DEMOGRAPHY AND POPULATION VIABILITY OF POLAR BEARS IN LANCASTER SOUND AND NORWEGIAN BAY, NUNAVUT

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Abstract: We used mark-recapture and population viability analyses to estimate demographic parameters, abundance, and harvest risks for two adjacent populations of polar bears (*Ursus maritimus*) inhabiting Lancaster Sound and Norwegian Bay, Canada, from 1972 to 1997. We marked 1,871 bears during the period of study. Our best-fitting mark-recapture model specified sex and age effects in probabilities of survival, and an effect of prior recapture (dependence) on capture probability. The most parsimonious solution in our analysis of survival was to pool survival rates between the Lancaster Sound and Norwegian Bay populations. Total (harvested), annual survival rates ($\pm$ 1 SE) for females included: 0.749 ± 0.105 (cubs), 0.879 ± 0.050 (ages 1–4), $0.936 \pm 0.0.019$ (ages 5–20), and 0.758 ± 0.054 (ages 20+). Mean litter size was 1.69 ± 0.01 cubs for females of Lancaster Sound and 1.71 ± 0.08 cubs for females of Norwegian Bay. By age 6, on average 0.31 ± 0.21 females of Lancaster Sound were producing litters (first age of reproduction was 5 years); females of Norwegian Bay did not reproduce until ages 7+. Total abundance (1995–1997) averaged 2,541 bears $\pm$ 391 in Lancaster Sound and 203 ± 44 bears in Norwegian Bay. We calculated the stable-age, zero-harvest population growth rate for Lancaster Sound, λ_N, as 1.024 ± 0.010 and harvested population growth rate, λ_H, as 1.001 ± 0.013. The stable-age, zero-harvest population growth rate for Norwegian Bay was 1.006 ± 0.015 and harvested population growth rate was 0.984 ± 0.024. We incorporated demographic parameters into a harvest risk analysis to model likelihoods of persistence. Our harvest simulations suggest the current harvest (approximately 70 bears/year) in Lancaster Sound is sustainable. The much smaller Norwegian Bay population, which is likely declining, should be subjected to a harvest that does not exceed 3 bears/year.

Introduction

Management of large, long-lived mammals (e.g., bears, pinnipeds, and cetaceans) often involves controls on hunting. The typical conservation goal is persistence at current numbers, or, in cases where the population has declined, recovery. Determining harvests that are sustainable depends on several factors, including population size, natural rates of birth and death (vital rates), and the sex and age composition of the harvest. Unfortunately, because vital rates and population size are regularly estimated with error, deterministic estimates of sustainable yields are rarely of value for managing populations. An alternative approach would be to manage for harvests that provide for some reasonable likelihood of population persistence some time into the future. Models of probability of persistence, such as stochastic Population Viability Analysis (PVA [review in White 2000]), are ideal for incorporating uncertainty of input parameters into harvest models. When information is uncertain (e.g., due to sampling error or environmental and demographic stochasticity), any harvest level poses some risk to a population. PVA has the flexibility to provide managers with harvest compositions that are sustainable with an associated probability, but also consequences should a harvest later be deemed too severe (e.g., required length of moratorium to restore the population [Taylor et al. 2002, 2005]).

Here we used mark-recapture data (1,871 marks-at-risk) collected from 1972 to 1997 to estimate demographic characteristics of polar bears (*Ursus maritimus*) inhabiting Lancaster Sound and Norwegian Bay, Nunavut, Canada (Fig. 1). We incorporated demographic parameters as input into harvest risk analyses designed to take into account demographic, environmental, and sampling uncertainty in generating outcomes, which amounted to a stochastic, harvested, PVA.

Materials and methods

Study area and animals

Polar bears in the study area were distributed primarily over the sea ice of Lancaster Sound and Norwegian Bay, Nunavut, Canada (Fig. 1). The geographic boundaries of the Lancaster Sound population and adjacent Norwegian Bay polar bear population were previously established using mark-recapture movement data (Taylor & Lee 1995), DNA analysis (Paetkau et al. 1999), and cluster analysis of radio-telemetry data (Bethke et al. 1996, Taylor et al. 2001*a*). The Norwegian Bay population was identified as having an unique genetic structure when compared to Lancaster Sound (Paetkau et al. 1999), which confirms movement data suggesting little exchange of individuals between the two areas (Taylor et al. 2001*a*).

