



January 31, 2025

Nunavut Wildlife Management Board  
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IQALUIT, NUNAVUT X0A 3H0  
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Dear Chairman Shewchuk and Board Members:

**RM001-2025 – TAB3 KRWB Harvest Accumulation and Credits**

The Government of the Northwest Territories (GNWT) recently became aware of the above-referenced agenda item that potentially affects polar bear management and harvesting in the Northwest Territories (NWT). The Kitikmeot Regional Wildlife Board (KRWB) has requested a decision from the Nunavut Wildlife Management Board (NWMB) regarding issuance of credits accumulated for the Viscount-Melville Sound (VM) polar bear subpopulation, which has a Total Allowable Harvest (TAH) that is shared with Inuvialuit harvesters in the NWT. Although the Harvest Accumulation and Credit Calculation System exists in Nunavut (NU), no equivalent system exists in the NWT for accumulations of unused polar bear tags year over year.

The current TAH for the VM subpopulation is 7, which is divided between the NWT and NU (4 and 3, respectively). As noted in the KRWB's submission, a new estimate for the VM subpopulation has recently been published (Regehr et al. 2024) and we have encouraged the Inuvialuit Game Council to reach out to their colleagues in NU to discuss recommendations for any changes to the TAH, and any additional management actions for the VM subpopulation, under the terms of the *Polar Bear Management Agreement for the North Beaufort Sea and Viscount Melville Sound Polar Bear Populations* (2006). According to this agreement, this user-to-user group is to meet annually to "review the best available information...and make recommendations for research and management." These recommendations would then feed into the respective co-management structures established under the *Nunavut Land Claims Agreement* and *Inuvialuit Final Agreement*. Unfortunately the Commissioners have not met since the publication of the new abundance estimate.

The GNWT has some concerns about the KRWB recommendation for issuance of 16 credits for the VM subpopulation. With the addition of 16 credit tags, the potential harvest from the VM subpopulation could be as high as 23 bears (4 NWT + 3 NU + 16 credits), which represents nearly 10% of the updated population estimate in Regehr et al. (2024) of 235 (Bayesian 95% CI 148-569).

.../2

Polar bears are not fast-reproducing animals, and the removal of a substantial portion of the breeding population (particularly females) can take years to recover from (Taylor et al. 2002) and can lead to changes in population composition and demographics (Regehr et al. 2024). Research has suggested that the VM subpopulation was previously overharvested at harvest levels of 8.2 bears annually (Regehr et al. 2024, Taylor et al., 2002), which reduced the subpopulation down to the numbers seen in the Taylor et al. (2002) estimate. This past overharvest resulted in a harvest moratorium in this subpopulation from 1995-1999. The VM polar bear subpopulation is a small population and has previously demonstrated sensitivity to overharvesting. Taylor et al. (2002) estimated the unharvested growth rate of this subpopulation at barely above replacement levels (1.059).

We would also note that KRWB's assertion that "Because communities have not harvested Viscount-Melville in recent years, it is likely the population has continued to increase" is unlikely to be accurate for the VM polar bear subpopulation. Evidence suggests that this subpopulation is near its environmental carrying capacity (Regehr et al. 2024), which is related to the availability of suitable habitat and food. Low levels of harvest in the area suggest that this subpopulation is not limited by human harvest. Taking a precautionary principle approach, we should not assume that this subpopulation has increased since the last assessment, unless there is evidence that has not been presented.

In light of the best available information for the VM subpopulation and given that the joint Commission for the Inuit and Inuvialuit have not had a chance to jointly review and discuss any changes to management in the VM area since the publication of Regehr et al. (2024), the GNWT feels it would be premature at this time to grant the KRWB's request for issuance of 16 polar bear credits. We acknowledge the desire to "promote harvesting opportunities and encourage harvesting and travel to Hadley Bay" for harvesters, but this needs to be balanced with the sustainability of polar bears in a relatively low productivity area like the VM.

Thank you for your consideration of our comments.

Sincerely,



Heather Sayine-Crawford  
Director, Wildlife Management  
Environment and Climate Change

## Enclosures

- Polar Bear Management Agreement for the North Beaufort Sea and Viscount-Melville Sound Polar Bear Populations between the Inuit of the Kitikmeot West Region in Nunavut and the Inuvialuit (2006).
- Regehr, E. V., Baryluk, S., Boulanger, J., Branigan, M., d'Eon-Eggertson, F., Pongracz, J., Thom, A., & Richardson, E. S. (2024). Modeling movements improves capture–recapture estimates for mobile species with sparse data: Polar bears (*Ursus maritimus*) in Viscount Melville sound. *Population Ecology*.
- Taylor, M. K., Laake, J., Cluff, H. D., Ramsay, M., & Messier, F. (2002). Managing the risk from hunting for the Viscount Melville Sound polar bear population. *Ursus*, 185–202.

**POLAR BEAR MANAGEMENT AGREEMENT**

**for the NORTH BEAUFORT SEA AND VISCOUNT-**

**MELVILLE SOUND POLAR BEAR POPULATIONS**

**between the Inuit of the Kitikmeot West Region in Nunavut  
and the Inuvialuit**

**Signed by the Kitikmeot Hunters and Trappers' Association**

**and**

**Inuvialuit Game Council**

The Parties to this agreement are the Inuvialuit and the Inuit of the Kitikmeot West Region in Nunavut:

*Noting* that both groups have traditionally harvested a portion of polar bears from the North Beaufort Sea and Viscount-Melville Sound polar bear populations;

*And Noting* that the continued hunting of polar bears is essential to maintain the dietary, cultural, and economic base of the groups;

*And Noting* that the maintenance of a sustained harvest for traditional users in perpetuity requires that the number of polar bears taken annually not exceed the productivity of the population;

*And Noting* that the US and Canadian management authorities have accepted the *Inuvialuit-Inupiat Polar Bear Management Agreement in the Southern Beaufort Sea* and it has proven to be an effective user-to-user agreement in the shared management of that polar bear population;

*And Noting* that nothing in this Agreement shall be read to abrogate the responsibilities of Federal or Territorial authorities under existing or future statutes;

*And Noting* that the Inuit of the Kitikmeot West Region in Nunavut and the Inuvialuit will have a long-term fundamental influence on the maintenance and use of this resource and that the efforts of other parties will also be required to ensure effective conservation;

*the Parties have agreed as follows:*

## ARTICLE I

(a) The species considered in this Agreement is the polar bear (*Ursus maritimus*).

(b) The area covered by this Agreement is the area within the boundaries of the North Beaufort Sea and Viscount-Melville Sound Polar Bear Populations as defined in the appropriate legislation.

(c) The people covered by this Agreement are the Inuit of the Kitikmeot West Region in Nunavut and the Inuvialuit.

(d) The settlements and their outpost camps whose hunting practices may be affected by this Agreement are Cambridge Bay, Kugluktuk, Sachs Harbour, Ulukhaktok, and Paulatuk.

(e) Sustainable yield means a harvest level which does not exceed net annual recruitment to the population and accounts for all human-caused forms of removal from the population, and which considers the status of the population, based on the best available scientific information and Traditional Knowledge/Inuit Qaujimajatuqangit.

(f) A Joint Commission with responsibility to implement this agreement will be formed and shall consist of three (3) representatives designated by each of the Inuvialuit Game Council and the Kitikmeot Hunters and Trappers Association. A Technical Advisory Committee with responsibility for ensuring the collection and evaluation of all relevant management data, including Traditional Knowledge/Inuit Qaujimajatuqangit, and making recommendations to the Joint Commission, shall be appointed by the Joint Commission.

## ARTICLE II

### Objectives:

- (a) To maintain the North Beaufort Sea and Viscount-Melville Sound polar bear populations at healthy viable levels in perpetuity.
- (b) To manage polar bears on a sustained yield basis in accordance with all the best information available.
- (c) To provide protection to female polar bears by encouraging that the female proportion of the harvest not exceed one third of the sustainable total.
- (d) To encourage the collection of adequate scientific, Traditional Knowledge/Inuit Qaujimagatuqangit, and technical information in a timely manner to facilitate management decisions.
- (e) To minimize detrimental effects of human activities on polar bears and their habitat.
- (f) To identify research priorities.
- (g) To allocate the total sustainable yield between the two jurisdictions.
- (h) To encourage the wise use of the polar bear populations and all polar bear products.
- (i) To facilitate the import into the USA of hides and other products from polar bears harvested in the Kitikmeot West Region in Nunavut and in the Inuvialuit Settlement Region.
- (j) To meet annually to review the best available information on the aforementioned polar bear populations, and make recommendations for research and management.
- (k) To review this Agreement every 5 years, or sooner if requested by either Party.

## ARTICLE III

### Collection of Data and Sharing of Information:

- (a) The following data will be recorded for each bear killed: sex, date, and location of the kill.
- (b) The following specimens shall be collected from each bear killed: the lower jaw or an undamaged post-canine tooth to be used for age-determination, ear tags, lip tattoos, radio collars if present, the baculum from each male, and other specimens as agreed to by the hunters of either jurisdiction for additional studies.
- (c) A summary of all harvest information and pertinent research plans or results from each jurisdiction shall be exchanged annually, normally at the annual meeting referred to in Article II (j).
- (d) The number of collars deployed for research purposes shall be limited to the minimum number necessary to reach management objectives.
- (e) There shall be notification and consultation prior to undertaking research.

## ARTICLE IV

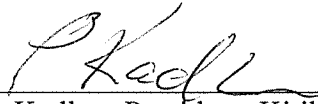
### Duration and Administration of Agreement:

- (a) This Agreement shall enter into force when it has been signed by the duly authorized representatives of each Party.
- (b) This Agreement shall remain in force unless either Party requests it be terminated.
- (c) Amendments to the Agreement may be proposed by either Party, then accepted or rejected by mutual agreement of the Parties. Formal written notification of any amendments to the Agreement approved and accepted by both Parties should be made to the Nunavut Wildlife Management Board, the Government of Nunavut Department of Environment, the Wildlife Management Advisory Council (NWT) and the GNWT Department of Environment and Natural Resources.

The signatories of this document have no authority to bind, and do not purport to bind, the respective regulatory authorities to any agreement which would otherwise be in violation of their management authority, but are acting solely as representatives of the local traditional user groups of the polar bear resource in furthering the goals of conservation, consultation, management, and information exchange.

SIGNED on this, the 4<sup>th</sup> day of February, 2006 in the city of Yellowknife.

On behalf of the Inuit of the Kitikmeot West Region in Nunavut:



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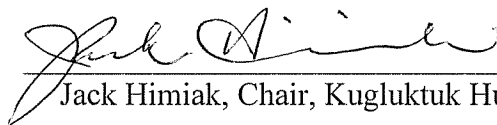
Philip Kadlun, President, Kitikmeot Hunters and Trappers' Association

Witnessed by:



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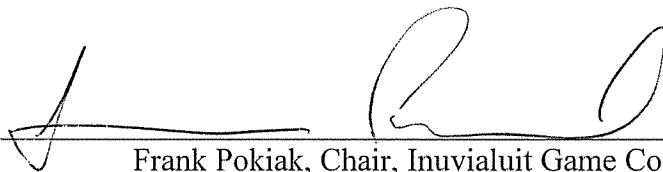
Attima Hadlari, Chair, Cambridge Bay Hunters and Trappers' Organization



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Jack Himiak, Chair, Kugluktuk Hunters and Trappers' Organization

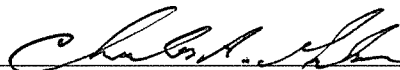
On behalf of the Inuvialuit:



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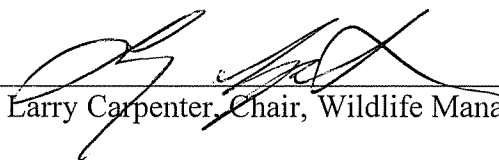
Frank Pokiak, Chair, Inuvialuit Game Council

Witnessed by:



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Charles A. Gruben, Member, Inuvialuit Game Council



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Larry Carpenter, Chair, Wildlife Management Advisory Council (NWT)

# Modeling movements improves capture–recapture estimates for mobile species with sparse data: Polar bears (*Ursus maritimus*) in Viscount Melville sound

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## Funding information

University of Washington; Environnement Canada; Polar Continental Shelf Program; Indigenous and Northern Affairs Canada; Wildlife Management Advisory Committee (NWT); Nunavut Wildlife Management Board; Government of the Northwest Territories; World Wildlife Fund; Indigenous and Northern Affairs Canada; Environment and Climate Change Canada

## Abstract

Wildlife management requires estimates of demographic parameters that are difficult to obtain for mobile species at low densities. Biased parameter estimates often result from capture–recapture (CR) studies due to small sample sizes and unequal recapture probabilities, the latter of which can be caused by animal movements with respect to the sampling area. We developed a multi-state CR model designed to minimize biases by including multiple data types (capture, harvest, natural mortality, and telemetry) and accounting for temporary emigration. We applied the model to data collected intensively from 2012 to 2014, and intermittently since the 1970s, for the Viscount Melville (VM) subpopulation of polar bears (*Ursus maritimus*) in the Canadian Arctic. The number of bears within the VM subpopulation boundary likely increased from an average of 145 (Bayesian 95% credible interval [CRI] [109, 221]) in 1989–1992 to 235 (95% CRI [148, 569]) in 2012–2014. Survival probability increased for all sex and age classes except adult females, for which estimates declined due to unknown reasons. Polar bear movements exhibited Markovian dependence with approximately 28% of the subpopulation located outside of the sampling area each spring. This contributed to inaccurate parameter estimates when using a simpler, single-state CR model that only included capture data. Although the interpretation of demographic status was complicated by statistical uncertainty and changes in study design, our findings suggest that—as of 2014—the VM polar bear subpopulation had likely recovered from an earlier period of overharvest, was stable, and had not exhibited detectable negative effects of climate warming.

## KEYWORDS

capture–recapture, polar bear, radiotelemetry, temporary emigration, wildlife management

Marsha Branigan: Retired.

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## 1 | INTRODUCTION

Periodic estimates of vital rates (e.g., reproduction and survival) and population abundance are needed for the management and conservation of wildlife (Runge, 2011). This is especially important for adaptive or state-dependent management (e.g., adjusting harvest levels in response to changing abundance) of species exhibiting spatial and temporal variation in population status due to climate warming (e.g., Sekercioglu et al., 2012). Capture–recapture (CR) studies are commonly used to investigate wildlife demography (Williams et al., 2002). For many species, climate warming is concurrently affecting demographic status as well as animal movements and distribution (Pandey & Papes, 2018). If not accounted for during the design and analysis of CR studies, heterogeneous recapture probabilities caused by movements can lead to biased estimates of vital rates (Kendall et al., 1997; Schaub et al., 2004) and uncertainty about the definition of the study population (e.g., whether estimates of abundance represent the number of animals in an area at a specific time vs. the number of animals that use the area over an extended period; Regehr et al., 2009).

Polar bears exemplify the challenges discussed above. The species is considered Threatened under the U.S. Endangered Species Act (USFWS 2008) and Vulnerable by the International Union for the Conservation of Nature due to observed and forecasted sea-ice loss (Regehr et al., 2016). Although climate warming is the primary threat to polar bears (PBRs, 2015) and expected to negatively impact most bears in the long term (Atwood et al., 2016; Molnár et al., 2020), the status of the world's 19 polar bear subpopulations is currently variable due to differences in the rate of habitat change, ecosystem productivity, human-caused mortality, and other factors (Durner et al., 2018). Some subpopulations have declined due to sea-ice loss (e.g., Bromaghin et al., 2021; Lunn et al., 2016) while others, particularly those at high latitudes where biological productivity was historically limited by heavy ice, have remained stable (Dyck et al., 2023) or increased (Laidre et al., 2020; Wiig et al., 2022). Polar bears are among the most mobile quadrupeds (e.g., Amstrup et al., 2000; Wilson et al., 2022) and climate-mediated changes in sea-ice availability are affecting their seasonal distributions as well (Laidre et al., 2020). This may increase the chances that animal movements, especially nonrandom temporary emigration from the sampling area, will introduce bias into demographic parameter estimates (Peñalosa et al., 2014). Regehr et al. (2009) used a combination of empirical data and computer simulation to demonstrate that movement-related bias can be large for some CR studies of polar

bears and can potentially lead to incorrect conclusions about population status.

The Viscount Melville (VM) polar bear subpopulation occurs in Nunavut and the Northwest Territories (NWT), Canada. The most recent abundance estimate was 161 bears (standard error [SE] = 34 bears) for the period 1989–1992 based on Cormack-Jolly-Seber (CJS) CR models (Taylor et al., 2002). This makes VM one of the smallest polar bear subpopulations, increasing vulnerability to negative demographic effects and leading Taylor et al. (2002) to question the value of future CR studies due to the low precision of parameter estimates resulting from small sample sizes. Like other polar bear subpopulations in Canada, VM is subject to a legal and regulated subsistence harvest by Indigenous Peoples, which is guided by the *Polar Bear Management Agreement for the North Beaufort Sea and Viscount-Melville Sound polar bear populations between the Inuit of the Kitikmeot West Region in Nunavut and the Inuvialuit*, signed in 2006. Relatively high harvest levels from 1973 to 1992 (mean 8.2 bears/year) led to changes in population composition suggesting overharvest (Taylor et al., 2002), which resulted in the management decision to implement a harvest moratorium from 1995 to 1999, followed by reduced quotas corresponding to a mean harvest of 4.3 bears/year from 2000 to 2019 (Government of the Northwest Territories and Nunavut, unpublished data). Updated demographic information is needed to estimate the current sustainable harvest level and understand the impacts of climate warming on VM bears.

