class.

### *Sampling – Preparations and Analysis*

To detect the harvest recovery of previously marked bears (e.g., the initial mark-recapture study from 1998 to 2000 or from biopsy-darting in 2014–16), small muscle tissue samples were submitted by hunters for all bears harvested in MC and surrounding subpopulations such as GB, Lancaster Sound (LS), and Viscount Melville Sound (VM) through the Nunavut polar bear harvest-monitoring program.

To identify live-recaptured bears initially marked during the 1998–2000 population study, we examined individuals from the 1998–2000 population inventory, removed bears that we knew were dead (e.g., through a recovered ear tag or lip tattoo by harvest), and selected the remaining individuals that could be still alive in 2014 (e.g., ≤ 34 yr. of age) for genetic analyses.

Briefly, a lentil-size piece of skin (~1–1.5 mm thick) or tissue was obtained from either the biopsy sample, the ear plug (e.g., a small tissue core that is obtained when applying ear tags), or the muscle tissue using a scalpel blade, transferred onto a shipping card (Avery, 70 × 35 mm), and attached with Scotch tape. Each sample card was labelled with a unique identification number, placed into a coin envelope (57 × 89 mm), and left to dry at room temperature for up to three days. Individual genotyping and sex determination of each dried specimen was done by Wildlife Genetics International Inc. (Nelson, British Columbia). The tissue samples were genotyped at eight previously published dinucleotide microsatellite loci (REN145P07, CXX20, MU50, G10B, G10P, G10X, MU59, G10H; Paetkau and Strobeck, 1994; Paetkau et al., 1995, 1998; Breen et al., 2001) and analysis of individual identity followed a three-phase protocol previously validated for bears and described elsewhere (Paetkau, 2003; Kendall et al., 2009). Once the genotyping and error-checking were complete, we defined an individual for each unique eight-locus genotype.

### *Abundance*

We estimated abundance using a closed population mark-recapture model (Otis et al., 1978) in a Bayesian framework (Kéry and Schaub, 2011) for independent animals (> 2 yr. old) encountered during two primary sampling periods that occurred during the spring field seasons for the years 1998 – 2000 (early sampling period) and 2014 – 16 (late sampling period). We used annual time-steps referenced to the springtime field seasons, resulting in three capture occasions within the early (1998, 1999, 2000) and late period (2014, 2015, 2016). The model allowed for capture probability to vary by sex but was held constant across capture occasions within each primary sampling period. We fit separate models for the early and late sampling periods. Abundance estimates for the two sampling periods were derived separately without any shared parameters. Furthermore, we split each abundance estimate by sex to obtain separate estimates of capture probability and abundance by sex. We made no assumptions about the change in population between the periods nor did we assume equal capture probability. We fit a total of four separate closed population models, one for each sex and time period.

The model assumed that the MC subpopulation was a geographically and demographically closed population within each three-year period of sampling. Therefore, the model assumes there is no movement in or out of the study area and no birth or death. Polar bear survival is generally higher for adults (Amstrup and Durner, 1995), which should reduce bias associated with violation of the demographic closure assumption. However, lower survival rates for younger polar bears (Regehr et al., 2010) and recruitment of juvenile animals into the study population could be expected to cause positive bias in estimates of abundance (Pollock et al., 1990). Furthermore, potential violations of the geographic closure assumption due to movement of animals in and out of the study area mean that the estimate of abundance does not represent the number of animals within the study area at any given time, but rather represents the total number of bears available for capture across the three-year period (i.e., the “superpopulation”; Kendall et al., 1997).

Despite potential biases, we estimated abundance ($N$) using closed models because the data were sparse and insufficient to parameterize an open population model. Moreover, because the survey area changed annually with changing weather and effort, common estimators such as the Horvitz-Thompson for $N$ from each year’s sampling were not appropriate because the estimator’s results would conflate changing survey area with population size in unknown ways. We chose to estimate abundance using data from the two primary sampling periods rather than from all data from 1998 to 2016 because the 13-year gap between the 1998 – 2000 and 2014 – 16 surveys will overstate permanent emigration causing survival ($\phi$) to go down and capture probability ($p$) to go up. Therefore, the population size will be underestimated because the estimate of $p$ will be too high. While not ideal, using the closed models provides the best estimate with the available data.

To fit the closed population capture-recapture models, we performed Markov chain Monte Carlo (MCMC) analysis using JAGS (Plummer, 2003) through the R package R2jags. Each model was run for 20,000 iterations with the initial 2000 discarded for burn-in. We used diffuse normal prior distributions on a logit link for all parameters (Kéry and Schaub, 2011). We checked for model convergence using  statistics and by examining MCMC chain plots (Gelman et al., 2013).