There have been two major capture programs in Lancaster Sound and Norwegian Bay yielding data for use in this study: a general arctic polar bear study conducted from 1972 to 1985 (Schweinsburg et al. 1981, 1982, Furnell & Schweinsburg 1984), and a more recent inventory conducted from 1989 to 1997 (Lancaster Sound) and 1993 to 1997 (Norwegian Bay). Captures from 1972 to 1992 were centralized around logistic bases (communities) and areas where bears concentrated, whereas from 1993 to 1997 captures were the result of a systematic, geographically uniform search of the entire study area.

We chemically immobilized all bears and their dependent cubs for capture, and marked bears according to procedures described by Stirling et al. (1989) following Animal Care Protocol No. 950005 of the University of Saskatchewan (under guidance of the Canadian Council on Animal Care). Bears captured from 1972 to 1985 were immobilized with phenylcyclidine hydrochloride (Furnell & Schweinsburg 1984). We used Telazol

(tiletamine hydrochloride and zolazepam hydrochloride in combination) to immobilize

bears from 1989 to 1997 (Stirling et al. 1989). Upon initial capture, we assigned an unique

identification number to each bear and marked the animals accordingly using a plastic ear

tag and permanent lip tattoo. We also marked each bear with a wax crayon on the fur to

ensure bears were not captured more than once per year. We considered a bear's age as

known if the bear was captured as a cub of the year (i.e., cub) or yearling, or if age was

estimated by counting the annular rings of an extracted vestigial premolar (Calvert &

Ramsay 1998).

Mark-recapture analysis

Estimates of survival and abundance were constructed from capture-recapture data

(1972–1997) using the Cormack-Jolly-Seber (CJS) formulation implemented in program

MARK (White & Burnham 1999). The CJS likelihood for capture-recapture data is

conditioned on initial capture events (i.e., the initial capture is treated as a release). The

likelihood is based solely on recapture events of marked (i.e., previously caught) animals,

and is defined by user-specified models for survival (S) and (re)capture probabilities (p)

that may be expressed as functions of covariates such as sex, age, and time.

Captures of bears from 1972 to 1985 were used as initial captures, but population

estimates were restricted to recaptures from 1993 to 1997 because captures were

geographically non-random and non-uniform prior to this time. Models were initially

developed by including a 'population' term, in addition to the covariates described below,

to test for differences in capture or survival probabilities by demographic unit (i.e.,

Lancaster Sound or Norwegian Bay).

For 1993–1997 data, we examined a series of models for capture probability that incorporated several additional covariates. We expected that capture probability would vary by year because capture teams were different each year. 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 all years. 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 areas of high use. Because these factors were also likely to vary for different family classes, we categorized bears into three classes: 1) females, cubs and yearlings; 2) sub-adults (2–4) of both sexes; and 3) adult males, and considered models in which capture probability varied for these classes. We also considered models in which bears with transmitters (radios) had a higher capture probability because their location was known at various times throughout the year (only females were equipped with radios), or bears that were previously captured which may have had higher capture probability for a variety of reasons (dependence). 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. More males were harvested than females, but this was captured by including the harvest explicitly. Survival was also likely to vary by age. We expected cubs to have lower survival than non-cubs. We considered an age-specific model which included different survival for cubs, subadults (aged 1–4 years), prime adults (5–20 years), and older adults

(21+ years). Annual differences in environmental conditions could create variation in

survival, so we considered models with distinct annual survival rates.

We fitted a series of CJS models using each capture probability model with each

survival probability model (White & Burnham 1999). We considered additive models with

main effects (e.g., sex + year) and a limited number of interactions (e.g., sex × age);

however, there were too few data to support higher order models. We used Akaike's

Information Criterion adjusted for sample size and over-dispersion ($QAIC_c$) as a guide for

model selection (Burnham & Anderson 2002). The data were likely to be over-dispersed

(i.e., greater than binomial variation) because survival and capture events of family groups

(e.g., females with cubs or yearlings) were not independent. We estimated the over-

dispersion coefficient, $\hat{c}$, based on the number of dependent cub captures (N_c) relative to all

captures, N (i.e., $\dfrac{N}{(N - N_c)}$; see Appendix in Taylor et al. 2002). We ranked the model

with the lowest $QAIC_c$ as best, and we used differences in $QAIC_c$ between the best-fitting

model and every other model ($\Delta QAIC_c$) to identify other likely models. We followed

Burnham & Anderson (2002) in selecting likely models, where $\Delta QAIC_c < 2.0$, 2.0–4.0,

4.0–7.0, and >7.0 can be said to exhibit strong, some, little, or no support, respectively. We

also used program MARK to calculate the $QAIC_c$ weight for each candidate model; these

weights sum to 1.0 and represent the relative likelihood of each model (Burnham &

Anderson 2002). For models with $\Delta QAIC_c \leq 4.5$ we used model averaging to present

parameter estimates, weighted according to $QAIC_c$ weights (Burnham & Anderson 2002).