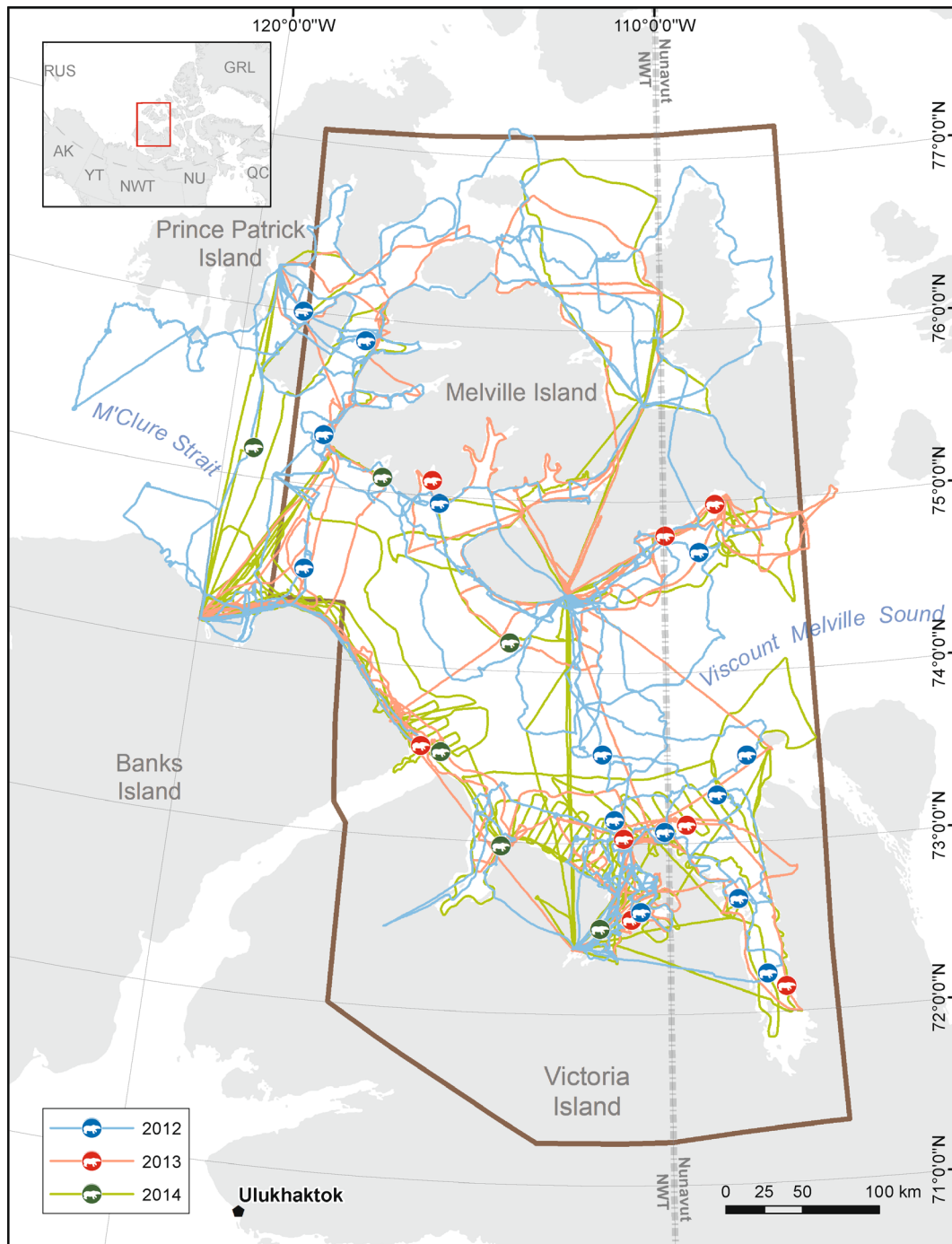
We conducted physical CR sampling on the VM subpopulation and applied satellite radiocollars to a limited number of adult females from 2012 to 2014. We analyzed these data, together with capture data collected intermittently since the 1970s, using a multistate model implemented in a Bayesian framework that sought to minimize potential biases associated with animal movements while maximizing the value of available data and knowledge. The model included multiple geographic states, used radiotelemetry data to inform transitions among states, included harvest data and observations of natural mortalities of research-marked animals, and used informative prior distributions for survival probability. Because the data were too sparse for time-dependent models, we explored long-term changes in demographic parameters using a two-period approach (1974–1999 and 2000–2019). Consistent with findings for other species (e.g., Bird et al., 2014), our analyses demonstrate that combining multiple data types and modeling movements can improve estimates of demographic parameters from CR studies of polar bears when sample sizes are small and animals move in and out of the sampling area.

## 2 | METHODS

### 2.1 | Study area

The VM polar bear subpopulation inhabits a marine area of approximately 101,000 km<sup>2</sup> (Stern & Laidre, 2016)

surrounding Melville Island, eastern Prince Patrick Island, northern Victoria Island, and VM Sound (Figure 1). It is considered part of the archipelago ecoregion for polar bears (Amstrup et al., 2008), which is characterized by heavy annual and multiyear sea ice that historically provided a year-round platform from which



**FIGURE 1** Management boundary of the Viscount Melville (VM) polar bear subpopulation (brown line) with global positioning system flight tracks (colored lines) and capture locations (colored symbols) from capture–recapture sampling conducted 2012–2014. The VM subpopulation occurs in the Northwest Territories (NWT) and Nunavut (NU), Canada. The inset in the upper left shows the depicted area in relation to Russia (RUS); Alaska, USA (AK); the Yukon Territory (YT) and Province of Quebec (QC), Canada; and Greenland (GRL).

polar bears could hunt (Messier et al., 1992). Areas of thick ice are generally poor habitat for ringed seals (*Pusa hispida*; Kingsley et al., 1985), the polar bears' primary prey (Amstrup, 2003), and therefore support relatively low densities of polar bears (Stirling, 2002; Stirling & Parkinson, 2006). From 1979 to 2016, the duration of the open-water season within the VM subpopulation boundary, as calculated from remote-sensing data using the methods of Stern and Laidre (2016), increased by an average of 11.2 days per decade. Concurrently, sea-ice concentration at the yearly minimum sea-ice extent declined by 6% per decade (Cavalieri et al., 1996, updated yearly). Similar shifts from heavy, multiyear sea ice to lighter, annual sea ice have been associated with improved body condition (i.e., fatness, a key indicator of reproductive success and survival) and increased abundance in some other high-Arctic subpopulations of polar bears (Dyck et al., 2021; Laidre et al., 2020).

## 2.2 | Field methods and data sources

We analyzed live-capture, radiotelemetry, and dead-recovery data collected from multiple sources over the period 1974–2019. Live-encounter data were available from CR programs conducted during the spring on the sea ice in 1974–1976, 1989–1992, and 2012–2014 using standard chemical immobilization techniques, as described in Taylor et al. (2002). Data were collected during 1989–1992 and 2012–2014 as part of a designed study with relatively large sample sizes. In contrast, live-capture data from 1974 to 1976 were collected opportunistically and did not include recaptures of previously marked individuals. Therefore, for analyses we pooled the 1974–1976 data into a single sampling occasion referenced to 1975 and modeled initial captures only by fixing recapture probability to 0 during this period (see Section 2.4). Live captures during 2012–2014 were approved by the Northwest Territories Wildlife Care Committee and conducted under research permit numbers WL005411, WL005418, and WL500236.

During physical captures, dependent young (cubs-of-the-year [C0] and yearlings [C1]) were aged based on body size and dentition. Independent bears (i.e.,  $\geq 2$  years-old) were aged by counting the growth annuli in an extracted vestigial premolar (Calvert & Ramsay, 1998). From 2012 to 2014, sampling effort was distributed throughout the current VM subpopulation boundary, as evidenced by capture locations and global positioning system (GPS) tracklogs from the helicopter used for captures (Figure 1). In contrast, from 1974 to 1976 and 1989 to 1992, sampling effort was restricted to marine regions within the VM subpopulation boundary south of 76° latitude, excluding the small

marine region that is south of 76° but north of Melville Island. Changes over time in the geographic region exposed to sampling meant that the definition of the study population changed as well, which has ramifications for interpreting estimates of population abundance and trend (see Sections 3 and 4).

Some captured adult ( $\geq 5$  years) female polar bears were fitted with satellite radiocollars (Platform Transmitter Terminal tags that provided data through the Argos system [[www.argos-system.org](http://www.argos-system.org)] using Doppler-derived location estimates [1989–1992; Messier et al. (1992)] or GPS locations [2012–2014]). We used location data from telemetry to determine whether collared bears were inside, or outside, the VM subpopulation boundary during each spring sampling occasion. The sampling occasion during year  $t$  was determined by the first and last live captures in the spring of that year. For each female fitted with a collar in year  $t$ , we used location data to determine whether she was in or out of the sampling area in subsequent years for which the collar functioned. A bear was considered in the sampling area on occasion  $t$  if more than 50% of the total distance it traveled during the 1–3-week sampling occasion was inside the VM subpopulation boundary. Regehr et al. (2018) performed similar in-versus-out calculations while accounting for differences in collar transmission schedules and location accuracy using a continuous-time correlated random walk model. However, such standardization was not necessary in our analyses because location data for most collared bears were unambiguous (e.g., for the subset of bears considered “in,” on average 98% of the distance traveled by each bear during the spring sampling occasion was within the VM subpopulation boundary).

In addition to live-capture and radiotelemetry data, we included data from research-marked bears that were harvested for subsistence purposes or were found by researchers after apparently dying without human involvement. Although physical captures ended in 2014, we modeled dead recoveries through 2019. In the NWT and adjacent Nunavut, subsistence harvest was implemented at a target 2:1 male–female sex ratio under a quota system with standardized reporting requirements including sex, age, and the presence of research marks (i.e., lip tattoos and ear tags with unique identification numbers, and satellite telemetry devices). Harvest reporting was mandatory and nearly 100% (S. Baryluk, unpublished data) although it is possible that physical research marks were lost or became illegible over time (see Section 4). We included harvest data for all bears previously marked in the VM subpopulation, even if they were harvested and reported in an adjacent subpopulation. When logistically feasible from 2012 to 2014, we also investigated the fate of bears wearing GPS collars that

appeared stationary during the field season (i.e., to determine whether the bear was dead or had dropped its collar).

### 2.3 | Multistate capture–recapture model structure

We developed a multistate CR model to estimate survival and abundance (e.g., Lebreton et al., 2009; Warlick et al., 2023). Because of small sample sizes and extended periods without live captures we used a relatively simple model structure and, unlike some other analyses for polar bears (e.g., Bromaghin et al., 2021), did not model vital rates as a function of environmental covariates (e.g., sea-ice concentration) due to the risk of spurious correlations. To account for demographic stochasticity, we modeled population processes as binomial and multinomial outcomes, as described below.

The model included six states: (1) alive and in the sampling area, (2) alive and out of the sampling area, (3) recently harvested and reported in the sampling area, (4) recently harvested and reported out of the sampling area, (5) recently dead of natural causes and found by humans (all such observations occurred in the sampling area), and (6) an absorbing dead state. The state transition matrix (Table 1) focused on modeling movements in and out of the VM subpopulation boundary because reducing potential bias due to nonrandom temporary emigration was a primary objective. The structure of the multistate model did not include sex, age, or reproductive states reflecting the polar bear life cycle (Regehr et al., 2010) because the data were too sparse to fit highly parameterized models. However, we derived sex- and age-specific estimates of some parameters using individual- and group-based covariates (see Section 2.4).

Parameters in the state transition matrix were referenced to annual timesteps from the spring of year  $t$  to the

spring of year  $t + 1$ . Individual bears of all ages entered the dataset when captured, marked, and released for the first time. Transitions among states were determined by five parameters. Total survival ( $\phi$ ) represented the probability of surviving, considering all types of mortality. Movement probabilities allowed individuals in the sampling area in year  $t$  to either remain inside ( $\Psi_1$ ) or move outside ( $1 - \Psi_1$ ) in year  $t + 1$ , conditional on survival. Similarly, individuals outside the sampling area could either remain outside ( $\Psi_2$ ) or move inside ( $1 - \Psi_2$ ). Estimating  $\Psi_1$  and  $\Psi_2$  separately meant that the model allowed for Markovian dependence in movement probabilities. The final two parameters were conditional on death: harvest recovery probability,  $r$ , defined as the probability that a bear was killed by a human and reported to the responsible management authorities; and the parameter  $\kappa$ , defined as the probability that a bear that died of natural causes was detected by a human. We modeled harvest recoveries as states, which led to  $r$  appearing in the state transition matrix rather than in the observation matrix, because this parameterization can improve numerical estimation in some Bayesian implementations of live-recapture dead-recovery models (Kéry & Schaub, 2012). Although there were only two known natural mortalities, we accounted for them in the model structure because of the sparseness of VM data in the 2010s. We considered  $\kappa$  a nuisance parameter because it was a function of a nonrandom search process and did not have a biological meaning.

Processes leading to bear observations were represented by the observation matrix, which included eight possible observation types (Table 2). Parameters in the observation matrix included  $p$ , the probability of physical recapture conditional on being alive and in the sampling area. There were no physical captures outside of the sampling area. The observation matrix also included the individual time-varying covariate  $Tel$ , which was set to 1 if an adult female bear was wearing a radiocollar that

TABLE 1 State transition matrix for the multistate capture–recapture model of Viscount Melville polar bears.

	1	2	3	4	5	6
	Alive in	Alive out	Harvested and reported in	Harvested and reported out	Known-natural mortality	Dead (absorbing)
1 Alive in	$\phi \Psi_1$	$\phi (1 - \Psi_1)$	$(1 - \phi) \Psi_1 r$	$(1 - \phi) (1 - \Psi_1) r$	$(1 - \phi) \kappa$	$(1 - \phi) (1 - r - \kappa)$
2 Alive out	$\phi (1 - \Psi_2)$	$\phi (\Psi_2)$	$(1 - \phi) (1 - \Psi_2) r$	$(1 - \phi) \Psi_2 r$	$(1 - \phi) \kappa$	$(1 - \phi) (1 - r - \kappa)$
3 Harvested and reported in	0	0	0	0	0	1
4 Harvested and reported out	0	0	0	0	0	1
5 Known-natural mortality	0	0	0	0	0	1
6 Dead (absorbing)	0	0	0	0	0	1

Note: Rows and columns represent model states. The parameters in cell  $i, j$  define the probability of transitioning from the state in row  $i$  at year  $t$ , to the state in column  $j$  at year  $t + 1$ . Parameters are defined in the main text.

TABLE 2 Observation matrix for the multistate capture–recapture model of Viscount Melville polar bears.

	1	2	3	4	5	6	7	8
	Capture in, no telemetry data	Capture in, known in due to telemetry	Not captured in, known in due to telemetry	Known out due to telemetry	Harvested and reported in	Harvested and reported out	Known-natural mortality	No observation
1 Alive in	$p(1-Tel)$	$p Tel$	$(1-p) Tel$	0	0	0	0	$(1-Tel)(1-p)$
2 Alive out	0	0	0	$Tel$	0	0	0	$(1-Tel)$
3 Harvested and reported in	0	0	0	0	1	0	0	0
4 Harvested and reported out	0	0	0	0	0	1	0	0
5 Known-natural mortality	0	0	0	0	0	0	1	0
6 Dead (absorbing)	0	0	0	0	0	0	0	1

Note: Rows represent model states and columns represent observation types. The parameters in cell  $ij$  define the probability of the observation type in column  $j$  at year  $t$ , conditional on being in the state in column  $i$  at year  $t$ . Parameters and covariates are defined in the main text.

confirmed she was alive and provided location data (i.e., that indicated whether the bear was in or out of the sampling area) and set to 0 otherwise.

The live-encounter, radiotelemetry, and dead-recovery data were analyzed jointly by expressing the state of individual  $i$  in year  $t$  as a categorical random variable:

$$z_{i,t} | z_{i,t-1} \sim \text{Cat}(\Theta_{z_{i,t-1}}), \quad (1)$$

where  $\Theta_{z_{i,t-1}}$  is the vector of state transition probabilities for an individual that was in state  $z_{i,t-1}$  in year  $t-1$ , as defined by parameters in the state transition matrix. Observation data for individual  $i$  in year  $t$ ,  $y_{i,t}$ , were modeled as a function of its state in year  $t$  as well as covariates (e.g., presence of a functional radiocollar, see below). We assumed  $y_{i,t}$  was a categorical random variable:

$$y_{i,t} | z_{i,t} \sim \text{Cat}(\Pi_{i,t,z_{i,t}}), \quad (2)$$

where  $\Pi_{i,t,z_{i,t}}$  is the vector of detection probabilities for individual  $i$  in year  $t$ , as defined by the observation matrix. From 1989 to 1992, very high frequency (VHF) transmitters on radiocollars were used to locate several collared bears for physical capture. The resulting increase in  $p$ , compared to non-collared bears, was accounted for using an individual time-varying covariate ( $rad$ ) that was

set to 1 if an adult female was wearing a functional radio collar 1989–1992, and set to 0 otherwise.