### *Survival*

We estimated annual, apparent survival for independent bears over 2 yr. old using all encounters from 1998 to 2016 by grouping our data into the two primary sampling periods (1998 – 2000 and 2014 – 16) and using available dead recoveries from 1998 to 2016. Data were sparse with respect to live recaptures and dead recoveries and there was a 13-year gap (i.e., 2001 – 13) in sampling between the capture-mark-recapture studies. The gap period was characterized by a very low harvest rate resulting in minimal dead-recovery opportunities (e.g., three bears per year as harvest). Additionally, $p$ is essentially equal to zero because the closed population model does not allow any recaptures during the gap period between sampling efforts. Because we did not have radiotelemetry data, and very few or no data on recoveries of previously marked animals, we could not estimate fidelity ($F$; the probability that an animal does not permanently emigrate from the sampling area and remains available for live observation in the future) to our study area. Therefore, estimates are not true survival but rather apparent survival, which is the probability of a bear remaining alive and available for capture, given that it was alive at the previous sampling time. Bears that permanently leave the study area and remain alive but are unavailable for recapture cannot be separated from mortality when estimating apparent survival. Therefore, apparent survival will be lower than true survival due to likely emigration.

We used a Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) and considered apparent survival ($\phi$) varying by sex (i.e., male or female) or remaining constant, and capture probability ($p$) varying by sex, study period (i.e., early versus late period), or remaining constant. The commonly used Burnham model was not applicable for estimating MC survival rates because the harvest rate changed, yet we had insufficient data to estimate multiple recovery probabilities. Consequently, the survival from the Burnham model would be unreliable and would reduce to a CJS model in the absence of additional data. We fit six models representing all combinations of $\phi$ and $p$ in Program Mark (White and Burnham, 1999) through the Rmark package in R (Laake, 2013; R Core Team, 2019). We used AIC to rank models with the lowest AIC value suggesting the strongest support (Burnham and Anderson, 2002). All models differed by a single, nested parameter, therefore we evaluated whether that parameter resulted in a model improvement based on ΔAIC and parameter estimates.

### *Reproduction*

We calculated reproductive indices for MC polar bears using data for the early and late sampling periods by using reproductive metrics that have been identified as important for monitoring (Vongraven et al., 2012). The annual observations of dependent young during the sampling periods were few and variable, which limited our ability to estimate many reproductive indices. We calculated the mean number of C0 and C1 per adult female (AF) by year and study period (± SE) using the observed sampling data. Adult females were a) bears identified genetically as females, and b) bears classified in the field in the age class "adult" with high confidence. We also calculated mean C0 and C1 litter size by study period, although the data were too sparse to evaluate patterns in litter size as function of biological, environmental and temporal factors.

### *Population Growth*

We estimated population growth rate in two ways to understand differences between observed changes in abundance and demographic rates. First, we estimated the empirical growth rate as the ratio of the late sampling period abundance over the early sampling period abundance separately for males and females. We then computed an average annual growth rate ($\lambda$) by taking the 17th root of the growth rate to account for the length of time between the two study periods. We estimated separate growth rates for males and females because the abundance estimates differed by sex. Second, we computed an asymptotic growth rate from a four-stage matrix model (C0, C1, 2 yr., 3+) based on the demographic rates estimated in this study (Mills, 2012). For rates that were not available from our study, we used values from Taylor et al. (2006). The population matrix was defined as:

$$L = \begin{bmatrix} 0.00 & 0.00 & 0.00 & 0.17 \\ 0.62 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.88 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.88 & 0.88 \end{bmatrix}$$

where C0 survival probability = 0.62 (Taylor et al., 2006), 2+ yr. old survival probability = 0.88 (present study), and recruitment = 0.39 C0 per AF (present study). The value of 0.17 in the upper right of the matrix is the product of AF survival (0.88), recruitment (0.39; see reproduction methods above), and sex ratio at birth (0.5). We solved for asymptotic growth rate by calculating the dominant eigenvalue of the matrix (L) assuming a stable stage distribution.

### *Body Condition*

We compiled body condition score (BCS) data for the early (1998–2000) and late (2014–16) sampling periods. Bears were classified with a BCS, and their sex, age, and reproductive classes were assigned as described in the sample collection section above. Observers who participated during biopsy sampling had either participated in both study periods or were experienced in polar bear observations through other studies.

The BCS raw values were binned into three classes: "poor" (corresponding to a 1–2 classification on the 5-point scale) (Stirling et al., 2008), "average" (3), and "good" (4–5) to facilitate comparison between previous studies (Laidre et al., 2020a, b). We did not include dependent offspring in analyses because their body condition is dependent on maternal condition (Laidre et al., 2020a), and we excluded within-year observations of the same individual.