Our estimates of total survival (S) derived from capture-recapture data and included

losses from harvest. We were interested in estimating natural survival, S_N, to investigate

potential impacts of alternative harvest strategies (see Harvest risk analysis, below). Since

total harvest of Lancaster Sound and Norwegian Bay polar bears was known, we used the

approach outlined by Taylor et al. (2002) to estimate the mean and standard error (SE) of

natural survival, S_N, from the average annual harvested population size and total survival,

which assumed that harvest and natural mortality occur in two separate time periods.

Abundance estimates were stratified by population, sex, and age. For cases where

we stratified the population into k strata, the total estimated population was the sum of

stratum estimates and the variance estimator was extended to include covariances between

estimated capture probabilities in the k strata (see Taylor et al. 2002). We used a similar

estimator to construct a variance estimate for the average population size over several

years.

Reproduction and population growth rate

We estimated reproductive parameters from the standing age distribution based on

captures and recaptures from 1993 to 1997 that occurred inside the study area (Fig. 1).

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 2 2-year-old cubs.

Our methods for estimating litter size, age-specific litter production rates (for

females aged 4, 5, 6 and 7+ years), and sex ratio at birth from the standing age distribution

are described in Taylor et al. (1987*a,b*), and available as the software package 'Vital Rates'

(Taylor et al. 2000). Standard errors of summary reproductive parameters were determined

from Monte Carlo simulations with 1,200 iterations.

The geometric mean, zero-harvest population growth rate (λ_N) and harvested (i.e., total) population growth rate (λ_H) at stable-age distribution were calculated according to Taylor et al. (1987*b*, 2001*b*). We ran 1,200 Monte Carlo simulations to estimate the geometric mean of λ using the life table-based (Caughley 1977), Visual Basic program 'RISKMAN' (Taylor et al. 2001*b*; see Eastridge and Clark 2001, Howe 2002, Taylor et al. 2005). We described variability about λ by presenting the bootstrapped standard deviation (SD) of λ (i.e., standard error; Manly 1997).

Harvest risk analysis

We also used RISKMAN to model risks of future declines in polar bear populations given population parameters and uncertainty in data (i.e., population viability). RISKMAN can incorporate stochasticity into its population model at several levels, including sampling error in initial population size, variance about vital rates due to sample size and annual environmental variation (survival, reproduction, sex ratio), and demographic stochasticity. RISKMAN uses Monte Carlo techniques to generate a distribution of results (Manly 1997), and then uses this distribution to estimate population size at a future time, population growth rate, and proportion of runs that result in a population decline set at a predetermined level by the user. We adopted the latter to estimate persistence probability.

Our approach to variance in this simulation was to pool sampling and environmental variances for survival and reproduction. We did this because: 1) our estimator of variances for reproductive parameters did not lend itself well to separating the sampling component of variance from environmental variance, and 2) we were interested in quantifying the risks of population decline including all sources of uncertainty in the data.

For each simulation, the frequency of occurrence of unacceptable outcomes (based on a threshold value of decline that was >20% of initial population size) was monitored and reported as the cumulative proportion of total runs over the threshold after 15 years. We chose to conduct model projections using these criteria because: 1) the population inventory cycle for this population is currently planned to be 15 years in duration, 2) we do not advocate using PVA over long time periods in view of potential significant changes to habitat regarding climate change in the Arctic, and 3) we felt most readers would appreciate a >20% decline in population size over 15 years as an unacceptable outcome. Individual runs could recover from 'depletion', but not from a condition where all males or all females or both were lost. 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, the sex ratio of cubs, initial population size, and demographic distribution of the harvest.

The standing age distribution was female-biased, as expected from long-term, sex-biased harvesting (Table 1). Because we wished to err on the side of caution, for all simulations we used the stable age distribution expected to be achieved by the population for a given harvest rate as the initial age/sex distribution (i.e., initializing the population at the stable age distribution produced more conservative outcomes compared to that of the existing standing age distribution). The harvest selectivity and vulnerability array was identified by comparing the standing age distribution of the historical harvest to the total mortality, stable age distribution. Harvest was stratified by sex, age (cubs and yearlings,

ages 2–4, ages 5–20, and ages 21+) and family status (alone, or with cubs and yearlings, or with 2-year-olds).