Finally, we modeled counts of individuals physically captured in the sampling area (state 1) in year  $t$  ( $n_t$ ) as a binomially distributed random variable, with recapture probability  $p$  and latent abundance  $N_t$ :

$$n_t \sim \text{Binomial}(p, N_t). \quad (3)$$

Annual values of  $N_t$  were considered a Poisson-distributed random variable with rate parameter  $\lambda_t$ . We specified a time-constant rate parameter within each period of intensive CR sampling during which abundance estimation was possible (i.e., 1989–1992 and 2012–2014). Therefore, we report a mean value of  $N_t$  over each period of interest (e.g.,  $\bar{N}_{2012-2014}$ ). The values of  $n_t$  and  $p$  used here refer to bears that were physically captured and released alive after being randomly encountered while searching the sampling area by helicopter. To account for the small number of bears that were more likely to be detected from 1989 to 1992 due to the assistance of VHF telemetry (i.e., bears with  $rad=1$ ), we adjusted estimates of  $N_t$  by adding numbers of radiocollared bears ( $N_t^{rad}$ ) estimated using a Horvitz-Thompson equation (McDonald & Amstrup, 2001), as follows:

$$N_t^{rad} = n_t^{rad} / p_t^{rad}, \quad (4)$$

where  $n_t^{rad}$  is the number of radiocollared bears that were captured and  $p_t^{rad}$  is their corresponding recapture probability.

The parameter  $N_t$  represents the number of bears that used the sampling area during sampling occasion  $t$ . Because some polar bears were located outside of the sampling area each spring,  $N_t$  was necessarily smaller than the “superpopulation,”  $N_t^S$ , defined as the number of bears with a non-negligible probability of using the sampling area over a multiyear period (Kendall et al., 1997). We were interested in  $N_t^S$  because it is commonly estimated in CR studies of geographically open populations when using simpler models that do not account for movements in and out of the sampling area. Specially, the previous VM abundance estimates in Taylor et al. (2002) represent  $N_t^S$ . To derive approximate values of  $N_t^S$ , we created a  $2 \times 2$  matrix model that included in and out states, with transitions among states defined by the posterior distributions of  $\Psi_1$  and  $\Psi_2$  from the multistate model. We then estimated the proportion of the superpopulation located within the sampling area on occasion  $t$  ( $prop.in_t$ ) based on the matrix’s asymptotic stable-stage distribution, and subsequently calculated superpopulation size as  $N_t^S = N_t / prop.in_t$ .

## 2.4 | Model fitting and parameter estimation

We constructed a model for inference using the state transition and observation matrices (Tables 1 and 2, respectively). Parameters in the matrices were modeled as linear equations of covariates using a logit link function. Model structure was informed by biological and study-design considerations for the VM subpopulation as well as patterns in polar bear vital rates from other studies (e.g., sex- and age-specific variation in survival). The model was parameterized as follows, where the terms in parentheses represent parameter-specific submodels:

$$\begin{aligned} & \varphi \left( COC1^{per1} + SF^{per1} + AF^{per1} + SM^{per1} + AM^{per1} \right. \\ & \quad \left. + \beta_{(t)}^{per1} + COC1^{per2} + SF^{per2} + AF^{per2} + SM^{per2} \right. \\ & \quad \left. + AM^{per2} + \beta_{(t)}^{per2} \right) \psi_1(per1 + per2) \psi_2(per1 + per2) \\ & \quad \times r(F^{per1} + M^{per1} + F^{per2} + M^{per2}) \kappa(per2) p(per1 + per2 + rad^{per1}). \end{aligned} \tag{5}$$

Notation for sex is females ( $F$ ) and males ( $M$ ). Age classes consisted of C0s and C1s grouped together, due to small sample sizes ( $COC1$ ); subadults (2–4 years;  $S$ ), and adults ( $\geq 5$  years;  $A$ ). Terms used together represent

combined sex- and age-classes (e.g.,  $SF$  refers to subadult females, whereas  $F$  without an age modifier refers to all females). For the survival submodel, the choice of age classes was based on previous demographic studies for polar bears (e.g., Regehr et al., 2007; Taylor et al., 2009). A sex effect was included because the VM subpopulation is subject to sex-selective harvest, a common management tool for polar bears (Taylor et al., 2008). The sex effect was not extended to dependent young because harvesting females with cubs was prohibited. We included a two-level fixed effect for period ( $per1$  and  $per2$ ) to evaluate changes in mean survival over time. We selected the year 2000 as a cutoff because it divided the overall study into periods of comparable length and marked the end of a harvest moratorium (Government of the NWT, unpublished data). When used as superscripts, the terms  $per1$  and  $per2$  denote demographic parameters for the periods 1974–1999 and 2000–2019, respectively. For example,  $\varphi(S^{per1})$  represents subadult survival for the early period. Temporal random effects in survival were formulated as  $\beta_{(t)} \sim Normal(0, \sigma^2)$ , where  $\sigma^2$  is the period-specific variance. The movement submodels included a period effect only because most location data were from adult females, which precluded more detailed sex and age structure. The harvest recovery submodel included period and sex effects because harvest of the VM subpopulation was selective and changed over time. The parameter  $\kappa$  was fixed to 0 in all years except during the second period of intensive CR sampling, for which it was modeled using an intercept only. Finally, the submodel for recapture probability included a period effect because of changes in sampling effort between the two periods of intensive CR sampling (1989–1992 and 2012–2014). Recapture probability was fixed to 0 in all other years.

We used informed prior distributions for survival corresponding to mean values and standard deviations (SD) on the probability scale of 0.72 (SD = 0.21) for C0s and C1s of both sexes, 0.87 (SD = 0.09) for SFs, 0.93 (SD = 0.04) for AFs, 0.80 (SD = 0.13) for SMs, and 0.89 (SD = 0.05) for AMs. These priors were developed using moment-matching methods based on the point estimates and SEs of apparent survival (i.e., including harvest mortality but generally not including emigration) for 12 other polar bear subpopulations with available data (Supporting Information S1). Because the demographic status of these subpopulations varied, our use of priors did not represent a specific assumption about the VM subpopulation (e.g., that it was growing or declining), but rather represented the assumption that survival of VM polar bears was within the range of empirical estimates of survival for the global population of polar bears. Non-informative priors were used for all other parameters in the model (Supporting Information S1).

To understand the effects of modeling multiple data types and accounting for animal movements, we compared our results with those from a single-state model that included live-encounter data only and was analogous to a traditional CJS model with time-constant structures for  $\phi$  and  $p$  in the early and late periods of the study (Williams et al., 2002; Supporting Information S1). Goodness-of-fit (GOF) tests are not well developed for multistate models with individual covariates. Therefore, we also used the CJS-analog model to evaluate GOF based on tests derived from logistic regression in the R package *mra* (McDonald, 2018). Finally, we evaluated the sensitivity of results to the choice of priors by refitting the multistate model using non-informative priors for survival.

Models were fit in a Bayesian framework using JAGS (Plummer, 2017) with the *jagsUI* (Kellner, 2019) and *saveJAGS* (Meredith, 2021) packages, accessed through R version 4.02 (R Core Team, 2020). We used 40 parallel Markov Chain Monte Carlo simulations, each of which included 10,000 adaptive and burn-in iterations, and 200,000 posterior iterations, thinned by 20 to reduce file size. Chain convergence was evaluated visually and by confirming that values of the Gelman-Rubin statistic (Gelman et al., 2004) were less than 1.01 for all parameters. We report results as posterior modes (McElreath, 2020) and 95% Bayesian credible intervals (CRI) unless otherwise noted.

## 2.5 | Population growth rate

We performed post-hoc analyses to interpret estimates of vital rates for the period 2000–2019, for the purpose of informing management of the VM subpopulation. First, we used live-encounter data from 2012 to 2014 to estimate C0 litter size and litter production rate ( $lpr$ ), defined as the proportion of adult females available to breed in year  $t$  that successfully produced a litter of C0s in year  $t + 1$  (Taylor et al., 1987). We estimated variance in C0 litter size and  $lpr$  using a nonparametric bootstrap procedure with 1000 iterations during which live-encounters of individual bears were resampled with replacement. Second, we used estimates of  $\phi$  from the multistate model, which included harvest mortality, to estimate un-harvested survival as  $\phi^* = \phi + r \times (1 - \phi)$  (Peacock et al., 2013). This equation assumes that harvest of research-marked bears is reported, and that harvest mortality is additive (i.e., that no harvested bears would otherwise have died during a given interval). Finally, we used estimates of C0 litter size,  $lpr$ , and  $\phi$  (or  $\phi^*$ ) to estimate the mean population growth rate ( $gr$ ), defined as log of the dominant eigenvalue of a 10-stage

matrix projection model for polar bears, as developed by Regehr et al. (2017), populated with vital rates from the current study. We estimated variance in  $gr$  by repeating calculations using 1000 samples from the posterior distributions of survival together with the bootstrap distributions of C0 litter size and  $lpr$ . During this process, we retained the existing covariance structure within estimates of reproductive rates and within estimates of sex- and age-specific survival. The resulting estimates of  $gr$  represented the time-constant, asymptotic intrinsic growth rate at a stable stage distribution, including harvest mortality (when using estimates of  $\phi$ ) and excluding harvest mortality (when using estimates of  $\phi^*$ ). Estimates of  $gr$  calculated using  $\phi^*$  can be interpreted as the potential growth rate of the VM subpopulation at its current relative density if harvest were stopped.

## 3 | RESULTS

### 3.1 | Data

A total of 166 unique females and 119 unique males were included in the VM polar bear dataset from 1974 to 2019. There were 45, 205, and 71 physical captures (i.e., including both initial captures and recaptures) in 1974–1976, 1989–1992, and 2012–2014, respectively. The number of research-marked bears that were re-encountered either alive or dead was low, especially in the later period (Table 3). Total sample sizes for observation types 1–7 (as defined in the Methods and column headers of Table 2) were 338, 13, 22, 10, 26, 9, and 2, respectively. From 1990 to 2019, the average number of research-marked bears reported in the harvest (observation types 5 and 6) was 1.2 per year (SD = 1.3) and the average proportion of females among research-marked bears reported in the harvest was 0.26.

### 3.2 | Abundance

Estimates of mean abundance in the sampling area were  $\bar{N}_{1989-1992} = 145$  (95% CRI [109, 222], coefficient of variation [CV] = 0.19) and  $\bar{N}_{2012-2014} = 235$  (95% CRI [148, 569], CV = 0.37; Table 4). This corresponds to a probability of 0.94 that abundance within the VM subpopulation boundary was higher in the 2010s, although interpretation is complicated by the expansion of the geographic sampling area (see Section 4). The corresponding estimates of superpopulation size were  $\bar{N}_{1989-1992}^S = 221$  (95% CRI [152, 917]) and  $\bar{N}_{2012-2014}^S = 340$  (95% CRI [214, 815]).

TABLE 3 Summary of observational data for Viscount Melville polar bears in a modified m-array format, 1975–2019.

Year	R	89	90	91	92	94	95	97	99	00	01	02	06	09	12	13	14	15	16	17	19	r	
75	45	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
89	42	-	13	9	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	27
90	22	-	-	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
91	68	-	-	-	22	2	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	26
92	79	-	-	-	-	2	3	1	0	1	2	1	2	1	1	1	0	1	0	0	0	0	16
12	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	1	2	1	2	0	0	19
13	38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	1	0	0	0	0	13
14	36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	0	0	1	0	9
15	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	0	0	0	5
16	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1

Note: Counts for bears released alive (R) include physical captures in the sampling area without (observation type 1) or with (observation type 2) knowing the bear’s location due to telemetry, and bears that were alive and had a known location due to telemetry but were not physically captured inside (observation type 3) or outside (observation type 4) of the sampling area. Counts for re-encountered bears (r) include bears that were observed alive (observation types 1–4), bears that were harvested inside (observation type 5) or outside (observation type 6) of the sampling area, and known natural mortalities (observation type 7). Columns are excluded for years with no re-encounters. The symbol “-” is used for years preceding the year that releases occurred in a given row.

### 3.3 | Vital rates and movements

Estimates of survival varied by sex, age, and period (Table 4). Point estimates of  $\phi$  increased between the early period (1974–2000) and late period (2001–2019) for all bears except adult females, for which estimates went from 0.95 (95% CRI [0.90, 0.98]) to 0.89 (95% CRI [0.81, 0.95]). Considering statistical uncertainty, this corresponds to a 0.92 probability that estimates of adult female survival declined. Although the mode of survival estimates for the combined C0 and C1 age class also declined, the posterior distributions were skewed such that their other moments increased between the early and late periods (e.g., mean values of 0.83 and 0.86 for the early and late periods, respectively). Modeling of temporal random effects in survival probability led to imprecise variance estimates that were similar for the early ( $\sigma^2 = 0.08$ , 95% CRI [0.00, 3.10]) and late periods ( $\sigma^2 = 0.04$ , 95% CRI [0.00, 2.3]; time-varying estimates of survival for adults are displayed in Figure S1). Because this variation likely reflected sampling uncertainty associated with sparse data between short periods of CR sampling, we report mean estimates of time-constant  $\phi$  (i.e., with  $\sigma^2 = 0$ ; Tables 4 and 5). Harvest recovery probabilities were higher for males than females, and similar across periods for both sexes.

Movement probabilities exhibited Markovian dependence and some estimates changed over time (Table 4). Most notably, the probability that a previously marked bear was located outside the VM subpopulation boundary on occasion  $t + 1$ , conditional on being located outside on occasion  $t$  (the parameter  $\Psi_2$ ), was 0.88 (95% CRI [0.14, 0.98]) for the early period and 0.06 (95% CRI [0.01, 0.71]) for the late period, corresponding to an 0.89

probability of decline and potentially reflecting increased fidelity to the sampling area (i.e., a “rubber-band” effect). However, interpretation is complicated by large statistical uncertainty. The estimated proportion of the superpopulation located inside the VM subpopulation boundary (*prop.in*) was 0.72 (mean = 0.62, 95% CRI [0.19, 0.86]) in the early period and 0.73 (mean = 70, 95% CRI [0.52, 0.83]) in the late period, corresponding to an 0.64 probability of an increase and therefore providing little evidence for a biologically meaningful change.

We calculated mean intrinsic growth rate (*gr*) to help interpret the demographic status of the VM subpopulation. Reproductive parameters estimated from capture data collected 2012–2014 included mean litter production rate (*lpr*) = 1.0 (95% CRI [0.29, 1.0]) and C0 litter size = 1.67 (95% CRI [1.38, 1.92]). Use of these estimates in a matrix projection model, together with estimates of  $\phi$  from the multistate model, resulted in an estimate of  $gr = 0.00$  (95% CRI [−0.09, 0.06]). Alternatively, this metric can be expressed as the finite population growth rate:  $\exp(gr) = 1.00$  (95% CRI [0.91, 1.06]). We also used estimates of  $\phi$  and *r* from the multistate model to estimate un-harvested survival ( $\phi^*$ ; Table 5). The corresponding estimate of un-harvested intrinsic growth rate was 0.01 (95% CRI [−0.06, 0.07]; alternatively, finite population growth rate = 1.01 [95% CRI [0.94, 1.07]]).

### 3.4 | Details of model fitting and sensitivity analyses

Demographic parameters in the multistate model were estimated using informed prior distributions on survival

**TABLE 4** Estimated demographic parameters for the Viscount Melville polar bear subpopulation from the multistate capture–recapture model using informed prior distributions for survival probability.