We modeled BCS using ordinal logistic regression with package MASS (Ripley et al., 2021). To evaluate if differences between sampling periods existed, we included the covariate period (early sampling period = 1998–2000 or late sampling period = 2014–16) and reproductive status, age, and sex were combined into a four-level categorical variable, *reproclass* (ADM = adult male, ADFI = independent adult female, ADFWO = adult female with offspring, and SUB = subadults of both genders). The day of the year the bear was sampled (*cap_day*) was included as a continuous covariate to reflect the amount of time a bear spent on their preferred sea ice hunting platform before being sampled in year *t*. The sampling season (April–June) in this study also coincided with the annual seal-pupping period, which is known to be a prime feeding period for bears (Pilfold et al., 2012; Reimer et al., 2019). Thus, we predicted that increased time on the ice prior to sampling would be associated with higher BCS. Given previous studies suggesting decreased body condition with increased ice-free days and lower sea ice concentrations (Rode et al., 2012; Laidre et al., 2020a), we included a covariate ($icetm_{t-1}$), which represents the number of days between the summer sea ice retreat and fall sea ice advance in sampling year $t - 1$ for MC per Stern and Laidre (2016; updated unpubl. data through 2016 provided by Environment and Climate Change Canada). Briefly, sea ice retreat and advance in MC were defined as the point at which the sea ice concentration for a given year fell below the halfway point between the averaged 1979 and 2016 March sea ice concentration (representative of annual sea ice maximum) or exceeded the average September sea ice concentration (annual minimum). For MC, that transition threshold sea ice concentration was 59%. Using the covariates described above, we generated a global model and performed ordinal regression-specific goodness-of-fit tests (Hosmer-Lemeshow test $p > 0.1$; Pulkstenis-Robinson test $p > 0.1$; Fagerland and Hosmer, 2017) on our global model to ensure our initial model adequately fit our data. Then, using package MuMIn in R, we performed model selection to obtain the most supported models based on ΔAICc < 4 (Barton, 2009). Coefficients from the most supported models were averaged and used to calculate predicted probabilities across the covariates and BCS levels using package MuMIn (Table 1).

## RESULTS

### *General Overview*

We conducted fieldwork between 20 April and 18 June of 2014–16, where we flew 72.5–97.5 hours each year searching for polar bears, with an average distance flown per year of 12,300 km (range 10,100–12,600 km; Fig. 2). The highest bear encounter rate occurred during 2014, though polar bears were not distributed evenly across the study area (Table 2, Fig. 2). Most bears across all study periods were encountered from Franklin Strait southward to Victoria Strait and Jenny Lind Island (Fig. 2). We observed very few tracks and only one bear during the reconnaissance flight into M’Clintock Channel proper in 2016, which did not suggest high bear density at that time. However, it remains uncertain if sea ice is used by bears with higher intensity north of Gateshead Island during early spring at times when we were not present.

### *Samples Examined*

We analyzed a total of 953 (319 biopsies, 102 samples from early sampling period, and 532 harvest) tissue samples collected from 1998 to 2016 for genetic identification. We identified 244 individual bears through the biopsy sampling activities 2014–16. All 102 tissue samples from physical captures during the early study period (1998–2000) were successfully analyzed and, of the 532 harvest samples, 99% produced reliable genetic results. Overall, the success rate of extracting DNA material from all study samples (research and harvest) was 97.8%.

TABLE 1. Model-averaged coefficient estimates for ordinal logistic regression model of body condition for the M’Clintock Channel polar bear subpopulation. See Methods for parameter descriptions.

| Parameter | Coefficient | SE | $p$ |
|---|---|---|---|
| periodEarly | 0.75 | 0.98 | 0.45 |
| reproclassADFWO | −0.41 | 0.25 | 0.11 |
| reproclassADM | −0.38 | 0.21 | 0.07 |
| reproclassSUB | −0.35 | 0.27 | 0.19 |
| cap_day | 0.01 | 0.004 | < 0.01 |
| $icetm_{t-1}$ | −0.007 | 0.005 | 0.10 |
| periodearly: $icetm_{t-1}$ | −0.01 | 0.009 | 0.10 |
| periodearly:reproclassADFWO | −0.51 | 0.45 | 0.26 |
| periodearly:reproclassADM | 1.12 | 0.51 | 0.03 |
| periodearly:reproclassSUB | 0.10 | 0.42 | 0.78 |

TABLE 2. Overview of encountered polar bears during the 2014–16 polar bear study in M’Clintock Channel, Nunavut (Note: listed bears include biopsied and non-biopsied individuals).