We ran harvest simulations using natural survival rates, upon which incrementally increasing rates of harvest (i.e., human-caused mortality from all sources) were added. We present our harvest risk analysis as the estimated probability of decline (>20%) from initial population size after 15 years vs. annual kill of bears. Simulations were time referenced to the last year of study (1997).

Results

Captures, recaptures, and harvest

We captured 984 females in Lancaster Sound and 85 females in Norwegian Bay from 1972 to 1997 (Table 1). Of these females, 153 and 21 bears, respectively, were recaptured at least once during the period 1993–1997. Of 191 and 25 recaptures of females in Lancaster Sound and Norwegian Bay, 39 and 5 were equipped with radio-collars. We captured 739 male bears in Lancaster Sound and 63 in Norwegian Bay from 1972 to 1997, of which 81 and 20 males were recaptured at least once during 1993–1997. The harvest between 1993 and 1997 was highly selective for male bears and averaged 71.6 bears/year (SE = 5.7) in Lancaster Sound and 3.2 bears/year (SE = 1.3) in Norwegian Bay (PBTC 2001).

Survival and abundance

Our best-fitting model specified sex and age effects in probabilities of survival and an effect of prior recapture (dependence) on capture probability (Table 2). Three additional

models were sufficiently close to the best-fitting model to be included in a model average (Table 2): a model identical to the above with an added age effect for capture probability, and models identical to the first that included interaction effects for age and sex in survival probability (one model with cubs stratified by sex and one without). The most parsimonious solution in our analysis of survival was to pool survival rates between the Lancaster Sound and Norwegian Bay populations (Table 2). Model averaged, annual mean total survival rates (S) and mean natural survival rates (S_N) for the period 1993 to 1997 are presented in Table 3.

Annual estimates of total abundance (1995–1997) averaged 2,541 bears ± 391 (mean ± 1 SE) in Lancaster Sound, of which 1,538 ± 242 bears were female and 1,001 ± 158 bears were male. Of these, 502 ± 87 bears were cubs and 822 ± 134 bears were adult females (5+ years), suggesting an average natality (cubs per adult female) of 0.61. The Norwegian Bay population was much smaller, averaging 203 ± 44 bears from 1995 to 1997. The Norwegian Bay population was composed of an average of 107 ± 25 females and 92 ± 23 males, including 35 ± 11 cubs and 66 ± 16 adult females. We estimated natality for Norwegian Bay polar bears at 0.53 cubs per adult female.

Reproduction and population growth rate

Summary reproductive parameters for the Lancaster Sound and Norwegian Bay populations based on analysis of the standing age distribution of captures from 1993 to 1997 are presented in Table 4. We calculated the stable-age, zero-harvest population growth rate for Lancaster Sound, λ_N, as 1.024 ± 0.010 (mean ± 1 SE). The harvested population growth rate for Lancaster Sound, λ_H, was 1.001 ± 0.013. The stable-age, zero-

harvest population growth rate for Norwegian Bay was 1.006 ± 0.015. The harvested

population growth rate for Norwegian Bay was 0.984 ± 0.024.

Harvest risk analysis

Our results suggest the current harvest of polar bears in Lancaster Sound is

sustainable. For the immediate future (i.e., next 15 years), the population can be expected

to be stable or slightly increasing if harvest remains at present levels (Fig. 2). We observed

a much higher likelihood of population decline under current harvest rates for the smaller

Norwegian Bay population (Fig. 3). Current harvest levels present a substantial likelihood

of near-term population decline (Fig. 3).

Discussion

The most parsimonious solution in our analysis of survival was to pool survival

rates between the Lancaster Sound and Norwegian Bay populations of polar bears. Despite

pooling survival rates, unharvested population growth rates continued to differ substantially

between the two populations. We attributed lower population growth rate in Norwegian

Bay to delayed age of reproduction and reduced productivity of Norwegian Bay females,

relative to females of Lancaster Sound. Whereas females reproduced as early as age five in

Lancaster Sound, in Norwegian Bay females did not reproduce until at least age seven, and

only then with a litter production rate that was more variable and 25% less than that of

females in Lancaster Sound (Table 4). A similar phenomenon of reduced age at first

reproduction, relative to more southerly Canadian polar bear populations, was also

observed for polar bears inhabiting Kane Basin directly to the east and north of Norwegian

Bay (M.K. Taylor, unpublished data), on the opposite side of Ellesmere Island (Fig. 1).