Parameter	Mode	Lower CRI	Upper CRI
$\phi(COC1^{per1})$	0.99	0.57	0.99
$\phi(SF^{per1})$	0.87	0.67	0.97
$\phi(AF^{per1})$	0.95	0.90	0.98
$\phi(SM^{per1})$	0.84	0.65	0.96
$\phi(AM^{per1})$	0.87	0.79	0.97
$\phi(COC1^{per2})$	0.94	0.58	0.98
$\phi(SF^{per2})$	0.97	0.75	0.99
$\phi(AF^{per2})$	0.89	0.81	0.95
$\phi(SM^{per2})$	0.98	0.80	1.00
$\phi(AM^{per2})$	0.92	0.83	0.96
$\psi_1(per1)$	0.89	0.72	0.94
$\psi_2(per1)$	0.88	0.14	0.98
$\psi_1(per2)$	0.73	0.56	0.84
$\psi_2(per2)$	0.06	0.01	0.71
$r(F^{per1})$	0.06	0.02	0.19
$r(M^{per1})$	0.29	0.18	1.00
$r(F^{per2})$	0.09	0.04	0.25
$r(M^{per2})$	0.31	0.12	0.79
$\kappa(per2)$	0.09	0.03	0.42
$p(per1)$	0.32	0.23	0.45
$p(rad^{per1})$	0.75	0.50	0.90
$p(per2)$	0.11	0.06	0.22
$\lambda_{1989-1992}$	142	103	218
$\bar{N}_{1989-1992}$	145	109	221
$\bar{N}_{1989-1992}^S$	222	152	917
$\lambda_{2012-2014}$	239	147	570
$\bar{N}_{2012-2014}$	235	148	569
$\bar{N}_{2012-2014}^S$	340	214	815

Note: Values are posterior modes and 95% credible intervals (CRI). Parameters include total survival probability ( $\phi$ ), movement probabilities ( $\psi$ ), harvest recovery probabilities ( $r$ ), detection probability of known–natural mortalities ( $\kappa$ ), recapture probability ( $p$ ), rate parameter for Poisson distributions of abundance ( $\lambda$ ), mean abundance in the sampling area ( $\bar{N}$ ), and mean abundance of the superpopulation ( $\bar{N}^S$ ). Early (1974–1999) and late (2000–2019) periods of the study are denoted *per1* and *per2*, respectively. Sex- and age-classes are denoted as follows: cubs-of-the-year of both sexes (CO), yearlings of both sexes (CI), females (F), males (M), subadults (2–4 years; S) and adults ( $\geq 5$  years; A). Detailed parameter definitions are provided in the main text.

probability. The same model with non-informative priors led to estimates of mean  $\phi$  for the period 2012–2014 that were lower (mean percent relative difference

**TABLE 5** Estimates of un-harvested survival probability ( $\phi^*$ ) for the Viscount Melville polar bear subpopulation from the multistate capture–recapture model using informed prior distributions for survival probability.

Parameter	Mode	Lower CRI	Upper CRI
$\phi^*(COC1^{per1})$	0.99	0.57	0.99
$\phi^*(SF^{per1})$	0.89	0.69	0.97
$\phi^*(AF^{per1})$	0.96	0.91	0.98
$\phi^*(SM^{per1})$	0.89	0.75	1.00
$\phi^*(AM^{per1})$	0.91	0.85	1.00
$\phi^*(COC1^{per2})$	0.94	0.58	0.98
$\phi^*(SF^{per2})$	0.97	0.78	0.99
$\phi^*(AF^{per2})$	0.90	0.83	0.96
$\phi^*(SM^{per2})$	0.99	0.85	1.00
$\phi^*(AM^{per2})$	0.96	0.87	0.99

Note: Values are posterior modes and 95% credible intervals (CRI). Early (1974–1999) and late (2000–2019) periods of the study are denoted *per1* and *per2*, respectively. Sex- and age-classes are denoted as follows: cubs-of-the-year of both sexes (CO), yearlings of both sexes (CI), females (F), males (M), subadults (2–4 years; S) and adults ( $\geq 5$  years; A). Detailed parameter definitions are provided in the main text.

[MPRD] = –4%) and considerably less precise (MPRD in the CV = 35%). Estimates of  $\bar{N}_{2012-2014}$  using non-informative priors also were lower (MPRD = –10%) and slightly less precise (MPRD[CV] = 1%) compared with estimates using informative priors.

Estimates of survival for the period 2012–2014 from the CJS-analog model (Supporting Information S1) were much lower (MPRD = –46%) and less precise (MPRD [CV] = 73%) than corresponding estimates from the multistate model. Mean estimates of superpopulation size ( $\bar{N}_{2012-2014}^S$ ) from the CJS-analog model, calculated using a Horvitz-Thompson equation (McDonald & Amstrup, 2001), also were lower (MPRD = –52%) and slightly less precise (MPRD[CV] = 4%) compared with estimates of  $\bar{N}_{2012-2014}^S$  from the multistate model. We did not find evidence for a lack of fit in the CJS-analog model. The Osius-Rosjek test ( $p = 0.51$ ) and overall Chi-square test ( $p = 1.0$ ) were not significant, and the receiver operating characteristic test indicated good discrimination (0.82).

## 4 | DISCUSSION

Climate warming is affecting the movements, distribution, and status of wildlife populations around the globe (Brodie et al., 2013). The rapid rate of change presents challenges to research and management (LeDee et al., 2021), especially for large carnivores and other

mobile species that occur at low densities in remote areas (e.g., Laidre et al., 2022). In this paper, we present a CR model designed to accommodate animal movements and maximize the use of available data and knowledge. Similar models have been shown to reduce bias in estimates of demographic parameters for other species (e.g., Bird et al., 2014). We applied the model to longitudinal data from live captures, radiotelemetry, observations of natural mortalities, and harvest for the VM polar bear subpopulation to estimate the demographic parameters needed for management and conservation.

## 4.1 | Abundance

Abundance of polar bears within the VM subpopulation boundary, as estimated from the multistate model, was significantly higher in 2012–2014 ( $\bar{N} = 235$ ) compared to 1989–1992 ( $\bar{N} = 145$ ). Although the assessment of population trend is complicated by expansion of the geographic sampling area in the latter period, several factors suggest that abundance has increased in recent decades. First, during 2012–2014, no bears were observed in the area north of 76° latitude that was not sampled in the earlier periods, meaning that the search effort expended here did not contribute to the estimated number of animals. Second, a harvest moratorium from 1995 to 1999 and subsequent reduction in subsistence harvest levels from 1999 to 2019 likely allowed for growth of a previously overharvested subpopulation (Taylor et al., 2002). Another potential explanation for increasing abundance is that sea ice throughout the Canadian Arctic Archipelago is transitioning to be younger and thinner (Howell & Brady, 2019), leading to declines of approximately 5% and 10% per decade in total sea ice and multiyear sea ice, respectively, in VM Sound for the period 1986–2016 (Derksen et al., 2018). In some other high-latitude regions, lighter sea-ice conditions resulting from climate warming have led to transient increases in biological productivity (Ardyna & Arrigo, 2020) and environmental carrying capacity for polar bears (Dyck et al., 2021; Laidre et al., 2020). In an assessment of body condition and diet composition of VM polar bears using biological samples from physical captures 2012–2014, Florko et al. (2021) did not find evidence that declining sea ice has had a positive effect on foraging conditions. However, the short time series, high interannual variability, and lack of historical data in that study precluded drawing strong conclusions. Other scientific data are not currently available on how climate warming may be affecting the ecology of VM bears.

## 4.2 | Vital rates

Total survival (i.e., including harvest mortality) of all sex and age classes except adult females increased between the early and late periods (Table 4; noting that, although the mode of  $\phi$  for the combined C0C1 age class decreased, the mean and median increased). For bears other than adult females, point estimates for the latter period (2000–2019) were, on average, 11% higher than the mean survival rates from other case studies for polar bears (Table S1). This suggests relatively high survivorship for most VM bears, although interpretation is complicated by the fact that some case studies estimated apparent survival (i.e., the probability of surviving and remaining in the sampling area), whereas our inclusion of harvest data from outside the VM subpopulation boundary meant that estimates of  $\phi$  represented biological survival that was not affected by emigration. Harvest recovery probability ( $r$ ) was higher for males than females due to sex-selective harvest. Estimates of mean  $r$  were similar for the early (1974–1999) and latter (2000–2019) periods, which may be due to small sample sizes, variable harvest levels within each period, or the underreporting of harvested bears due to tag loss during the species' 20–30-year lifespan (see below).

Point estimates of adult female survival declined from 0.95 in the early period to 0.89 in the latter period, which is below the mean value of 0.93 from other case studies (Table S1). We do not know to what extent this represents a true biological change versus bias or a statistical artifact. It is possible that lower adult female survival is related to a combination of changing harvest levels and a subpopulation that is nearing environmental carrying capacity. Taylor et al. (2002) reported a low proportion of adult males in the 1989–1992 capture sample and suggested this was due to relatively high, sex-selective harvest (63% male) from 1973 to 1992. We found that the proportion of males in the subpopulation increased from approximately 0.36 to 0.52 between the early and latter periods, likely due to recovery of males following reduced harvest quotas. More adult males, which have twice the body mass of adult females and exhibit social dominance (Derocher et al., 2005), may have increased competition for hunting opportunities or displaced females and family groups from preferred habitats (Stirling et al. 2004). Estimated harvested and un-harvested intrinsic growth rates for the latter period were  $gr = 0.00$  and  $0.01$ , respectively, suggesting strong population regulation. However, the possibility that density dependence would disproportionately impact adult females is confounding given that, for long-lived species, density effects typically first appear in subadult survival and recruitment (Eberhardt, 2002;

Fowler, 1987), both of which were high in the latter period of our study (although with large uncertainty).

### 4.3 | Movements

One of our primary objectives was to evaluate temporary emigration with respect to the sampling area which, if nonrandom, can introduce bias into demographic parameters (Peñaloza et al., 2014). To accommodate animal movements, we modeled a quasi-unobservable state, defined as the area outside of the VM subpopulation boundary where live captures did not occur (i.e., where  $p = 0$ ) and a bear could be detected only if it was wearing a functional radiocollar or reported dead in the harvest. Estimates of the movement parameter  $\psi_1$  (Table 4) were greater than 0.50 in both periods, indicating that animals inside the sampling area in year  $t$  were more likely to be inside again in year  $t+1$ , compared with animals that were outside in year  $t$ . This suggests that VM bears exhibit a moderate degree of seasonal fidelity, similar to some other polar bear subpopulations (e.g., Amstrup et al., 2000). The probability that a bear outside sampling area in year  $t$  returned to the sampling area in year  $t+1$  (i.e.,  $1 - \psi_2$ ) increased between the early and late periods, although uncertainty was large and the estimated proportion of the VM subpopulation located inside the sampling area during spring did not change significantly. Regehr et al. (2009) found evidence for Markovian dependence in movements based on 175 bear-years of telemetry data from springtime CR studies of polar bears in the Southern Beaufort Sea. They also demonstrated that heterogeneity in recapture probabilities resulting from these movements can lead to meaningful bias in estimates of demographic parameters. This is consistent with our finding that the point estimate of mean superpopulation size for the period 2012–2014 derived from the multistate model ( $\bar{N}_{2012-2014}^S = 340$ ) was higher than the abundance estimate from the CJS-analog model ( $\bar{N}_{2012-2014}^S = 227$ ; Supporting Information S1), which did not account for movements. Similarly, our estimate of  $\bar{N}_{1989-1992}^S = 222$  for the early period was higher than the corresponding estimate of  $\bar{N}_{1989-1992}^S = 165$  from the CJS models of Taylor et al. (2002).

### 4.4 | Modeling considerations

The multistate CR model was designed to incorporate multiple data types and account for key sources of variation. Nonetheless, estimated demographic parameters should be interpreted with caution for several reasons. Sparse data necessitated the use of a relatively simple

model structure that did not reflect extended maternal care in polar bears or allow vital rates to be linked to stage-specific abundances, a common feature of integrated population models (e.g., Regehr et al., 2018). The low number of recaptures, especially in the latter period (Table 3), likely increased susceptibility to bias resulting from un-modeled heterogeneity in the data (Pollock et al., 1990). Also, recaptures and harvest recoveries were identified using physical marks rather than genetic analysis (e.g., Atkinson et al. 2021), raising the possibility of tag loss given that lip tattoos can fade over time and plastic ear tags can be removed, especially by males during intra-specific competition for mates. Although this issue can be addressed analytically for doubly marked animals (Conn et al., 2004), it was not possible to do so for VM bears due to small sample sizes. Consequently, tag loss may have introduced negative bias in survival estimates and positive bias in abundance estimates (McDonald et al., 2003). Another caveat is that most movement information was obtained from radiocollars, which were applied to adult females only because collars can potentially injure growing bears and are often shucked by adult males due to the large circumference of their necks. Although data are limited, several studies have suggested sex-specific differences in polar bear movements during the spring (Laidre et al., 2013; Wilson et al., 2022). Finally, the assumption of independent data sources was violated because some adult females provided both capture and telemetry data, although other studies suggest that lack of independence generally has a minimal impact on parameter estimates (Abadi et al., 2010).

On the positive side, several other factors likely increased the accuracy of parameter estimates, including the use of multiple data types (Zipkin & Saunders, 2018) and the availability of accurate age information from vestigial premolar teeth collected during physical captures (i.e., as opposed to CR studies that use biopsy sampling and have relied on subjective estimates of age class, e.g., Dyck et al. (2023)). Precision also was increased by using informed prior distributions for survival probability, which constrained estimates to a range that was realistic for long-lived animals. Use of informed priors represented the assumption that survival of VM bears was not outside the range of empirical estimates for the species (e.g., that climate warming or other factors have not had unprecedented impacts on VM bears). This assumption was justified on the basis that VM is in the archipelago polar bear ecoregion, where negative effects of climate warming are expected to be delayed (Amstrup et al., 2008; Atwood et al., 2016), and that Traditional Ecological Knowledge of Indigenous Peoples in the region suggests that the VM subpopulation is recovering or increasing (SARC, 2021; York et al., 2016). Although it

is possible that some of the survival estimates used to develop informed priors (Table S1) were biased by unmodeled animal movements or other factors, the consequences of this were likely negligible compared to the alternative approach of using a model that did not reflect preexisting scientific information about polar bear life history.

The multistate model in this paper provided reasonable estimates of demographic parameters, in contrast with the CJS-analog model, which produced estimates that were less precise, biologically implausible, and conformed to expected patterns of bias. This underscores the importance of including multiple data types and modeling animal movements. Given that radiotelemetry data are increasingly rare for polar bears due to ethical concerns about chemical immobilization and the application of radiocollars (Laidre et al., 2022), we recommend that scientists, managers, Indigenous partners, and stakeholders consider the pros and cons of applying telemetry tags during the design phase of CR studies. In addition to potentially reducing bias, contemporary movement data are required to differentiate between the number of bears in the sampling area versus the superpopulation. Such calculations are necessary if the goal is to compare estimates of abundance that were obtained using different study methods (e.g., distance-sampling aerial survey vs. open-population CR). Our analyses also emphasize the importance of a functional management system capable of enumerating harvested bears, especially for CR studies with long intervals between periods of intensive sampling (Peacock et al., 2012).

#### 4.5 | Management implications

Taken together, our findings suggest that, as of 2014, the VM subpopulation had likely recovered from an earlier period of overharvest, was stable, and had not exhibited detectable, negative demographic effects of climate warming. There was some evidence for changing movement patterns, which may be attributable to sea-ice loss but require additional data to understand. The low body condition of VM bears compared to the adjacent Northern Beaufort Sea subpopulation (Florke et al., 2021) and the decline in estimates of adult female survival (this study) are potential concerns that warrant further investigation. Updated parameter estimates from this analysis provide a basis for near-term management and conservation decisions and could be used in a quantitative harvest risk assessment (e.g., Regehr et al., 2021). Harvest risk assessments provide information on tradeoffs between higher harvest, which can lead to negative demographic effects—and lower harvest, which can limit opportunities

for the nutritional, cultural, and economic use of polar bears by Indigenous Peoples. Because our model estimated the number of animals within the VM subpopulation boundary as well as the corresponding superpopulation size, which was 44% higher but much less precise, management authorities will be able to evaluate which estimate is appropriate for informing harvest quotas. It is important to recognize that use of the former can underestimate the biological population capable of supporting harvest, whereas use of the latter can “double-count” animals that were enumerated as part of adjacent subpopulations. In contrast to questions raised by Taylor et al. (2002), our findings suggest that CR studies of polar bears can be useful even when the number of captures is relatively low, provided that radiotelemetry and harvest data are available. Given the rapid pace of climate warming and high cost of research in the Arctic, the methods presented here are likely applicable to other polar bear subpopulations as well as other mobile species.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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# MANAGING THE RISK FROM HUNTING FOR THE VISCOUNT MELVILLE SOUND POLAR BEAR POPULATION

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**Abstract:** Managers of harvested polar bear (*Ursus maritimus*) populations are required to determine current status and sustainable harvest levels. Time series population estimates are unavailable or suspect for most polar bear populations, including the Viscount Melville Sound (VM) population in Canada. Between 1974 and 1992, 194 polar bears were captured within VM. We used mark-recapture and standing age analyses to estimate population size and the rates of birth and death for this population. Both the current and historical harvest were also recorded. From mark-recapture data, we estimated (1) age and sex-specific natural and total survival and (2) population size from estimated capture probabilities that varied by year and were higher for females with satellite transmitters. The average population estimate for 1989–92 was 161 bears (SE = 34). We used a simulation model to estimate the population growth rate without harvest at 1.059 (SE = 0.063). Historical harvest levels and changes in the population standing sex and age distribution and sex ratio indicated that the population had been reduced by over-hunting. Using Monte Carlo simulations that utilized the estimated variability in demographic parameters, we explored the risk to this population associated with a range of harvest rates. Because of uncertainty in our estimates, we found that the population was at risk at harvest levels less than the estimated sustainable kill. The estimated risk was proportional to harvest level. Large harvest rates increased the risk of further reductions to the population and extended the recovery period that would likely be required to return the population to its current number relative to lesser harvest rates. We question the value of frequent population inventory for Viscount Melville Sound because the small size of this population constrains both the precision and the accuracy of demographic estimates. We recommend instead conservative and precautionary harvest policies to reduce the risk of harvest and enhance long term recovery of this population.