| | Field season | | |
|---|---|---|---|
| Sex/age group | 2014 | 2015 | 2016 |
| Adult female | 42 | 35 | 36 |
| Subadult female | 6 | 4 | 8 |
| Adult male | 63 | 29 | 31 |
| Subadult male | 13 | 11 | 6 |
| Cubs-of-the-year | 16 | 23 | 9 |
| Yearlings | 6 | 12 | 11 |
| Unknown | 2 | 1 | 2 |
| Total | 148 | 115 | 103 |

Dead recoveries of marked bears through the harvest resulted in 22 bears being identified, seven of these were recovered in subpopulations outside MC (32% of total recoveries; four in LS, one in northern Beaufort Sea, one in Foxe Basin, and one in Viscount Melville Sound). No harvest recoveries were identified in the neighboring GB subpopulation area though as a note of interest, seven bears that were originally marked in MC from 2014 to 2016 were resampled in GB during that population inventory study conducted between 2015 and 2017 (Dyck et al., 2020). We resampled six bears initially marked in MC 1998–2000 and 33 bears initially marked in 2014–15 during our MC 2014–16 study.

### *Population Demographic Information*

**Abundance**: Estimated total (males and females combined) abundance was 325 (95% Credible Interval (CRI) = 220–484) for 1998–2000, and 716 (95% CRI = 545–955) for 2014–16. The CRIs around the total abundance did not overlap between the two study periods, providing substantial evidence for an increase. Estimated recapture probability was 0.13 in both sampling periods with higher precision in the later period (95% CRI = 0.03–0.19 [early], 95% CRI = 0.10–0.18 [late]).

We estimated sex-specific abundance to obtain additional insight into population dynamics. Between the two study periods, the female segment of the MC

TABLE 3. Model selection results for Cormack-Jolly-Seber models of polar bear capture-recapture data from 1998 to 2016 used to estimate apparent survival of independent bears older than 2 yr. *K* is the number of parameters in the model. For descriptions of parameters see Method section.

| Model | *K* | AICc | ΔAICc | Weight | Deviance |
|---|---|---|---|---|---|
| Phi(constant) p(constant) | 2 | 425.53 | 0.00 | 0.28 | 26.46 |
| Phi(sex)p(constant) | 3 | 426.22 | 0.69 | 0.19 | 420.15 |
| Phi(constant)p(period) | 3 | 426.40 | 0.87 | 0.18 | 25.30 |
| Phi(sex)p(period) | 4 | 427.02 | 1.49 | 0.13 | 418.90 |
| Phi(sex)p(sex) | 4 | 427.25 | 1.72 | 0.12 | 419.13 |
| Phi(constant)p(sex) | 3 | 427.46 | 1.94 | 0.10 | 421.39 |

subpopulation increased from 219 (95% CRI = 124–405) to 327 bears (95% CRI = 230–487). The males showed a larger increase from 134 (95% CRI = 74–256) to 360 bears (95% CRI = 244–550).

**Survival**: We estimated apparent survival for independent bears aged two and older from 1998 to 2016. The best-supported model included constant survival and detection probabilities across time and sex (Table 3). All other models showed no support given that the AIC values increased when a single parameter was added. Apparent survival from the top model was 0.88 (SE = 0.02) and detection probability was 0.17 (SE = 0.02). Following internal best practices for animal care, C0s were not biopsy-sampled; thus, their survival was not possible to estimate.

**Reproduction and Recruitment**: During the 1998–2000 mark-recapture study, 23 family groups, representing a total of 38 (19 C0 and 19 C1) dependent offspring were encountered. During the 2014–16 genetic biopsy sampling study, we sampled 45 family groups representing a total of 75 (46 C0 and 29 C1) dependent offspring (Table 4). For the 1998–2000 period, C0 and C1 mean litter sizes were 1.62 (SE = 0.14) and 1.71 (SE = 0.14), respectively. For 2014–16, mean C0 and C1 litter sizes were 1.76 (SE = 0.09) and 1.59 (SE = 0.11), respectively. For 1998–2000, mean C0 and C1 per AF were 0.38 (SE = 0.02) and 0.39 (SE = 0.10), respectively (Table 4). The mean C0 and C1 per AF for 2014–16 were 0.43 (SE = 0.10) and 0.27(SE = 0.06), respectively. The overall mean C0 recruitment was 0.39 (SE = 0.11).

**Population Growth**: Based on the estimated increases for the female and male proportions of the subpopulation between the two time periods, the average annual growth rate (λ) was 1.025 for females and 1.064 for males. The four-stage matrix population model results suggest a declining population λ = 0.97 using our calculated recruitment value of 0.39 for C0 per AF, an apparent survival rate of bears 2 yr. or older of 0.88, and C0 survival of 0.62. These results represent a discrepancy between observed demographic rates and our calculated abundance. To explore this discrepancy, we calculated what level of adult survival would be needed to achieve the estimate of female λ = 1.02 based on changes in abundance across study periods. The new adult survival probability of 0.93 provides a population growth of λ = 1.02. That survival value is consistent with survival in the absence of harvest from Taylor et al. (2006). Flat population growth λ = 1.0 occurs when survival is 0.91.