The Norwegian Bay and Kane Basin populations of polar bears represent the northernmost

range of polar bears in North America.

In extreme environments, like the high Arctic, female bears should allocate

resources for reproduction in a safer, but less-productive, manner (Ferguson & McLoughlin

2000). Changes in life history that affect timing of reproduction (e.g., later age at maturity,

longer inter-birth intervals, greater longevity; Cohen 1970, Phillipi & Seger 1989, Sajah &

Perrin 1990) reduces effects of extreme or stochastic environments, such that the geometric

mean fitness of individuals is increased (Yoshimura & Jansen 1996). For example,

increased age at first reproduction has been observed for grizzly bear populations in

response to reduced productivity and increased seasonality of the environment (Ferguson &

McLoughlin 2000). Polar bears in Norwegian Bay exhibit life history traits that appear

adapted to extremes of the species' fundamental niche, including late reproduction relative

to other polar bear populations. We did not, however, detect any difference between the

survival rates, longevity, or litter size of Norwegian Bay polar bears and other polar bear

populations.

For large mammals, the outcome of life history adaptations to extreme

environments is relatively low natural (unharvested) rates of population increase when

populations are below carrying capacity. The unharvested finite rate of increase observed

for polar bears inhabiting Norwegian Bay is an example ($\lambda_N = 1.006$), which compares

similarly with polar bears of Kane Basin to the northeast ($\lambda_N = 1.009$; M.K. Taylor,

unpublished data). Due to long periods of historical harvest, we do not believe either

population is currently at carrying capacity. These rates contrast significantly with

unharvested population growth rates obtained for adjacent, more southerly populations of polar bears, including Lancaster Sound ($\lambda_N = 1.024$) and the Baffin Bay population to the immediate southeast ($\lambda_N = 1.055$; Taylor et al. 2005). Intraspecific variation in life history entails that not all populations of a species can, or should, be harvested at the same rates. Populations with relatively low intrinsic (Malthusian) rates of increase may not be safely harvested at levels that appear sustainable for conspecific populations. We caution against applying harvest rates to polar bears within Norwegian Bay that were originally developed from data on polar bears from outside the Norwegian Bay boundary.

Although the difference between the annual harvest rate and unharvested growth rate of a population plays a primary role in determining sustainability of a given harvest, it is not the only consideration when we estimate likelihoods of population persistence. If populations are small, population size requires special consideration when developing hunting quotas that allow for acceptable probabilities of population persistence. Discrete demographic units that are small in size are more susceptible to population decline due to the phenomenon of increasing importance of random chance in survival and reproduction in determining population trends as population size decreases (i.e., demographic stochasticity; Caughley 1977). Deterministic Allee effects (Allee 1931) may also contribute to 'extinction thresholds' for small populations, whereby individuals of populations that have been significantly reduced have difficulty finding mates, or are unable to engage in normal social interactions, resulting in per capita growth rates that approach or fall below zero at lower densities. The Norwegian Bay population is relatively small ($N = 203$), with an estimate of only 66 adult females. Previous authors have cautioned against hunting discrete

demographic units of bears approaching 100 individuals due to unknown and potentially

severe Allee effects or effects of demographic stochasticity (e.g., Wielgus 2002).

Although we predict a decline in the Norwegian Bay population of polar bears if the

average harvest rate is not decreased from present levels, it is possible through emigration

from the nearby and much larger Lancaster Sound population that polar bears may continue

to be harvested in Norwegian Bay without any observable decrease in population size.

Potential 'rescuing' of the population will depend on the degree to which individuals within

Norwegian Bay constitute a discrete demographic unit. Unfortunately, both cluster analysis

of movement data and genetic information suggests very low interchange between the two

populations (Paetkau et al. 1999, Taylor et al. 2001*a*). Thus, relying on population

interchange between Lancaster Sound and Norwegian Bay to improve prospects of models

of persistence for Norwegian Bay bears is probably not warranted.

Our risk assessment is an expression of the uncertainty in demographic processes

and parameters. Our simulations suggest that the current quota of approximately 70

bears/year is reasonable for Lancaster Sound; however, a quota of <3 bears/year is

recommended in Norwegian Bay if the management goal also includes recovery to a higher

level of abundance. Higher harvest rates constitute an increased risk (fewer acceptable

outcomes) to the population, and will result in slower recovery rates. If managers and

stakeholders are willing to accept a very long recovery time, or a large degree of risk

associated with the recovery, harvesting is possible; however, the shortest recovery time

and smallest risk obviously comes from instituting a harvest moratorium.