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**Key words:** demography, harvest, life-table, mark-recapture, polar bear, population viability analysis, recruitment, survival, *Ursus maritimus*

Management of large long-lived mammals, like bears, usually involves controls on hunting. Habitat and population density are always important factors in determining natural demographic rates. However, in arctic and marine environments, it is often not possible or practical to manage habitat. When habitat cannot be managed, the typical management goal for harvested marine mammal populations is persistence at current numbers or recovery, in cases where the population has declined. When numbers are relatively constant over time, density effects need not be considered in determining sustainable harvest levels. For relatively stationary populations, habitat and current densities determine the natural (unharvested) rates of birth and death. The sustainable harvest depends on the sex and age composition of the harvest (Caughley 1994). The population size and vital rates can be estimated and the harvest can be monitored each year. This demographic information can be used to estimate the sustainable harvest (Caughley 1977).

However, such an approach neglects the uncertainty of the information. If the information were perfect and constant each year, the estimated sustainable harvest could be taken forever without risk to the population. When demographic estimates are based on samples collected over several years, both sampling and annual variability are

present. Hence, the estimate of sustainable yield will also be uncertain. Population growth rate and the maximum sustainable yield are summary parameters that are estimated but rarely measured directly for bear populations. The uncertainty of both the population growth rate and the sustainable yield estimates may be calculated using Monte Carlo methods when estimates of both vital rates and the harvest sex and age composition are known (Boyce 1992, Caughley 1994).

Our approach recognizes that there is no single correct harvest level. Because our information is uncertain, each harvest level poses a different level of risk for the population. Some harvest levels may be so low that the risk is essentially zero. Other harvest levels may be so high that the population will certainly decline rapidly. The most interesting harvest levels to managers are those that pose an acceptable risk to the population and still provide an acceptable number of harvest opportunities.

We summarize the available demographic information for the Viscount Melville Sound (VM) polar bear population and compare our estimates to published values from other populations. We show how our demographic information can be used to estimate the risk of various harvest levels for the VM population and discuss options for management.

<sup>1</sup> Deceased

## STUDY AREA

VM polar bears are mainly distributed on the sea ice north of Banks and Victoria Islands and south of Melville Island (Fig. 1). The western portion of this area is part of the Inuvialuit Settlement Area and the eastern portion is part of Nunavut. The geographic boundaries of the VM polar bear population (Fig. 1) were established using mark-recapture movement data (Taylor and Lee 1995), DNA analysis (Paetkau et al. 1999), and cluster analysis of radiotelemetry data (Bethke et al. 1996, Taylor et al. 2001a).

The first polar bear population inventory ever conducted by the Government of the Northwest Territories included part of the area currently identified as the Viscount Melville Sound (VM) polar bear population (Taylor et al. 2001a). Hadley Bay and portions of Wynniatt Bay (Fig. 1) were investigated as part of a wider Central Arctic study (Schweinsburg et al. 1981, 1982; Furnell and Schweinsburg 1984). The boundaries of this population were uncertain until satellite radio-tracking technology became available (Bethke et al. 1996). Because the initial research in VM covered only a fraction of the population area, that initial work is difficult to interpret. This study constitutes the only polar bear research that included the entire VM population area.

Heavy multi-year ice is poor habitat for polar bears (Kingsley et al. 1985; Messier et al. 1994; Ferguson et al. 1998, 1999, 2000a,b, 2001;). Although polar bears can cross heavy multi-year ice, the concentration of good habitat inside a large expanse of poor habitat tends to restrict the movements of polar bears to relatively local areas. No permanent emigration from this population (i.e., bears that left the population and did not return during the time the radio collar was active) were recorded from telemetry observations (Bethke et al. 1996, Taylor et al. 2001a) and movements of marked bears into or out of this population were rare (Taylor and Lee 1995, Taylor et al. 2001a). Melville Island forms a land barrier to the north. Victoria Island and Banks Island form land barriers to the south. The western sea ice is heavy multi-year pack ice in most years and the polar bear densities in the northeastern part of the North Beaufort population are relatively low (Lunn et al. 1995). Similarly, the sea ice in eastern VM is heavy annual and multi-year mixed, with low densities of polar bears in the winter and spring (M.K. Taylor, unpublished data). This effectively concentrates both seals (*Phoca hispida* and *Erignathus barbatus*) and polar bears in the bays and coastal areas where there are tide cracks, active ice, annual ice, and mixed annual and multi-year ice (Messier et al. 1992, Bethke et al. 1996, Taylor et al.

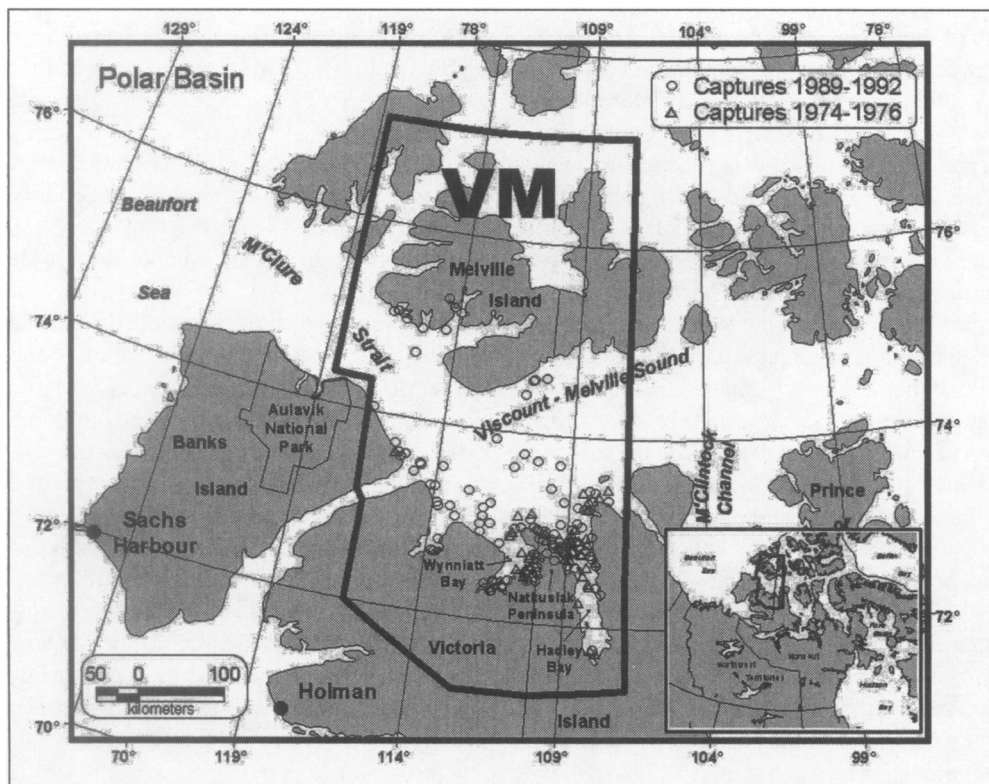


Fig. 1. Location of all captures and recaptures within the Viscount Melville Sound polar bear population, Canada, 1974–76 and 1989–92.

2001a).

Historically this population was hunted occasionally by aboriginal residents of Victoria Island; however, Usher (1974) found little evidence of year-round use in pre-settlement times. An annual harvest quota of 8 bears was allocated for Hadley Bay (Fig. 1) in the early 1970s and an additional harvest quota of 12 bears/year was allocated as the "Melville Quota" in the mid-1980s. Communities adjacent to this area could also harvest any number of their annual quota in VM until a distinct and exclusive VM quota was established in 1994. A 5-year harvest moratorium was implemented from 1995 to 1999 and the current total VM quota is 4 bears/year.

## METHODS

### Captures

Bears and their dependent cubs were captured from 1989–92 with tiletamine chlorohydrate and zolazepam chlorohydrate and marked according to procedures described by Stirling et al. (1989). Animal capture and handling procedures followed animal care protocol 950005 of the University of Saskatchewan, under the guidance of the Canadian Council of Animal Care. Bears and their dependent cubs were captured from 1974–76 with phenylcyclidine hydrochloride (Furnell and Schweinsburg 1984). Captures were opportunistic (every bear seen was captured or recaptured) during a systematic, geographically uniform search of the entire area in 1989–92. Captures from 1974–75 were restricted to the southeast portion of the population, mainly Hadley Bay (Fig. 1). Each bear was given a unique identification number, which was permanently tattooed on the upper inside lip and attached as a plastic ear tag. Each bear also was temporarily marked with a wax crayon on the fur to ensure that bears were not captured more than once per year. The bear's age was considered known if the bear was captured as a cub born that year (i.e., cub), or yearling, or was estimated by counting the annular rings of an extracted vestigial premolar (Calvert and Ramsay 1998).

### Mark–recapture Analysis

Estimates of survival rate and abundance were constructed from capture–recapture data using the Cormack–Jolly–Seber (CJS) model formulation implemented in program MARK (White and Burnham 1999). The CJS likelihood for capture–recapture data is conditioned on the initial capture events (i.e., the initial capture is treated as a release). The likelihood is based solely on the recapture events of marked animals (i.e., previously caught) and is defined by user specified models for survival and (re)capture probabilities, which can be expressed as func-

tions of covariates such as sex, age, and year.

We used MARK to analyze the capture–recapture data collected during 1974–76 and 1989–92 in VM. Captures of bears in 1974–76 were used as initial captures, but recaptures in 1975–76 were ignored because captures were restricted to a local subset of the entire population area in those early years. Recapture probability for 1975–88 was set to zero because recaptures were excluded and no recapture effort occurred in that interval.

For 1989–92, we examined a series of models for capture probability that incorporated potential covariates. We expected that capture probability would vary by year because the amount of capture effort varied between years. During 1989–90 the focus was deployment of satellite transmitters on adult females, whereas during 1991–92 transmitters were not deployed and all effort focused on captures. Therefore, we considered a model that allowed capture probability to vary for each year and another model in which capture probability was the same for 1989–90 and 1991–92. Within the area searched in a given day, bears were located by visual observation and tracking from a helicopter. Successful location and eventual capture were likely to be affected by the number of bears in a group, their reaction to the helicopter, movement patterns, and fidelity to known high use areas. Because these factors were likely to vary for different sex and age classes, we categorized bears into 3 classes: (1) females, cubs, and yearlings; (2) sub-adults (age 2–4) of both sexes; and (3) adult males. We considered models in which capture probability varied for these classes. We also considered models in which bears with transmitters had a higher capture probability because their location was known at various times throughout the year. Cubs and yearlings of a female with a transmitter were considered to have the same probability of capture as their mother.

For survival probability, we considered models that included sex, age, and year. Because more males were harvested than females, we expected their survival to be lower. Survival was also likely to vary by age; in particular, we expected cubs to have lower survival than non-cubs. We considered 2 age-specific models with different survival for cubs and non-cubs and another model in which non-cubs were further divided into yearlings, sub-adults (age 1–5 years), and adults ( $\geq 6$  years). Annual differences in harvest and environmental conditions could create variation in survival, so we considered models with 3 distinct annual survival rates for 1989–92 and a constant survival rate for the interval 1974–89.

We fitted a series of CJS models using each capture probability model with each survival probability model. We considered additive models with main effects (e.g., sex + year) but did not consider models with interactions because there were too few data to support the additional

complexity. We used Akaike’s Information Criterion adjusted for over-dispersion (QAIC<sub>c</sub>) (Burnham and Anderson 1998) as a guide for model selection. The data were likely to be overdispersed (i.e., greater than binomial variation) because survival and capture events of family groups (e.g., female with cubs or yearlings) were not independent. We estimated the overdispersion coefficient  $\hat{c}$  based on the number of dependent cub captures relative to all captures (Appendix).

Because the CJS likelihood does not include the probability distribution for the unmarked animals, it may not provide the best precision from the data for estimating abundance when survival and capture probabilities are not time dependent (i.e., constrained Jolly-Seber model). However, we used the CJS formulation because of its modeling flexibility in the MARK software and the Jolly-Seber estimator for abundance ( $\hat{N}$ ) using the estimated capture probabilities ( $\hat{p}$ ) from the marked animals in the CJS likelihood (Pollock et al. 1990) for each year  $i$ :

$$\hat{N}_i = \frac{n_i}{\hat{p}_i}$$

We computed variance estimates using a Taylor series approximation that contains a component of variance for the number observed and another for estimation of  $p$  (Thompson 1992:165):

$$\hat{Var}(\hat{N}_i) = \frac{\hat{n}(1-\hat{p}_i)}{\hat{p}_i^2} + \frac{\hat{N}_i^2}{\hat{p}_i^2} \hat{Var}(\hat{p}_i)$$

When we stratified the population into  $k$  strata (e.g., sex-age class), the total estimated population was simply the sum of the stratum estimates:

$$\hat{N}_i = \sum_{j=1}^k \frac{n_{ij}}{\hat{p}_{ij}}$$

The variance estimator was extended to include covariances between estimated capture probabilities in the  $k$  strata:

$$\hat{Var}(\hat{N}_i) = \sum_{j=1}^k \frac{n_{ij}(1-\hat{p}_{ij})}{\hat{p}_{ij}^2} + \sum_{j=1}^k \sum_{j'=1}^k \frac{n_{ij} n_{ij'}}{\hat{p}_{ij}^2 \hat{p}_{ij'}^2} \hat{Cov}(\hat{p}_{ij}, \hat{p}_{ij'})$$

Our extension is equivalent to the variance estimators used by Huggins (1989) and Borchers et al. (1998) for abundance estimates constructed in a similar fashion. We used a similar estimator to estimate the variance of the mean population size over several years. Our abundance estimator is equivalent to the one proposed by McDonald and Amstrup (2001), but our variance estimator is different than theirs.

The estimates of survival derived from the capture-recapture data include harvest losses. We were interested in estimating natural survival to investigate the impacts of alternative harvest strategies and levels. We estimated

natural survival  $S_n$  from the average annual harvest ( $H$ ), population size ( $N$ ), and total survival ( $S$ ) as:

$$S_n = \frac{S}{1 - \frac{H}{N}}$$

which assumed that harvest and natural mortality occurred in 2 separate time periods and  $h = H/N$  is the estimated harvest rate. We also used a Taylor series approximation for the variance of natural survival:

$$\hat{Var}(\hat{S}_n) = \hat{S}_n^2 \left[ \frac{\hat{Var}(\hat{S})}{\hat{S}^2} + \frac{\hat{Var}(\hat{N})h^2}{\hat{N}^2(1-h)^2} - 2 \frac{\hat{Cov}(\hat{N}, \hat{S})h}{(1-h)\hat{N}\hat{S}} \right]$$

where

$$\hat{Cov}(\hat{N}, \hat{S}) = - \frac{\hat{N} \hat{Cov}(\hat{S}, \hat{p})}{\hat{p}}$$

The variances and covariances for  $p$  and  $S$  were computed by program MARK after inflation by the over-dispersion coefficient. Non-symmetric 95% confidence intervals were constructed based on an assumed log-normal distribution (Burnham et al. 1987) to compensate for the skewed sampling distribution resulting from a lower bound on the estimate ( $N > n$ ) and correlation between the estimate and its estimated variance (Pollock et al. 1990).

### Standing Age Distribution Analysis

The standing age distribution was based only on captures and recaptures for 1989–92 that occurred inside the final VM boundaries. Only the 1989–92 captures and recaptures were used to estimate litter size and recruitment parameters. The sampling unit in this case was family units and individuals. Each individual or family group was recorded by age as a male, solitary female, female with a cub, female with 2 cubs, female with a yearling, female with 2 yearlings, female with a 2-year-old, or female with two 2-year-old cubs. One female with 3 offspring was observed and was treated as an observation of females with 2 offspring for the standing age distribution analysis.

Our method for estimating litter size, litter production rate, and cub survival from the standing age distribution is described in Taylor et al. (1987a, 2000) and available as the software package “Vital Rates” (Taylor et al. 2000). For comparison to the mark-recapture estimates of survival rate, the adult male and female survival rates (AMΦ and AFΦ respectfully) were estimated from the standing age distribution using the Chapman-Robson truncated method (Chapman and Robson 1960) from age 2 to the final age that had 5 or more records. We recognized that the Chapman-Robson survival estimate is actually not an age-constant survival rate, but is rather an age-constant survival rate divided by population growth rate for populations at stable age distribution (Caughley 1977). The

AF $\Phi$  value is required to determine other values which were based on standing age ratios and which were contingent on female survival (Taylor et al. 1987a).

The mean litter size of cubs (CLS) and yearlings (YLS) was used to estimate the survival rates of cubs (DeMaster and Stirling 1983; Taylor et al. 1987a, 2000). Dependent offspring survival rates were calculated based on the change in litter size observed from cubs to yearlings (cub individual survival, CISR) and yearlings to 2-year olds (yearling individual survival, YISR). Estimates of CISR and YISR are not affected by adult female survival rate because the entire litter is lost if their mother dies (i.e., no change in mean litter size). The cub standing age survival rate (CS $\Phi$ ) was also calculated as the ratio of yearlings/cubs in the standing age distribution. Similarly, an age ratio yearling survival rate (YS $\Phi$ ) was calculated as the ratio of 2-year olds/yearlings. CS $\Phi$  and YS $\Phi$  estimates are survival rate/population growth rate at stable age distribution, and include adult female mortality. The correction for adult female mortality and population growth rate is 1/AF $\Phi$  (Taylor et al. 1987a, 2000). Assuming stable age distribution and unbiased sampling, CISR, YISR, CS $\Phi$ , and YS $\Phi$  estimates are directly comparable to cohort estimates from telemetry or mark-recapture methods.