TABLE 4. Mean numbers of cubs-of-the-year (C0) and yearlings (C1) per adult female and litter size for the M'Clintock Channel polar bear subpopulation, 1998–2000 and 2014–16.

| | Offspring per adult female | | Litter size[1] | | | |
|---|---|---|---|---|---|---|
| Year | C0 | C1 | C0 | n | C1 | n |
| 1998 | 0.40 | 0.25 | 2.00 | 4 | 1.67 | 3 |
| 1999 | 0.40 | 0.33 | 1.20 | 5 | 1.67 | 3 |
| 2000 | 0.33 | 0.60 | 1.67 | 3 | 1.80 | 5 |
| 2014 | 0.41 | 0.15 | 2.00 | 8 | 1.50 | 4 |
| 2015 | 0.61 | 0.35 | 1.50 | 14 | 1.71 | 7 |
| 2016 | 0.26 | 0.32 | 1.80 | 5 | 1.57 | 7 |

[1] Litter sizes of 0 (whole litter loss) are not listed; all litters depend on at least one offspring being present.

**Body Condition**: We analyzed a total of 380 BCSs from the two study periods and the most supported model included *period*, *reproclass*, *cap_day*, and $icetm_{t-1}$ and interactions *period:reproclass* and *period:*$icetm_{t-1}$ (Table 1). The mean predicted probability (P) of being in poor body condition decreased for all reproductive classes from the early to the late sampling period ($P_{\text{Poor early period adult females and subadults}} = 0.50$ vs $P_{\text{Poor late period adult females and subadults}} = 0.14$), except for adult males ($P_{\text{Poor early period adult males}} = 0.15$ vs $P_{\text{Poor late period adult males}} = 0.17$; Fig. 3). Sampling later in the year was associated with better body condition (Fig. 4).

## DISCUSSION

### General

This study provides empirical evidence of the ongoing recovery of an overharvested polar bear subpopulation with estimates of demographic parameters including abundance, survival, population growth, reproductive indices, and body condition. Using data from surveys conducted in the MC polar bear subpopulation area between 1998–2000 and 2014–16, along with dead recoveries of harvested bears from 1998 to 2016, these results represent the second scientific inventory of the MC subpopulation to allow comparisons of population trend. We conducted our study similarly to the 1998–2000 survey and applied consistent analytical methods to both study sampling periods. Our results indicate the MC subpopulation experienced a

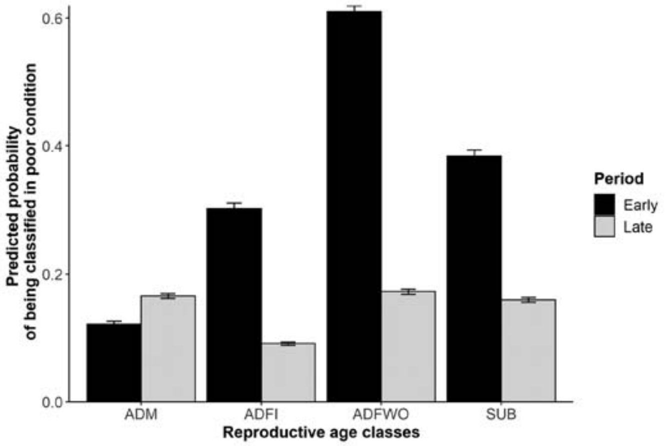

FIG. 3. Predicted probabilities of bears being classified in poor body condition in the early (1998–2000) and late (2014–16) sampling periods (ADFI = adult, independent female, ADFWO = adult female with offspring, ADM= adult male, SUB = subadults of both sexes).

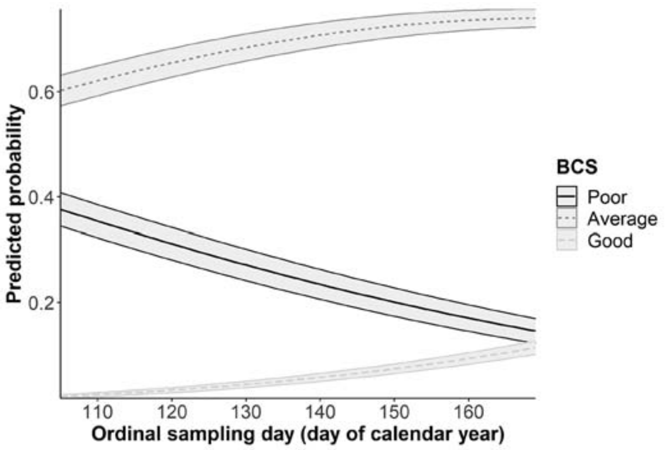

FIG. 4. Predicted probabilities of a bear being in poor, average, or good body condition when sampled at different days of the year.