Acknowledgements

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Table 1. Initial captures of polar bears classified by age and sex. The number of bears recaptured at least once in the years 1993–1997 is listed in parentheses. Bears initially captured in 1997 (last year of study) were never recaptured.

	Year	Cub	Yearling	2 yr old	3–4 yr old	5–20 yr old	>20 yr old	Total
Lancaster Sound								
Female	1972-1985	58(6)	35(3)	34(1)	47(3)	177(6)	10(0)	361(19)
	1989-1991	5(0)	1(0)	3(0)	0(0)	21(5)	3(2)	33(7)
	1992	7(2)	4(1)	1(0)	2(0)	20(10)	3(0)	37(13)
	1993	5(1)	3(1)	1(0)	7(3)	22(11)	0(0)	38(16)
	1994	14(4)	5(3)	4(0)	5(1)	34(20)	2(0)	64(28)
	1995	26(5)	12(4)	10(6)	9(2)	54(19)	7(2)	118(38)
	1996	40(10)	18(3)	12(4)	15(2)	59(11)	8(2)	152(32)
	1997	30	24	6	24	93	4	181
	Total	185(28)	102(15)	71(11)	109(11)	480(82)	37(6)	984(153)
Male	1972-1985	59(1)	32(2)	20(0)	41(2)	120(0)	5(0)	277(5)
	1989-1991	6(0)	2(0)	1(0)	1(0)	11(2)	0(0)	21(2)
	1992	7(1)	3(0)	2(0)	3(0)	13(6)	0(0)	28(7)
	1993	12(1)	4(0)	1(0)	4(3)	16(5)	0(0)	37(9)
	1994	20(1)	7(2)	1(0)	8(0)	35(9)	2(1)	73(13)
	1995	28(1)	7(4)	6(1)	5(2)	43(8)	0(0)	89(16)
	1996	32(11)	17(6)	6(0)	8(1)	43(9)	4(2)	110(29)
	1997	31	16	3	14	40	0	104)
	Total	195(16)	88(14)	40(1)	84(8)	321(39)	11(3)	739(81)
Norwegian Bay								
Female	1972-1985	0(0)	1(0)	1(0)	0(0)	6(0)	0(0)	8(0)
	1993	0(0)	5(3)	1(1)	3(1)	5(3)	0(0)	14(8)
	1995	3(1)	2(0)	3(1)	1(0)	15(7)	1(0)	25(9)
	1996	2(0)	2(0)	0(0)	3(2)	9(2)	0(0)	16(4)
	1997	3	3	0	2	12	2	22
	Total	8(1)	13(3)	5(2)	9(3)	47(12)	3(0)	85(21)
Male	1972-1985	0(0)	1(0)	1(0)	0(0)	3(0)	0(0)	5(0)
	1993	0(0)	2(1)	1(0)	1(1)	2(1)	0(0)	6(3)
	1995	4(2)	1(0)	3(0)	4(2)	9(6)	0(0)	21(10)
	1996	6(2)	1(1)	1(0)	0(0)	6(4)	0(0)	14(7)
	1997	6	3	0	4	4	0	17
	Total	16(4)	8(2)	6(0)	9(3)	24(11)	0(0)	63(20)

Table 2. $\Delta QAIC_c$ values for models fitted to Lancaster Sound and Norwegian Bay capture-recapture data, 1972–1997. The number of estimated parameters for each sub-model is shown in parentheses. Bolded values represent models used in model-averaging. Our estimate of the overdispersion coefficient, $\hat{c}$, was 1.65. $QAIC_c$ weights of the best four models, ranked from highest to lowest, were 0.590, 0.264, 0.092, and 0.054, respectively.

	Capture Model			
	Pop × Year + Radio	Dependence	Dependence + Age	Family + Age
Survival Model	(11)	(12)	(13)	(14)
Age (4)	22.6	7	8.5	20.2
Age + Sex (5)	13.9	**0**	**1.6**	8.7
[1]Age × Sex (7)	17.5	**3.7**	5	12.2
Age × Sex (8)	18.2	**4.5**	5.8	12.8

[1]Cub survival is the same for both sexes.