The estimates of age-specific litter production rate (LPR) were specific to females that were available to mate the previous year (i.e., those with no cubs or 2-year-olds), and did not include females with dependent cubs (i.e., cubs and yearlings). We viewed litter production rates for age 4 (LPR4) and age 5 (LPR5) as distinct (i.e., reduced) litter production rates. We assumed that by age 6, all females were producing litters at adult rates (LPR6). The average age of first birth (AFB) was determined for surviving females only.

Except as identified above, all rates were assumed to be age constant (i.e., no senescence). Because there were relatively few observations for older individuals, any reduction of rate estimates due to senescence was assumed to be negligible.

We also calculated 6 summary parameters based on the above values (DeMaster 1981; Taylor et al. 1987a, 2000): mean reproduction (litter production) interval (R-I), mean annual reproduction rate (R-R), mean mating (available to mate) interval (M-I), mean annual mating rate (M-R), proportion of females that reached adulthood but had only 1 litter (P<sub>1</sub> litter), and proportion of surviving females that reached adulthood but produced no litters (P<sub>0</sub> litter). The mark-recapture estimates of cub survival and adult survival were used to calculate the 6 summary parameters. The stable-age, zero-harvest population growth rate ( $\lambda$ ) was also calculated according to Taylor et al. (1987c, 2001b). Mean annual reproduction rate could be used in

an annual life-table model; however, projections would only be accurate if populations were at stable age distribution (Taylor et al. 1987b, but also see Testa 1996).

We used the jack-knife method (Arveson 1969) to estimate the variance of the life history parameters estimated from the standing age distribution (Taylor et al. 1987a, 2000). The data were stratified by year. Our estimate of variance pooled both sampling error and inter-year environmental variation. Most of our rate estimates were ratios; however, the jack-knife estimate is a mean of means and the error was assumed to be normally distributed. The variance of the corrected (for AF $\Phi$ ) cub survival estimate was calculated as the binomial variance of the corrected ratio. The variances of the summary parameters (R-I, R-R, P<sub>1</sub> litter, M-I, M-R, P<sub>0</sub> litter and  $\lambda$ ) were determined using the Monte Carlo method with 1200 iterations (Taylor et al. 2000, 2001b). All comparisons of binomial parameter means used chi-square tests with the Yates correction (SigmaStat 1997). Differences were considered not significant for  $P > 0.10$ . Monte Carlo simulations to estimate the mean and SE of population growth rate were performed with a Visual Basic program called "RISKMAN RISK MANAGEMENT" (Taylor et al. 2001b). Both the Vital Rates and RISKMAN programs are available from the senior author.

## Uncertainty Analysis

Monte Carlo simulations were used to explore harvest management options by estimating the risk of population reduction for various harvest scenarios. A population was considered at risk if the population trajectory after a set time interval left the population size below a threshold proportion ( $T$ ) of the target population size that would allow recovery within a specified number of years (recovery time). The expected time to recovery ( $Y$ ) from a reduced population size ( $N_r$ ) to a recovered target population size ( $N_t$ ) can be computed from the unharvested population growth rate ( $\lambda$ ):

$$Y = \frac{-\ln(P)}{\ln(\lambda)}$$

where  $P = N_r/N_t$ . The threshold proportion ( $T$ ) for a specified recovery time ( $Y$ ) is:

$$T = e^{-Y \ln(\lambda)}$$

If a population is reduced, so long as  $P \geq T$ , it would be expected to recover within  $Y$  years with deterministic growth.

RISKMAN (Taylor et al. 2001b) was used to estimate the proportion of population trajectories that were not reduced below the threshold proportion (acceptable outcome) for a range of harvest levels (annual quota: 0–25).

RISKMAN differs from other population viability

analysis (PVA) simulation models in that it allows correct simulation of the 3-year life cycle for polar bears and allows the estimated sex and age selectivity/vulnerability of the harvest to be modeled dynamically. RISKMAN was developed to estimate the uncertainty associated with various harvest management options using estimates of the standard error of the input parameters. RISKMAN is an individual based model, so demographic uncertainty (Caughley 1994) is incorporated. The uncertainty associated with estimates of survival and recruitment pools both sampling and environmental uncertainty (part of what Thompson et al. [1998] call process variation). RISKMAN allows the user to partition the total uncertainty (variance) into sampling and environmental uncertainty. Generally, sampling uncertainty reduces the geometric mean population growth rate, which increases the fraction of population projections that are unacceptable. Because the jack-knife method for estimating variance does not lend itself to partitioning the total variance estimate (White 2000), partitioning the variance estimates from the standing age analysis was not possible. However, the root difficulty was the small sample size for this population. The number of recapture years and number of bears caught were insufficient to partition the variance into its 2 components. The environmental variance component was estimated as essentially 0 from the variance components output of program MARK. However, other studies (Stirling and Lunn 1997, Stirling et al. 1999) have demonstrated environmental variability in vital rates for some polar bear populations. Rather than incorrectly assuming that there was no environmental variation, we subjectively specified that 75% of the variance was due to sampling uncertainty and 25% was environmental variation. To evaluate this specification, we explored the 2 boundary conditions by assigning the total variance to sampling uncertainty and alternatively to environmental variation.

For each year of the simulation, the frequency of occurrence of unacceptable outcomes (based on our threshold value) was monitored and reported as cumulative proportion of total runs over the threshold at that time. Individual runs could recover from "depletion", but not from a condition where all males or all females or both were lost. The total unacceptable outcomes over an indefinite period were also of interest for exploring management options that do not involve periodic monitoring. Required population parameter estimates and standard error inputs included: annual natural survival rate (stratified by age and sex as supported by the data); age of first reproduction; age-specific litter production rates for females available to have cubs (i.e., females with no cubs and females with 2-year-olds); litter size; sex ratio of cubs; sex, age, family status distribution of harvest; and initial population size.

The initial age distribution was identified by determining the stable age distribution using total mortality values. The harvest selectivity and vulnerability array was identified by comparing the total-mortality stable age distribution with the sex, age, and family status distribution of the historical harvest. Harvest was stratified by sex, age (cubs and yearlings, age 2–5, age 6–19, and age >20), and family status (alone, or with cubs and yearlings, with 2-year-olds).

Harvest simulations were conducted using the natural survival rates from this study. Although the final year of sampling was 1992, simulations were approximately time referenced to 1999 by allowing 5 years of harvest moratorium. The starting (1999) population size (215, SE = 57.5) was determined by running the model in stochastic mode (2,500 iterations) for 5 years. We then ran the simulations for 15 years beginning with 1999. We choose 15 years as a simulation interval because we estimated that the fraction of the VM population that would still be marked after  $15 + 7 = 22$  years (i.e., 7%) would be sufficient to re-estimate the population at the next population inventory. Adult survival rates of long-lived animals can be underestimated (J. Laake and M. Taylor, unpublished analyses) when there are few old marks in the population to observe and there is unmodeled heterogeneity in capture and survival probabilities. A range of harvest levels was used to estimate the harvest associated with a range of risk thresholds (i.e., proportions of unacceptable reductions to initial numbers). We also calculated risk over 75 years for annual harvest rates ranging from 0 to 25 bears to investigate the risk implications of irregular monitoring.

## RESULTS

From 1974 to 1976, 30 females and 16 males were captured in VM (Table 1). These 46 bears were insufficient to estimate total numbers or survival and recruitment rates from either the mark-recapture data or the standing age distribution. Thus, we pooled the 46 initial captures from 1974–76 with the 90 females and 58 males that were captured and recaptured between 1989 and 1992 (Table 1) for the mark-recapture estimates of numbers and survival rates (Tables 2, 3). The estimates from analysis of the standing age distribution using the 1989–92 data were:  $AM\Phi = 0.901$  (SE = 0.048),  $AF\Phi = 0.963$  (SE = 0.007),  $CISR = 1.0$  (SE = 0.0),  $CS\Phi = 0.773$  (SE = 0.046),  $YS\Phi = 0.920$  (SE = 0.033), and  $YLS = 1.752$  (SE = 0.064).

Changes in the VM polar bear population were reflected in the differences between the 1973–76 and 1989–92 capture samples. There were 4 observations of females with 3-year-old cubs in 1989–92, but none in 1973–76. The sex ratio among adults (age  $\geq 6$ ) declined from 49% to

**Table 1. Initial captures of polar bears by sex and age for 1974–76 and 1989–92 for Viscount Melville (VM) Sound population, Nunavut, Canada.**

Sex	Year	Age					Total
		Cub	Yearling	2-yr old	3-yr old	>3-yr old	
Females	1974–76	3	7	0	2	18	30
	1989	10	0	0	0	12	22
	1990	0	1	2	0	5	8
	1991	5	8	1	1	15	30
	1992	6	4	4	2	14	30
Total males		24	20	7	5	64	120
	1974–76	4	1	0	0	11	16
	1989	4	2	3	2	6	17
	1990	0	0	1	0	1	2
	1991	4	5	3	0	4	16
	1992	12	4	3	1	3	23
Total		24	12	10	3	25	74

**Table 2. The mean and standard error of natural (no harvest, upper rows) survival and actual (includes harvest, lower rows) survival rates for the Viscount Melville (VM) polar bear population in Nunavut Canada for the interval 1974–92.**

Sex and age	Mean annual survival rate (SE)	
	No harvest	Harvest
<b>Female</b>		
0	0.693 (0.183)	0.693 (0.183)
1–5	0.957 (0.028)	0.905 (0.026)
6–19	0.957 (0.028)	0.905 (0.026)
≥20	0.957 (0.028)	0.905 (0.026)
<b>Male</b>		
0	0.448 (0.216)	0.448 (0.216)
1–5	0.924 (0.109)	0.774 (0.081)
6–19	0.924 (0.109)	0.774 (0.081)
≥20	0.924 (0.109)	0.774 (0.081)

29% males ( $P = 0.061$ ,  $n = 161$ ). The adult sex ratio of captures from 1973–76 did not differ from 50% ( $P = 0.542$ ,  $n = 54$ ). However, the adult sex ratio of captures from 1989–92 was 14 different from 50:50 ( $P = 0.001$ ,  $n = 107$ ). The sex ratio of cubs was not different between the 2 periods ( $P = 1.000$ ,  $n = 122$ ) and did not differ from 50:50 ( $P = 0.543$ ,  $n = 122$ ). In the 1989–92 sample, the fraction of adult captures that were males (29%) was lower than the fraction of male cub captures (45%); ( $P = 0.010$ ,  $n = 230$ ). The adult (>5 years) fraction of the population was 44% in 1989–92 and 62% in 1974–76 ( $P = 0.053$ ,  $n = 110$ ). Estimates of the mean annual recruitment rate (and interval), mating rate (and interval), and unharvested population growth rate (Table 4) were based on the mark–recapture survival estimates from the selected model (Table 2) and standing age estimates of recruitment parameters (Table 3).

The harvest between 1973 and 1992 was highly selective for male bears (36.6% females and 63.4% males,  $n = 164$ ) and averaged 8.2 bears/year. However, the average annual harvest from 1985 to 1990 was 19.6 and the average annual harvest between 1980 and 1989 was 16.1. The relatively high harvest rates and strong selection for males

**Table 3. The mean and standard error of cub litter size (CLS), litter production rate for 4, 5, and adult (≥6) age strata, proportion of cub litters that are male (PCM), and total number (i.e. all cubs and adults of both sexes) of males and females for the Viscount Melville (VM) polar bear population in Nunavut, Canada for the interval 1989–92.**

Parameter	Mean (SE)
Cub litter size	1.64 (0.125)
Litter production rate:	
4-year olds	0.0 (0.0)
5-year olds	0.623 (0.414)
≥6-year olds	0.871 (0.712)
Proportion male cubs	0.535 (0.118)
Abundance average 1989–92	
Males	61 (16.6)
cubs	9 (9.5)
others	52 (15.2)
Females	100 (20.0)
cubs	21 (6.2)
others	79 (15.4)
Total	161.0 (34.5)

that occurred just before the population inventory in 1989–92 markedly reduced the number of adult males in the population.

Sixty-two percent of the 194 bears captured were females (Table 1). During 1989–92, 60 bears were recaptured (Table 5). Eleven percent of the bears initially captured from 1974–76 were recaptured at least once during 1989–92 and 44% of the bears initially captured from 1989–91 were recaptured at least once during 1990–92. There were 128 captures and recaptures for the years 1989–92 and of these 23 were cubs. The proportion of those captures that were not cubs was 0.82 and the estimate of the over-dispersion coefficient ( $\hat{c}$ ) was 1.22 (1/0.82).

The model with minimum QAIC<sub>c</sub> included survival parameters for males and females and capture probability parameters for year (1989–90 vs. 1991–92) and “transmitter” (i.e., capture probability was higher for females with satellite transmitters, Table 6). Several other models had QAIC<sub>c</sub> values close to the minimum, including a model with a parameter for differential cub survival. We

**Table 4. Estimates of the mean and standard deviation of polar bear reproduction parameters from uncorrected ANURSUS vital rate estimates for the Viscount Melville (VM) Sound population of polar bears in Nunavut, Canada, 1989–92. The vital rates estimates are: reproduction interval (R-I), litter reproduction rate (R-R), proportion of females that have only 1 litter ( $P_1$  litter), mating interval (M-I), mating rate (M-R), proportion of females that have no litters ( $P_0$  litter) and stable age unharvested population growth rate ( $\lambda$ ). The Monte Carlo method (1,200 iterations) was used to estimate the standard deviation of these values.**

	R-I (years)	R-R (litters/year)	$P_1$ litter	M-I (years)	M-R (matings/year)	$P_0$ litter	$\lambda$
Mean	2.976	0.338	0.119	2.545	0.397	0.049	1.059
SD	0.209	0.024	0.0753	0.255	0.039	0.030	0.063

**Table 5. Recaptures for 1989–92 summarized by sex and age (cub or other) at initial capture. A bear initially caught in 1975 and first recaptured in 1991 becomes an entry in the 1991 releases. Recaptured cubs are shown in the releases of non-cubs. Recaptures prior to 1989 were not used in the analysis. The percent recaptured over a long-time span (i.e., mid 1970s to 1989) illustrates differences in survival rate. A (-) indicates no recaptures possible.**

Sex	Age	Year	Released	Year of next recapture				Total	%
				1989	1990	1991	1992		
Females	cub	1974	0	0	0	0	0	0	-
		1975	0	0	0	0	0	0	-
		1976	3	0	0	0	0	0	0
		1989	10		2	3	0	5	50
		1990	0			0	0	0	-
	other	1991	9				2	2	22.2
		1974	6	1	0	0	0	1	16.7
		1975	17	1	0	1	1	3	17.6
		1976	4	0	0	1	0	1	25
		1989	14		4	4	3	11	78.6
Male	cub	1990	14			8	1	9	64.3
		1991					12	12	29.3
		1974	1	0	0	0	0	0	0
		1975	2	0	0	0	0	0	0
		1976	1	0	0	0	0	0	0
	other	1989	4		0	1	0	1	25
		1990	0			0	0	0	-
		1991	4				1	1	25
		1974	5	0	0	0	0	0	0
		1975	6	0	0	0	0	0	0
other	1976	1	0	0	0	0	0	0	
	1989	13		2	3	1	6	46.2	
	1990	4			2	0	2	50	
	1991	18				6	6	33.3	

believe it is more biologically reasonable to include a separate cub survival and we know that males were selected during harvest, so the model with age and sex parameters was selected as the best model.

Capture probability varied from 0.15 to 0.70 (Table 7) and annual estimates of total abundance ranged from 73 to 208 (1989:  $N = 208$ ,  $SE = 84$ ; 1990:  $N = 73$ ,  $SE = 30$ ; 1991:  $N = 165$ ,  $SE = 32$ ; 1992:  $N = 202$ ,  $SE = 40$ ) with a mean of 161 bears ( $SE = 34.5$ ) (Table 3). Female total survival rates (including harvest mortality) were higher than males. Nearly twice as many males were harvested annually than females (8.4 males vs. 4.3 females). The difference in natural survival rates of males and females was small (Table 2) and was well within the range of sampling error.

The unharvested population growth rate for VM ( $\lambda = 1.059$ ) determines the minimum time required for recovery from any reduction in numbers. The population growth

rate can be restated as the proportion of the original population required for recovery times of 0, 3, 5, 10, ... X years (Table 8). For example, a population reduced to 0.751 of original numbers would require 5 years to recover and a population reduced to 0.842 of original numbers would require 3 years to recover, if  $\lambda = 1.059$ . A unique distribution of outcomes is defined for any given harvest level. Some proportion of outcomes fall within recovery thresholds of 1, 2, 3, ... X years and these we termed "acceptable outcomes". That proportion of acceptable outcomes depends on the frequency of monitoring (e.g., 15 years, Table 8; 75 years, Fig. 2), starting population size, survival rates, recruitment rates, harvest sex and age composition, harvest number, uncertainty of these parameters, and recovery threshold value (i.e., years).