significant increase in abundance over time. The MC subpopulation also serves as an example in which the initial abundance estimates from the 1970s were scientifically unsound, and management, based on inaccurate estimates and unsupported ideas, led to overharvest (Taylor et al., 2006). The overharvest became clear in the 1990s when TEK indicated that bears were scarce. In response, a short moratorium (two years), followed by reduced harvest for approximately 13 years, was implemented. The cessation of an unsustainable harvest coupled with improved habitat productivity appears to have supported recovery.

Climate-induced sea ice loss is considered the principal threat to the persistence of polar bears (Regehr et al., 2016). However, unlike several polar bear subpopulations that are showing negative impacts from climate change (Regehr et al., 2007, 2010; Bromaghin et al., 2015; Lunn et al., 2016; Obbard et al., 2016, 2018), sea ice change in the MC region may have benefited polar bears. The region has shifted from primarily multiyear ice to one dominated by annual ice and reduced summer ice coverage (Rothrock et al., 1999; Stern and Laidre, 2016). Annual ice is relatively thin, susceptible to mechanical wind forcing and fracturing, and vulnerable to complete melting in the summer (Perovich et al., 2019; Richter-Menge et al., 2018). These changes may have increased Arctic marine productivity (Derocher et al., 2004; Häder et al., 2014; Frey et al., 2019) and the availability of seals, all of which may have played a role in population growth and improvement in body condition of MC polar bears between 1998–2000 and 2014–16. Similar observations were reported for polar bears that inhabit the Kane Basin, an area in the Canadian Arctic that also went through significant sea ice transitions during the past decades (Stern and Laidre, 2016; Laidre et al., 2020b). However, projected reductions in MC sea ice through the 21st century (Sou and Flato, 2009; Hamilton et al., 2014) suggest this region too may eventually cross a threshold such that reduced time to hunt seals will bring negative impacts similar to other polar bear subpopulations (Bromaghin et al., 2015; Lunn et al., 2016).

### *Abundance*

Polar bear abundance increased across the two study sampling periods with the male segment of the population increasing more rapidly than females. This difference may reflect recovery of the male segment after depletion due to general harvest overexploitation, which, when coupled with a sex-selective harvest (two males for each female in Nunavut) could have been further exacerbated (Taylor et al., 2005, 2006, 2008b). Male abundance was almost half of female abundance in the early period but grew to be equal to or slightly larger than female abundance during the late sampling period. Increases in male abundance over females reflect a higher growth rate for males during the study sampling period, potentially from reductions in harvest pressure or immigration of males into MC from other subpopulation units.

We estimated abundance of MC polar bears using closed population mark-recapture models. However, our sampling occurred across three-year periods, which means that the assumptions of demographic and geographic closure are almost certainly violated. The limited numbers of bears detected and the sparse recaptures within a year precluded fitting models that can potentially reduce bias in parameter estimates, such as the “robust design” or “spatially-explicit” capture-recapture models (Pollock, 1982; Efford and Fewster, 2013). Moreover, open population models that include an abundance estimate (e.g., forms of the Jolly-Seber model) require more years of data with more recaptures than our data had. Evidence from TEK (or Inuit *Qaujimajatuqangit*) and the few harvest-recovered marked bears indicates that the population is not in fact closed to emigration, but limitations with available data prevented more complex models being used, despite the potential advantages of these models in estimating demographic parameters of interest and reducing bias.

The consequences of assumptions violations in closed population models are well known (Otis et al., 1978; Kendall, 1999) and affect both the actual abundance and what that abundance geographically represents. A lack of demographic closure results in underestimated detection probability (for example, bears that die are no longer available for detection). The underestimated detection probability leads to an overestimated abundance for any given year. Despite these caveats, the total number of bears in the study area available for detection across the three years of our study appeared to have been unbiased (i.e., a similar number of bears frequented the study area while the study was conducted), and our estimated abundance of 325 bears for MC using a closed population model for the early period was similar to Taylor et al. (2006; 284 bears). A lack of geographic closure blurs the boundaries of the study area, causing our estimate to reflect the "superpopulation." A superpopulation is defined as all the animals with a chance (non-negligible probability) of occurring within a study area, regardless of where the animals were located at any given sampling occasion (Schwarz and Arnason, 1996). Thus, estimates of superpopulation size in year *t* likely reflect some animals that were temporary emigrants in year *t*. We were not able to estimate temporary emigration directly from the sampling area (Cooch and White, 2019) because our sample sizes were not sufficiently large to do so and there are no recent radiotelemetry data to provide location and movement data.