Table 3. Means and SE (in parentheses) of natural survival rates (S_N) and total survival

rates (harvest included, S) for polar bears of Lancaster Sound and Norwegian Bay,

Nunavut, 1993–1997. Estimates are the weighted-averaged four best MARK models

(pooled across populations as suggested by $QAIC_c$ model selection, Table 2).

Sex and Age	Mean Annual Survival Rate	
	S_N	S
Female		
0	0.750 (0.104)	0.749 (0.105)
1–4	0.898 (0.050)	0.879 (0.050)
5–20	0.946 (0.018)	0.936 (0.019)
21+	0.771 (0.054)	0.758 (0.054)
Male		
0	0.634 (0.123)	0.633 (0.123)
1–4	0.838 (0.075)	0.790 (0.073)
5–20	0.974 (0.030)	0.892 (0.030)
21+	0.715 (.095)	0.653 (0.085)

Table 4. Estimates of the mean and SE (in parentheses) of summary reproductive parameters of polar bears inhabiting Lancaster Sound and Norwegian Bay, 1972–1997. Parameters include cub litter size (LS), litter production rates (LPR) for females of age 4, 5, 6, and 7+, and the proportion of cub litters that are male ([P] male).

	LS	LPR4	LPR5	LPR6	LPR7+	[P] male
Lancaster Sound	1.688 (0.012)	0.000 (0)	0.107 (0.050)	0.312 (0.210)	0.954 (0.083)	0.531 (0.048)
Norwegian Bay	1.714 (0.081)	0.000 (0)	0.000 (0)	0.000 (0)	0.689 (0.534)	0.544 (0.066)

Figure captions

Fig. 1. Location of the Lancaster Sound (LS) and Norwegian Bay (NB) polar bear populations, Nunavut, Canada. Boundaries are defined as in Taylor et al. (2001*a*).

Fig. 2. Estimated likelihood of >20% decline from initial population size vs. annual harvest rate (bears/year) for polar bears inhabiting Lancaster Sound after 15 years. The dashed, vertical line indicates the mean annual harvest rate for the period 1993–1997.