We evaluated the sensitivity of risk estimates associated with a range of harvests to the relative apportionment of estimate uncertainty into sampling and

**Table 6. QAIC<sub>c</sub> values for some of the best Cormack-Jolly-Seber polar bear survival models fitted to the Viscount Melville Sound, Nunavut, Canada 1974–92 capture and recapture data. Age refers to cub and non-cub; capture model year refers to partitioning based on annual capture effort strata (i.e., 1989–90 different from 1991–92). Models with more refined age and year partitioning were not supported by the data (i.e., had higher QAIC<sub>c</sub> values for equivalent models).**

Survival model	Capture probability model <sup>a</sup>						
	Age–sex+ transmitter	Age–sex+ year	Transmitter + year <sup>b</sup>	Transmitter	Age/sex	Year	Constant
Age+sex <sup>b</sup>	228.3 (7)	228.4 (7)	220.4 (6) <sup>b,c</sup>	225.0 (5)	232.0 (6)	224.5 (5)	227.4 (4)
Age	230.3 (6)	229.8 (6)	221.7 (5) <sup>b</sup>	226.5 (4)	233.4 (5)	227.6 (4)	230.2 (3)
Sex	227.8 (6)	227.1 (6)	219.8 (5) <sup>b</sup>	224.6 (4)	230.7 (5)	223.4 (4)	226.5 (3)
Year	234.8 (6)	229.8 (6)	223.2 (5) <sup>b</sup>	230.7 (6)	234.8 (7)	229.8 (6)	233.6 (5)
Constant	230.3 (5)	228.7 (5)	221.5 (4) <sup>b</sup>	226.3 (3)	232.7 (4)	226.6 (3)	229.5 (2)

<sup>a</sup> Number of estimated parameters in parenthesis.

<sup>b</sup> Suite of best models.

<sup>c</sup> The selected model (Survival model: age + sex, Capture model: transmitter + year) also considered biological reality (QAIC<sub>c</sub> = 220.4).

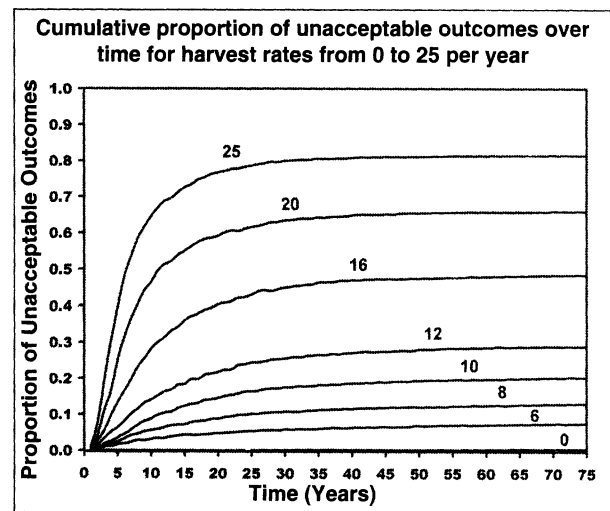
**Table 7. Capture probabilities and standard errors for best model of Viscount Melville Sound, Nunavut, Canada, polar bear population capture-recapture data.**

	Capture probability	
	Estimate	SE
1989–90 without transmitter	0.152	0.058
1989–90 with transmitter	0.407	0.141
1991–92 without transmitter	0.38	0.064
1991–92 with transmitter	0.702	0.132

environmental uncertainty (Table 9) for the case when a population reduction of 0.751 from initial numbers was judged “acceptable”. The estimate of risk was insensitive to how uncertainty was apportioned into sampling and environmental components for harvest rates that were clearly conservative (i.e., almost always sustained) and for harvest rates that were clearly excessive (i.e., almost always resulted in a dramatic decline). The maximum deviations (0.09 = maximum observed, Table 9) occurred for intermediate harvest levels.

## DISCUSSION

Currently, determination of population status and sustainable harvest levels of polar bears are based on estimates of vital rates that serve as input to a deterministic harvest simulation model (Taylor et al. 1987c). The vital rate estimates for the Taylor et al. (1987c) approach were



**Fig. 2. Estimated probabilities of a population reduction that would require >5 years to recover to original numbers for a range of harvest rates (0–25 per year) and time intervals (0–75 years) shows that risk increases with monitoring interval.**

based on an analysis of the pooled standing age distributions of essentially all of the polar bear capture data available at this time (Taylor et al. 1987a). Simulation results (Taylor et al. 1987a) indicated that the maximum sustainable harvest was about 1.5% of the total population of females (age ≥ 2+) and about 3% of the total population

**Table 8. Proportion of acceptable simulation outcomes for a range of annual harvest values for polar bears in Viscount Melville Sound (VM), Nunavut, Canada, from 1997. Acceptable outcomes left the population at or above the critical threshold after 15 years. For example, if the VM annual harvest were 6, the probability that the population would either increase or decline no more that could be recovered in 5 years is 0.97.**

Years to recovery <sup>a</sup>		Annual harvest								
		0	2	4	6	8	10	12	16	20
0	(1.000)	1.000	0.992	0.981	0.940	0.874	0.802	0.704	0.4884	0.300
3	(0.842)	1.000	0.997	0.984	0.966	0.921	0.859	0.757	0.542	0.348
5	(0.751)	1.000	0.998	0.991	0.972	0.938	0.877	0.804	0.575	0.393
10	(0.564)	1.000	1.000	0.997	0.987	0.961	0.932	0.868	0.686	0.476
15	(0.432)	1.000	1.000	0.999	0.993	0.979	0.948	0.895	0.765	0.554
20	(0.318)	1.000	1.000	0.998	0.996	0.986	0.967	0.929	0.807	0.612
25	(0.239)	1.000	1.000	0.999	0.998	0.989	0.977	0.944	0.846	0.703

<sup>a</sup> The proportion of original population associated with a given recovery time (i.e., critical threshold) is listed in parenthesis.

**Table 9. The proportion of runs that did not reduce initial population below 0.751 (i.e., not more than a 5-year recovery period at zero harvest) for harvest levels ranging from 0 to 20 bears/year for 3 simulations (2,500 iterations each) for which the ratio of sampling to environmental uncertainty was set to 1.0, 0.75, and 0.0 for Vicount Melville (VM) Sound population of polar bears, Nunavut, Canada.**

Sampling to environmental uncertainty ratio	Annual harvest								
	0	2	4	6	8	10	12	16	20
1.00	1.000	0.995	0.985	0.963	0.926	0.858	0.784	0.578	0.396
0.75	1.000	0.998	0.991	0.972	0.938	0.877	0.804	0.575	0.393
0.00	1.000	0.998	0.999	0.992	0.981	0.968	0.898	0.652	0.410

of males (age  $\geq 2$ ). A pooled data set was used because analysis of population-specific standing age distributions produced estimates of some parameters that were nonsense in all cases (i.e., for all populations). Subadult and adult survival rates were assumed rather than estimated because neither the standing age analysis nor the mark-recapture analyses provided estimates that were consistent with the observed long-term persistence of harvested polar bear populations (DeMaster et al. 1980; M. Taylor, unpublished analyses). Taylor et al. (1987c) assumed that vital rate estimates based on pooled data from all populations and logical assumptions would result in the most accurate estimates of sustainable harvest rates. It was recognized that better sampling protocols and improved mark-recapture models were needed for improved population-specific estimates. Comparison of the actual harvest to the 1.5% of the total population (females) and 3.0% of the total population (males) is still the accepted method by which the status of polar bear populations are determined (Lunn et al. In Press; 2001 Canadian Federal/Provincial Polar Bear Technical Meeting Minutes, 2002).

The present work uses the same standing age analysis approach and the population simulation model is a stochastic version of the same harvest simulation model described by Taylor et al. (1987c). The main differences from previous population inventory studies are the way the data were collected, the mark-recapture analysis, and the incorporation of uncertainty into the harvest management recommendations. It is relevant to compare our results to other demographic studies completed since 1987 so that the reader can evaluate both our estimates of parameter values and the risk estimates that are based on them.

### Mark-recapture Analysis

Only a few published studies report survival or abundance estimates from mark-recapture studies of polar bears after 1987 (Derocher and Stirling 1995, Lunn et al. 1997, Amstrup et al. 2001). Amstrup et al. (2001) suggested that previous mark-recapture studies of polar bears in the Beaufort Sea were compromised by unmodeled heterogeneity in survival and capture probabilities. Heterogeneity probably affects all mark-recapture studies to some degree but it was undoubtedly important for Amstrup et al. (2001) because they analyzed spring and fall capture

data collected by different researchers for different purposes from 1969 to 1998, and 38% of the 1,137 "captures" after 1981 were radio relocations. They modeled survival and capture heterogeneity of female polar bears and used a "modified" QAIC<sub>c</sub> procedure (McDonald and Amstrup 2001) to select from 82 different models that included combinations of potential covariates. Our analysis differed from that of Amstrup et al. (2001) and McDonald and Amstrup (2001) in that our data were specifically collected for mark-recapture analysis and included both sexes. We used a different variance estimator which produced larger variance estimates because we feel the variance estimator they used neglected covariance between the estimated capture probabilities of individuals. Our model selection criteria were according to Burnham and Anderson (1998), except that we did not model average for "tied" models. We did not understand the modified QAIC<sub>c</sub> method used by McDonald and Amstrup (2001) because QAIC<sub>c</sub> already attempts to optimize for both bias and variance. Our survival estimates are provided; the reader may judge if they are reasonable and consistent with other estimates and with what is known about polar bear life history.

Since the analyses of Derocher and Stirling (1995) and Lunn et al. (1997), the development of computer software packages like MARK have enabled researchers to develop more sophisticated analyses to account for heterogeneity. However, this capability should not be viewed as a way to avoid a proper study design. Heterogeneity can only be modeled if the data are sufficient. Further, we cannot model extreme heterogeneity whereby some animals have no chance of being captured. Although our analysis was similar to that of Amstrup et al. (2001), we believe our data were less heterogeneous. We did have much smaller sample sizes and thus would expect to be able to identify less heterogeneity. However, we believe our data were less heterogeneous because we attempted to survey the entire VM area from 1989–92 in a geographically uniform manner and we captured every bear we encountered. The flexibility of MARK allowed us to incorporate the earlier limited effort from 1974–76 by using the initial captures but excluding recaptures of those bears until the years with uniform sampling coverage.

Unfortunately, uniform coverage of the survey area does

not guarantee homogeneity. We did have temporal variability in capture probability because telemetry efforts in 1989 and 1990 reduced the helicopter time available for search and capture operations. Also, female polar bears who were given radiocollars and their cubs (as yearlings) were more likely to be recaptured than other bears. This was only partly because some of the collared adult females were located and recaptured using radio signals. Even after the radiocollars were removed, these individuals still had higher capture probabilities. This may have been because these individuals had a preference for a particular geographic area where they were easily located year after year. However, our data were not sufficient to establish the mechanism by which radiocollared bears and their offspring were more likely to be captured than other bears. We did not identify any sources of capture heterogeneity that would cause bias in the analysis of the standing age distribution. However, the small sample sizes may have resulted in the failure to fit more stratified models to detect additional sex, age, or family status effects.

Based on our unpublished analyses of larger populations in Lancaster Sound, Baffin Bay, and Gulf of Boothia, we anticipated that survival would vary by age and sex. The best model based on QAIC<sub>c</sub> only supported sex-specific rates, but we chose a closely competing model with separate cub (age 0) and non-cub (age 1+) survival rates. The failure of our analysis to identify additional age stratification in polar bear survival rates is probably because our data were too sparse to support additional model parameters. The population size imposes an obvious constraint on the number of captures. In turn, small numbers of captures limit analysis models to fewer parameters (e.g., simpler models). Thus, sample size can influence not only the precision, but also may influence the accuracy of the analysis.

### Vital Rate Comparisons

Our estimates of cub and yearling litter size, AMΦ, AFΦ, and to a certain extent total cub survival and age of first birth fall within the general range of published values in spite of differences in methodology and the possibility of non-representative sampling on other studies. Our standing age estimates of survival were not independent of our mark-recapture estimates because they were based on the same data. However, we did observe that the standing age Φ for both male and female non-cubs was larger than the mark-recapture survival estimates (harvest mortality included) for the same parameters. The higher values for the standing age estimates suggest that population growth rate (λ) was less than 1.0 for most of the years represented in the standing age distribution. We used the mark-recapture survival estimates for our simulations because mark-recapture estimates are potentially adjusted

for differential capture probabilities and because we had no independent estimate of λ to correct the standing age survival estimates.

Lunn et al. (1997) estimated the annual adult (age ≥ 2) total (natural + harvest mortality included) female survival rates to be 0.88 for females and 0.86 for males in western Hudson Bay. Although the survival estimates were within the sampling range of our equivalent survival rates for VM non-cubs for both sexes, this comparison is compromised because the harvest mortality rates for the 2 populations are likely different. Lunn et al. (1997) did not report natural survival estimates. We were unable to compare our estimates with those of Amstrup et al. (2001) because they did not report survival estimates except as a function of covariates that were not clearly defined. Amstrup et al. (1986) assumed a range of annual survival rates from 0.82 to 0.94 bracketed the true survival rate of polar bears in the Southern Beaufort Sea. Amstrup and Durner (1995) later estimated the natural survival rate of adult females in the same population to be 0.996 and the total survival rate of adult females to be 0.969; however, this telemetry based estimate was not consistent with the age distribution of polar bears in this area (Amstrup 1995).

Comparisons with other vital rate values in the literature were often difficult because most other researchers used different methods and different terminology for the estimates they reported (Stirling et al. 1980, 1999; Ramsay and Stirling 1988; Derocher and Stirling 1992, 1995; Amstrup 1995). Most of the published estimates that were based on the standing age distribution ignored the 3-year reproduction cycle of polar bears and published annual summary rates (i.e., mean natality = male and female cubs/female/year, as per Stirling et al. [1980] and Ramsay and Stirling [1988]). This mean natality rate (MNR) was calculated as:

$$MNR = (C_x + \frac{Y_{x+1}}{p_0}) (\frac{1}{N_x + N_{x+1}})$$

where  $C_x$  = cubs (male and female) with females of age  $x$ ;  $Y_{x+1}$  = yearlings (male and female) with females of age  $x+1$ ;  $p_0$  = survival rate of age class 0 (i.e., cubs);  $N_x$  = females of age  $x$ . The estimate for  $p_0$  was the standing age distribution ratio of yearlings (Y) to cubs (C), or Y/C. If the age distribution is stable and stationary, the ratio Y/C is actually  $p_0/\lambda$  (Caughley 1977). Additionally the mortality of females from age  $x$  to  $x+1$  was not considered, although this would clearly affect how many yearlings were counted because age 0 cubs are completely dependent on their mother. The mean annual natality rate is an abstraction for species with a 3-year reproduction cycle and we suggest that mean natality estimates using the method described in Stirling et al. (1977, 1980) and Ramsay and Stirling (1988) are only correct when female

mortality rates are zero and thus not directly comparable to the product of mean litter size and reproduction rate used in this paper.

The method of calculating natality rate has also varied. For example, the mean litter production rate for polar bears in the western Hudson Bay population for the interval 1980–84 was given as 0.69 in Derocher and Stirling (1992) and 0.70 in Derocher and Stirling (1995). However, Stirling et al. (1999: their Fig. 6) indicate that natality rates ranged between 0.93–0.98 from 1981 to 1985 in western Hudson Bay. Similar discrepancies in reported natality rates for the western Hudson Bay population were also apparent for other intervals (Derocher and Stirling 1992, 1995; Stirling et al. 1999). The natality rates reported by Derocher and Stirling (1992, 1995) and Stirling et al. (1999) were calculated to examine trends over time, so this discrepancy between papers does not affect their main points.

Amstrup and DeMaster (1988) discussed measures of reproduction and concluded that recruitment rate ( $m_x$ ) as calculated by pooling male and female cubs (i.e., litter size)/reproduction interval<sub>x</sub>) was a more appropriate measure of recruitment than the  $m_x$  defined by Taylor et al. (1987c) (i.e., [% females available<sub>x-1</sub>] [litter production rate<sub>x</sub>/females available<sub>x</sub>] [litter size<sub>x</sub>]) because the latter requires an estimate of the percent of females available for breeding which was not available in their study. Any estimate that depends on the relative frequencies of females with cubs, females with yearlings, females with 2-year-olds and unencumbered females (e.g., reproduction interval) will be biased if these frequencies are distorted by non-representative sampling. Amstrup (1995:191) discussed these same issues for the Beaufort Sea populations, but concluded that the low estimates of natality were “not entirely” due to the sampling problems mentioned in Amstrup and DeMaster (1988). Amstrup (1995) found that the age distribution estimates of natality were not different from estimates based on cohorts of polar bears followed through time using radiocollars. Amstrup (1995:192) stated that “females with cubs were under-sampled throughout the study”, although he applied a correction factor based on the survival of cubs in an attempt to remove this bias. If females with cubs were under-sampled, then family group classes and solitary adults must have been oversampled and it is unclear why biased standing age distribution estimates would be the same as unbiased estimates based on telemetry cohorts.