Lastly, the small proportion of the area that we were not able to survey—namely, the portions of M'Clintock Channel proper—contributes to the uncertainty surrounding our abundance estimate. Although we did not detect many signs of bear activity while conducting our reconnaissance flight, it is unknown how many bears (e.g., resident MC bears or bears that may temporarily move into this area from the neighboring LS subpopulation) may utilize this section of the study area throughout the timing of our surveys since we were able to conduct only one limited survey flight. Because we have no information on how many bears could have been in this area, we are unable to determine whether our abundance estimate would be affected negatively or positively and to what extent there may be bias. Taken together with the effects of demographic and geographic closure violation, the estimate of abundance is almost certainly larger than the actual number of animals within the MC subpopulation boundary at any given time. This should be taken into consideration when using these findings to inform management decisions, particularly for setting allowable harvest limits.

What is noticeable considering the areas searched during both sampling periods, is the difference in distribution of bears between the early versus the late sampling period (Figs. 1 and 2). Whereas bears were encountered mostly in northern Franklin Strait and M'Clintock Channel proper during the early study, they were observed from northern Franklin Strait through Larsen Sound and south as far as Jenny Lind Island, during 2014–16. Although we had no search tracks from the early study available for comparison, we have no reason to believe that our search efforts and activities differed significantly between the two study sampling periods in those areas searched during both studies. This apparent distributional shift on the sea ice is likely caused by the reduced presence of multiyear ice and the greater occurrence of thinner annual ice in these areas as compared to previous decades (Howell et al., 2016), which creates better seal habitat, hence providing better seal hunting opportunities for bears in this area (Smith, 1980; Ferguson et al., 2000).

### *Survival*

Our estimate of apparent survival (0.88) of polar bears from 1998 to 2016 is lower than biological survival estimated from other studies (Taylor et al., 2006). This is likely due to a combination of factors such as emigration away from the study area, which will cause apparent survival to be lower than biological survival (Lebreton et al., 1992), and unmodeled heterogeneity in recapture probability which is a well-known source of bias in estimates of survival (Devineau et al., 2006). Survival differs among sex and age classes; however, none of the models including differences in survival by sex were supported by our data. In addition, we were not able to test for differences in survival by age class. It is very likely that by pooling sexes and age classes the overall mean natural survival rate was also biased low (SWG, 2016). In MC, capture-recapture data were collected intensively for three years in two distinct sampling periods separated by 13 years. Therefore, few observations of bears exist between 2001 and 2013. The missing sampling years greatly reduce the power to estimate survival or estimate variation in survival across time, sex, or age classes. Unfortunately, with live capture-recapture data, limited harvest data, and no contemporary information on animal movements, few options exist to estimate biological survival. Our data were too sparse for joint live/dead models, and capture probability was too low for known fate models. These challenges were also recognized by Taylor et al. (2006) and are critical for managers to consider when creating monitoring plans.

### *Reproduction*

Our field observations of C0 and C1 litter sizes reveal interannual variation, with mean values similar to other subpopulations within the Canadian Arctic Archipelago (Table 4; Taylor et al., 2008a; SWG, 2016; Dyck et al., 2020), although our sample sizes were small. Our estimated reproduction rates based on counts of C0 and C1 observed with adult females are very similar across our study sampling periods and are within the ranges estimated by Taylor et al. (2006). Estimating the number of C1 per AF is considered a key reproductive parameter (Vongraven et al., 2012; Regehr et al., 2015) because it integrates cub production and cub survival. The C1 per AF in our sampling period of 0.27 is lower than during the earlier period (0.39), but drawing definite conclusions about whether reproductive parameters differ between the two studied periods is not recommended because of limited data. Nevertheless, our observed number of C1 per AF appears to be sufficient to maintain a viable subpopulation, provided that survival is within the normal range for healthy subpopulations (Regehr et al., 2015).

### *Population Growth*

We estimated population growth rate both empirically based on changes in abundance and using a matrix population model to compare observed changes in abundance to theoretical population growth rates arising from the vital rates. To estimate an asymptotic population growth rate based on the vital rates, we used a simplified matrix projection model. Although such a simplified model doesn’t fully reflect the multiyear reproductive cycle of polar bears and would not be suitable for stochastic projections (Taylor et al., 1987; Regehr et al., 2017), we believe it was sufficient for a general assessment of consistency between empirical and matrix-based estimates of population growth rate. The changes in abundance suggest that growth was approximately 2.5% per year for females and 6.4% per year for males for the period 1998–2016. Conversely, the estimated vital rates suggest a population growth rate of −3% per year (i.e., that a subpopulation with these vital rates would decline by 3% per year). Therefore, the demographic rates and abundance estimates are not internally consistent. The most likely explanation is negative bias in the estimate of true survival for adult females. If we replace estimated survival from Taylor et al. (2006), the model shows growth similar to our observed female population growth. The higher growth rate for males, combined with the low number of recaptures in the study area, suggests an unknown rate of male immigration from surrounding subpopulations.