Similar concerns were expressed about vital rate estimates for polar bear populations from the M’Clintock Channel and Gulf of Boothia (Furnell and Schweinsburg 1984). The parameter values reported in Taylor et al. (1987c) were calculated from a pooled data set that included all data collected in Canada, except western Hudson

Bay which was recognized as distinct. The available data in 1987 for individual population analysis (i.e., Southern Beaufort Sea, Northern Beaufort Sea, Viscount Melville Sound, M’Clintock Channel, Davis Strait, Lancaster Sound, Baffin Bay, and Davis Strait) using ANURSUS (Taylor et al. 1987a) produced results that were judged to be incorrect because of non-representative sampling. The pooled data estimates (Taylor et al. 1987c) were assumed to have compensating biases and represented the best available data at that time. The parameter values from Taylor et al. (1987a) gave a natality rate of 0.554. However, it is difficult to make meaningful comparisons to estimates that were based on pooled data with apparent but unquantified biases.

The discrepancies in reported estimates for mean annual natality rate estimates for the western Hudson Bay population (Derocher and Stirling 1992, 1995; Stirling et al. 1999) are unfortunate because an extensive database has been developed for this population. However, the values given by Derocher and Stirling (1995) (i.e., 1966–79: 0.75; 1980–84: 0.70; 1985–92: 0.52) for “mean annual recruitment” do seem comparable, in spite of the difference in methodology. A mean natality rate (i.e., cubs of both sexes produced/female/year) estimate of 0.849 was reported by Kolenosky et al. (1992) for the Southern Hudson Bay population. However, previously published estimates of natality rates reported by Kolenosky et al. (1992: Table 7) do not match the estimates reported in the references cited. Kolenosky et al.’s (1992) natality estimate was based only on females with cubs (as opposed to both females with cubs and yearlings as per Ramsay and Stirling [1988]). Stirling et al. (1980), also using both cub and yearling litters, estimated the natality rate (i.e., cubs of both sexes produced/female/year) of Davis Strait polar bears as 0.527; however, this estimate did not correct for cub to yearling survival.

The only previously published natality rate estimate that we view as unambiguous is the one presented by Amstrup (1995), because both the age distribution and the telemetry cohort estimates were not different. Amstrup’s (1995) mean annual natality rate (0.40, SE not reported) was marginally larger than our equivalent recruitment rate estimate of 0.356 (SD = 0.035). We were surprised that the 2 mean natality estimates were so close because Kingsley et al. (1985) reported that the habitat in VM has a lower density of seals than the Southern Beaufort Sea.

## Historical Harvest and Natural History

Although the VM polar bear population (Fig. 1) is currently few in number, it encompasses a very large geographic area (203,100 km<sup>2</sup>, of which 104,540 km<sup>2</sup> is sea ice). Wynniatt Bay has 3 polynya areas caused by current upwellings in shallow areas. Hadley Bay is separated from

Wynniatt Bay by the Natkusiak Peninsula. Both captures and the movements of radiocollared adult females suggested that most of the VM polar bear population was located in either Hadley or Wynniatt Bay or in the mixed annual and multi-year ice that extended about 50 km into VM in the same vicinity (Fig. 1). The concentration of bears may also explain why harvest quotas were so liberal in the 1970–95 years. Hunters had no difficulty harvesting polar bears in this area, even in the final years before the moratorium. One individual and his wife took 8 bears (5 females and 3 males) in the final year (1991) of the now discontinued Melville quota in a single hunting trip. The 20% shift in adult sex ratio (M/F) and 18% decline in the fraction of the population that were adults from 1974–76 to 1989–92 suggest that the population was severely over-harvested during this interval and that the initial numbers may have been between 500–600 bears.

It is unusual to find 4 females that kept their cubs to age 3, and we also observed one female that was accompanied by a cub of age 4. Only 3 other instances of females with 3-year-old cubs have been recorded previously in Canada; and no instances of females with 4-year-old cubs were known. Typically large males force 2-year-old cubs to leave their mothers during mating season. The reduced number of males in the population may have reduced encounter rates during mating season thus allowing cubs to remain with their mothers. Alternatively some females may have kept offspring an extra year in this area to increase their chance of survival post-weaning. A third possibility is that because the best habitat is concentrated in a relatively small area of VM, 2-year-old cubs re-associate with their mothers after mating and remain with females that do not enter maternity dens. We also observed a subadult male (age 5) accompanied by 3 females in estrous. Observations of multiple males with females are common, but we know of no other observations of a single subadult male with >1 adult female during the mating season. This observation is consistent with the suggestion that males were depleted in this population.

### Assumptions of Harvest Risk Analysis

The sensitivity of risk estimates to partitioning of the uncertainty in demographic parameters (Table 9) demonstrates the need to use estimation procedures that partition total variance (White 2000) and to collect sufficient data to enable that partitioning. However, when population and sample sizes are small, or when the sampling occurs over too few years, it may not be possible to estimate the proportion of total variance that is due to sampling error and environmental variability. Our data were too sparse to partition survival and population variance estimates. Our variance estimates of recruitment parameters were determined using the jackknife method, which

did not allow partitioning the variance estimate (White 2000). The risk estimates did vary as a function of how the uncertainty was partitioned (Table 9).

The magnitude of the deviation in the proportion of runs that were identified as unacceptable (i.e., reduction to levels requiring 5 or more years of no hunting to recover) between simulations that assumed independence and simulations that set environmental covariance to 1.0 ranged from 0.0 to 0.124 and averaged 0.058 for a range of annual harvest rates from 0 to 20. The largest deviations were observed at harvest levels close to the deterministic sustainable yield value. The smallest deviations occurred at harvest levels either so small that they were almost certainly sustainable or so large that they were almost certainly not sustainable.

Our estimate of the over-dispersion coefficient ( $\hat{c}$ ) is rational (Appendix), but is also somewhat subjective. The model based estimates of  $\hat{c}$  (i.e., 1.0) were clearly low, given that polar bear family groups are captured as groups, not individuals. Estimating  $\hat{c}$  as mean group size ( $\hat{c}=2.0$ ) was clearly too large because most polar bears are not captured as family groups and because once a cub was weaned, it was no longer likely to be captured with its mother or litter mates. Perhaps better estimates may be possible from these data as analysis models continue to develop.

An additional limitation in our simulation results is that our Monte Carlo simulations assumed independence in both sampling and environmental random deviates. The standing age vital rate estimates were based on the same data and non-zero covariance was apparent. Our simulation model was not able to incorporate co-variance directly; however, it did contain an option that forced all random deviates for a given year (i.e., environmental uncertainty) to be based on the same uniform random deviate. This option allowed us to view the extreme covariance assumption with respect to parameters that might be expected to increase or be reduced simultaneously by good and bad years. The effect of setting environmental covariance to 1.0 was to slightly increase the variance of the simulation and thereby also slightly increase the risk associated with a given harvest level.

### Harvest Risk

When information is uncertain, harvest presents a risk to the harvested population. Our field work was done in collaboration with local hunters and simultaneous with polar bear hunting. It was clear that the hunters were very adept at locating and harvesting polar bears. Although the area was large and the density of polar bears was relatively low, local hunters maintained high success rates in all years they hunted in Viscount Melville Sound. This hunt was legal and within the quota limitations set by the

Government of the Northwest Territories, Canada. The apparent over-harvest was not caused by a failure to obey conservation regulations. Rather, it was caused by lack of accurate information on the size and sustainable harvest rate for this population, which resulted in overly aggressive harvest quotas.

Although we were able to document that prior harvest had reduced the population and that the current harvest rate (4/year) is "likely" sustainable (Table 8), our information was too uncertain to identify an absolutely safe sustainable harvest rate for this population. The risk assessment is an expression of the uncertainty in the demographic process and parameters. The RISKMAN simulations indicated that even though the point estimate of population growth rate was  $>1$  (i.e., 1.059), the confidence interval includes values  $<1$ . The population is at some risk even if the annual harvest policy is zero (Table 8) because the uncertainty in demographic parameters causes a small fraction of the scenarios to result in unacceptable declines. Higher harvest rates constitute an increased risk (fewer acceptable outcomes) to the population. If managers and stakeholders are willing to accept long periods (e.g., decades) of no harvesting, the proportion of acceptable outcomes is increased. We indicated risk levels using recovery times (Table 8) rather than fractions of original numbers because this consequence of reduced numbers was more intuitive to many managers and stakeholders.

We suggest that these results are more realistic than a deterministic maximum sustained yield estimate that does not consider the uncertainty of the underlying information. Both managers and stakeholders must recognize that scientific information rarely provides exact and absolutely correct harvest rate or harvest quota values. Researchers have a responsibility to quantify the uncertainty of their measurements and the uncertainty of their management recommendations. Reporting scientific results in this manner identifies the distribution of solutions where local and traditional knowledge may be used to guide the final determinations.

## MANAGEMENT IMPLICATIONS

Even when risk has been quantified, periodic monitoring is still required if the harvest level poses a significant risk to the population. Small populations limit the possible sample size of demographic studies. Estimates developed from few data may not be sufficiently precise or accurate (i.e., certain) to justify the cost and ethical considerations involved in frequent mark-recapture sampling. There may be some polar bear populations that are simply too small to be inventoried with sufficient precision and accuracy to provide a meaningful harvest at an ac-

ceptable risk level. These small populations may require particularly risk-averse harvest management policies. These small populations may be best managed as non-hunted, or harvested at conservative (i.e., clearly safe) rates, so that monitoring resources can be shifted into the larger populations where the return (harvest levels) is greater. We believe that total anthropogenic mortality from all sources (i.e., harvest, defense, accidental, and illegal) would have to be reduced to levels that posed essentially no risk to the population before it would be justified to extend or terminate the inventory cycle.

We quantified the associated risks for the range of annual harvest levels that we deemed to be practical. Management decisions must also consider the long-term goals for the population and the resources available for monitoring. Shorter intervals between population inventories could allow more aggressive harvest policies with the same level of risk, but these inventories are expensive, invasive, and time consuming. Whatever harvest level is chosen, stakeholders should be informed that the quota recommendations are based on uncertain information and that long-term harvest moratoriums may be required to regain the current number of bears. If the management goal for the VM population is recovery to pristine levels, the harvest rate will have to be very conservative or the likelihood of recovery will be small. Immigration from adjoining populations is likely to be low because adjoining populations are currently harvested at the estimated maximum sustained rate (Anonymous In Press, Lunn et al. In Press) and permanent immigration between polar bear populations is rare (Taylor et al. 2001a).

Our risk analysis results were specific for a 15-year interval between analyses. Longer monitoring intervals would increase the risk of harvest to the population. A systematic exploration of the risk implications for the entire range of monitoring options is beyond the scope of this paper. However, the risk of longer monitoring intervals for a range of harvest levels was explored using a 5-year recovery at zero harvest as the "acceptable" criteria (Fig. 2) for a 75-year time interval. Even the risk from low harvest rates was greater over the longer monitoring interval and the risk from intermediate and large harvest rates increased dramatically. The risk of a given harvest rate depends on the monitoring interval, and more frequent monitoring is required to manage the risk of aggressive harvest policies.

We were surprised to estimate the unharvested population growth rate of this population at 1.059 (SE = 0.063) because relatively low seal densities and heavy multi-year ice that characterize VM make this area relatively poor habitat for polar bears. Although our estimate of the mean population growth rate had considerable variance, it is one of the highest estimates of polar bear population growth

rate ever published. One could speculate that the over-harvest reduced the population to the point that density effects have been relaxed. Most of the population seemed to be concentrated in a relatively small part of the area during our study (Fig. 1). However, our estimates of recruitment parameters were numerically (but not significantly) lower than estimates for recruitment parameters from other polar bear populations areas (M. Taylor, unpublished analyses). The high population growth rate estimate was due to the high natural survival rate estimates that were age constant for non-cubs of both sexes. Both survival and population estimates had relatively large standard errors because of sample size limitations.

Harvest quotas based on deterministic estimates of the maximum sustained yield are difficult to evaluate and dangerous because they do not consider the uncertainty of the underlying information. However, incorporation of the uncertainty of the underlying demographic estimates also requires assumptions about how the total variance of the estimates is partitioned, and the estimated variance depends, in part, on the over-dispersion coefficient. We tried to make reasonable assumptions that were consistent with the data, analysis models, and natural history of polar bears. We were unable to validate all of these assumptions and suggest that the risk values that we present be viewed as the best currently available, but also be employed cautiously for management.

For small populations, an alternative to population-based assessments is a meta-analysis or empirical Bayes approach that would use information from other populations to derive demographic estimates with greater certainty (Meyers and Mertz 1998) and potentially improve the certainty of harvest levels and risk. However, to move in that direction, researchers must report unbiased vital rate estimates, and standard estimation methods should be used to make the estimates comparable. Additionally, the estimates of vital rates for a given population should be examined when reported to confirm that the population trajectory they imply is rational.

For example, when the mark-recapture survival estimates for the Western Hudson Bay (WH) population (Lunn et al. 1997) are combined with the recruitment estimates for the same area (Stirling et al. 1999), they indicate a rapid decline in polar bear numbers (M. Taylor, unpublished simulation). This decline is not supported by the WH population estimates (Lunn et al. 1997), which employ those same survival rates, or by qualitative observations of residents and long-term researchers.

Development of a conservative polar bear model that could be used with confidence, even when data are sparse or absent, will require systematic accumulation of accurate and internally consistent vital rate estimates for the various polar bear populations. We urge those reporting

polar bear vital rate estimates to make an effort to reconcile new information with what has been published previously and to ensure that the information reported is internally consistent or that any discrepancies are explained.

An example of a default population dynamics model used for management of populations where scant or no data are available for direct estimates of vital rates is the "potential biological removal" (PBR) management policy that is part of the U.S. Marine Mammal Protection Act (16 U.S. Code 4041–4042; Wade 1998, Taylor et al. 2000). The PBR method regulates the risk of human-caused mortality to acceptable limits by restricting takes to a proportion of the current minimum population size (i.e., a lower confidence limit value of the population estimate). The allowable proportion is one-half the maximum population growth rate which may be scaled back by a recovery factor ( $F_r$ ) when the population status is unknown or the population is known to be recovering. Periodic monitoring allows adjustment of PBR based on population dynamics, or alternatively, values of  $F_r$  can be selected that would yield PBR values that would keep the population secure indefinitely (Wade 1998). This approach was designed as a management tool to prevent depletion of marine mammal populations from by-catch or other human-caused mortality and it is robust in terms of conservation. If PBR were applied as a tool for setting polar bear harvest quotas, it could greatly reduce harvest opportunities for populations that are recovering or where there is little information. However, the PBR approach or a similar "default" polar bear population dynamics model based on other polar bear populations could be a strong option for small populations where the cost:benefit ratio of population inventory research was prohibitive, or for large populations where the data were few or suspect.

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## APPENDIX

Various approaches for estimating the over-dispersion coefficient  $\hat{c}$  have been suggested (Lebreton et al. 1992, White et al. In Press). The bootstrap goodness of fit option in MARK currently under-estimates over-dispersion for reasons that are not currently understood (G.C. White, Colorado State University, Boulder Colorado, USA, personal communication, 2001). The use of Test2 + Test3 from program RELEASE (Lebreton et al. 1992) also has limitations in coping with age-structure and non-time dependent covariates because inclusion of these factors as strata will often yield an over-parameterized model that may underestimate  $\hat{c}$ . Preliminary investigations indicated that both the bootstrap option in program MARK and program RELEASE estimated  $\hat{c}$  as less than one, which is clearly an underestimate because of extended parental care in polar bears. McCullagh and Nelder (1991:125) show that the over-dispersion coefficient is bounded above by the cluster (group) size for a population in equal-sized clusters in which the binomial response varies by cluster. Thus, we could have used an upper bound of  $\hat{c} = 2.0$  bears per capture group. However, while captures of bears in groups are dependent, their survival and recapture are not necessarily linked except in the case of mothers and cubs.

To reflect this dependence, we chose to estimate  $\hat{c}$  as  $n/(n-n_c)$  where  $n$  is the total number of bear captures and recaptures and  $n_c$  is the number of initial cub captures. We used the 1989–91 data because recaptures were excluded prior to 1989 and captures in the final year were not used as trials in further years. We used  $\hat{c}$  in the computation of QAIC<sub>c</sub> and to inflate variance estimates. This  $\hat{c}$  adjustment effectively treats the survival and potential recaptures of cubs as entirely dependent on their mothers and can be viewed as a sample size adjustment. The use of mean group size as an upper bound would have yielded conservative (i.e., too large) variances and would have tended to favor simpler models. The alternatives (Lebreton et al. 1992, White et al. In Press) would have likely yielded underestimates of  $\hat{c}$  because the data were sparse. Underestimation of  $\hat{c}$  would lead to over-fitted models with optimistic estimates of precision that would be less useful for prediction. Our estimate of  $\hat{c}$  was subjective to a certain degree, but we feel it was justified until better methods for estimation of  $\hat{c}$  are developed.

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