The discrepancies in abundance and survival provide insight into the utility of each data type. Abundance data appear to be providing stronger inference into population dynamics of this polar bear population. The survival information contains too much bias relative to biological survival to be meaningful for polar bear management. If capture-recapture data were collected over a longer time period, then survival may become a more useful parameter. Other data-based and simulation studies for polar bears have documented that, although mean percent relative bias can be higher for estimates of abundance than survival, the resulting challenges to demographic inference are actually larger for bias in adult female survival because it is a primary driver of population growth for long-lived species like polar bears (Eberhardt, 1990).

Similar to estimates of abundance and survival, potentially high and variable levels of immigration and emigration across subpopulation boundaries can directly affect estimation and interpretation of population growth rate (Peñaloza et al., 2014). In some other subpopulation studies, radiotelemetry data have been critical to resolving these issues (Regehr et al., 2018). For regions where radiotelemetry is not available, performing a meta-analysis using updated capture-recapture and available harvest recovery data for all subpopulations within the region that are known to exhibit substantial levels of exchange (e.g., GB, MC, and LS) could help to reconcile these interpretation challenges and provide more accurate information to management decision makers.

### *Body Condition*

Polar bears observed during the recent study sampling period were in better body condition compared to 1998–2000, with the exception of adult males that remained in similar condition. This finding is not unexpected given that April–June represents the time males are searching for mates and breeding rather than only feeding (Stirling et al., 2016). For the other age and sex classes, rapid changes in sea ice characteristics in the last 15 years, from multiyear to more annual ice, may have provided improved seal habitat and contributed to an increase in the polar bear prey base. Polar bears occupying the Kane Basin subpopulation area appear to be experiencing similar improvements in body condition related to changing sea ice conditions (Laidre et al., 2020b). Our study occurred during the prime feeding period and annual seal-pupping period that occurs in mid-April–May. To our knowledge, there are no quantitative data about seal abundance from our study area available; however, our observations indicate ringed and bearded seals appear relatively abundant and demonstrate a preference for annual sea ice (Government of Nunavut, unpubl. data reports). The seal abundance and ice use potentially account for our finding that bears were more likely to be in better body condition when sampled later in the year (Stirling and Archibald, 1977; Pilfold et al., 2014; Reimer et al., 2019).

It is less likely that sampling method is responsible for changes in the observed BCS between time periods. First, in studies in which body condition was evaluated over time with earlier study period classification done by physical handling and later study period BCS classifications done via aerial observations, results have varied. This variation suggests there is not an inherent bias in aerial observation versus physical handling to classify body condition classification (Kane Basin: increase in BCS (Laidre et al., 2020b); Baffin Bay: decrease in BCS (SWG, 2016; Laidre et al., 2020a); Gulf of Boothia: increase in BCS; Dyck et al., 2020). Further, both MC sampling studies (i.e., early versus late) were conducted during similar times of the year and many of the same observers and biologists that participated in the early physical capture and handling study also participated in the aerial observation study, supporting reliability and consistency.

## CONCLUSION

These results provide direct feedback into an adaptive management framework with empirical estimates that confirm ongoing recovery of the MC polar bear subpopulation. Our study suggests that MC abundance increased since 2000, although with significant caveats and high uncertainty (e.g., biased survival rates, unknown emigration). Of particular importance to users setting harvest limits is the fact that the abundance estimate is almost certainly larger than the actual number of animals within the MC subpopulation boundary at any given time because of both data limitations and the nature of the MC subpopulation itself. Managers should consider factors such as density, area, and harvest levels. Bears in MC are sparsely distributed (low density) over a relatively large geographic area, directly affecting the ability to obtain accurate and reliable data for population monitoring. These factors require adaptive harvest, research, and management considerations. Shortening the research monitoring interval to under 15 years or introducing intermittent animal-marking sessions halfway between monitoring intervals would reduce some of the bias we encountered in estimating population parameters like survival and abundance. Resolving issues stemming from unknown movement in or out of MC is also critical for alleviating bias and improving accuracy of demographic parameters. A robust monitoring plan, as outlined above, improves understanding of the concurrent effects of management interventions and environmental change.

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