Fig. 3. Estimated likelihood of >20% decline from initial population size vs. annual harvest rate (bears/year) for polar bears inhabiting Norwegian Bay after 15 years. The dashed, vertical line indicates the mean annual harvest rate for the period 1993–1997.
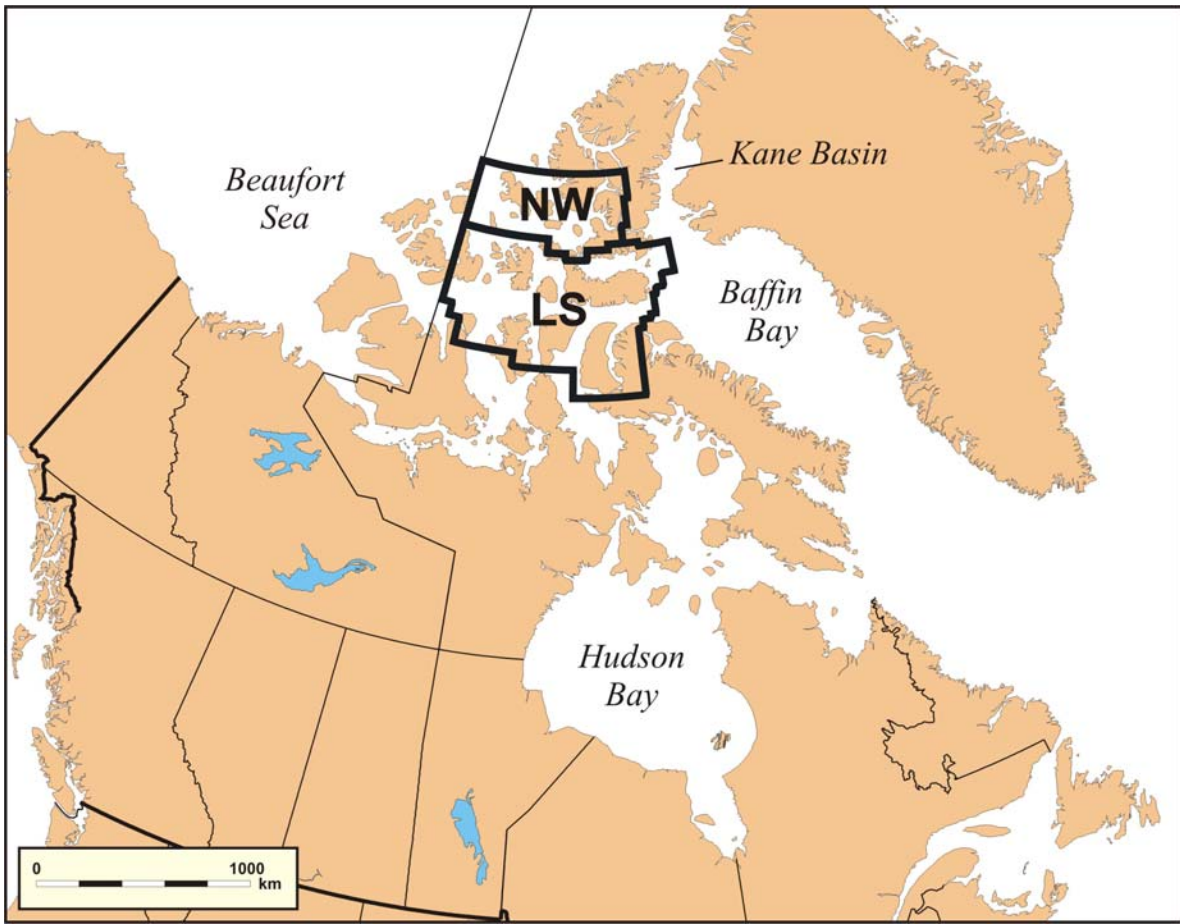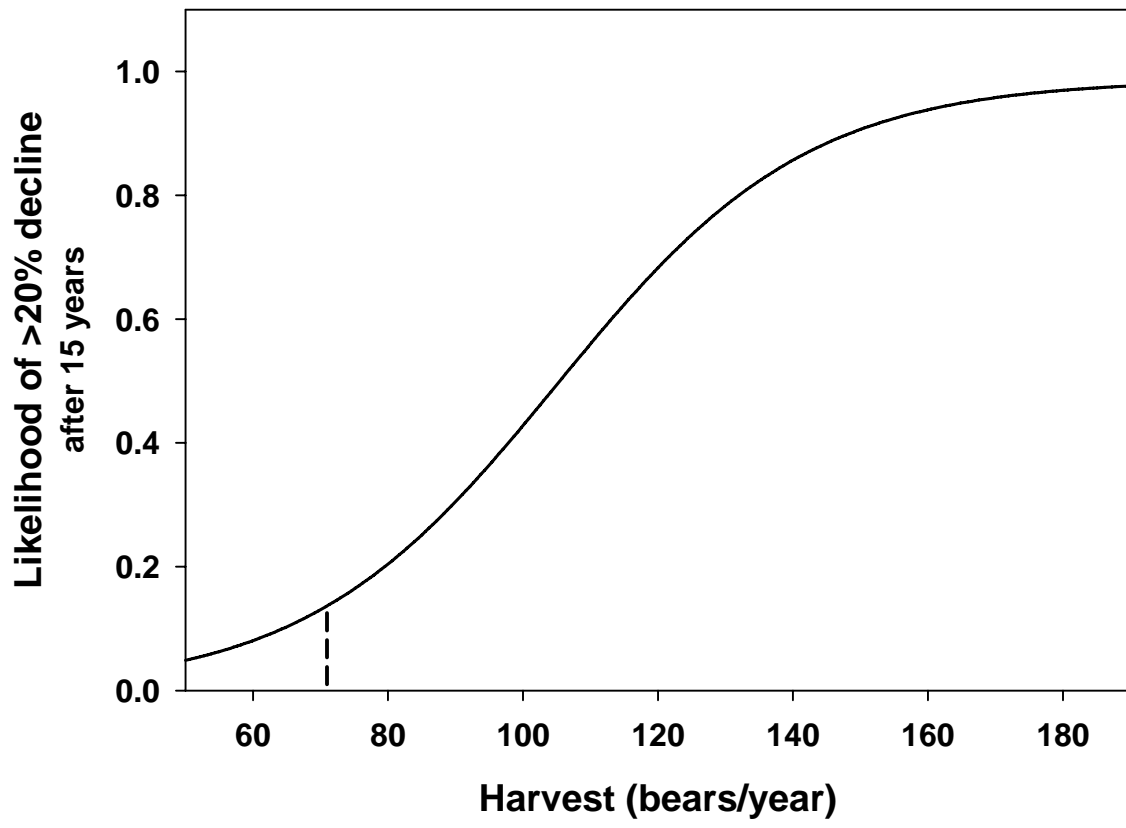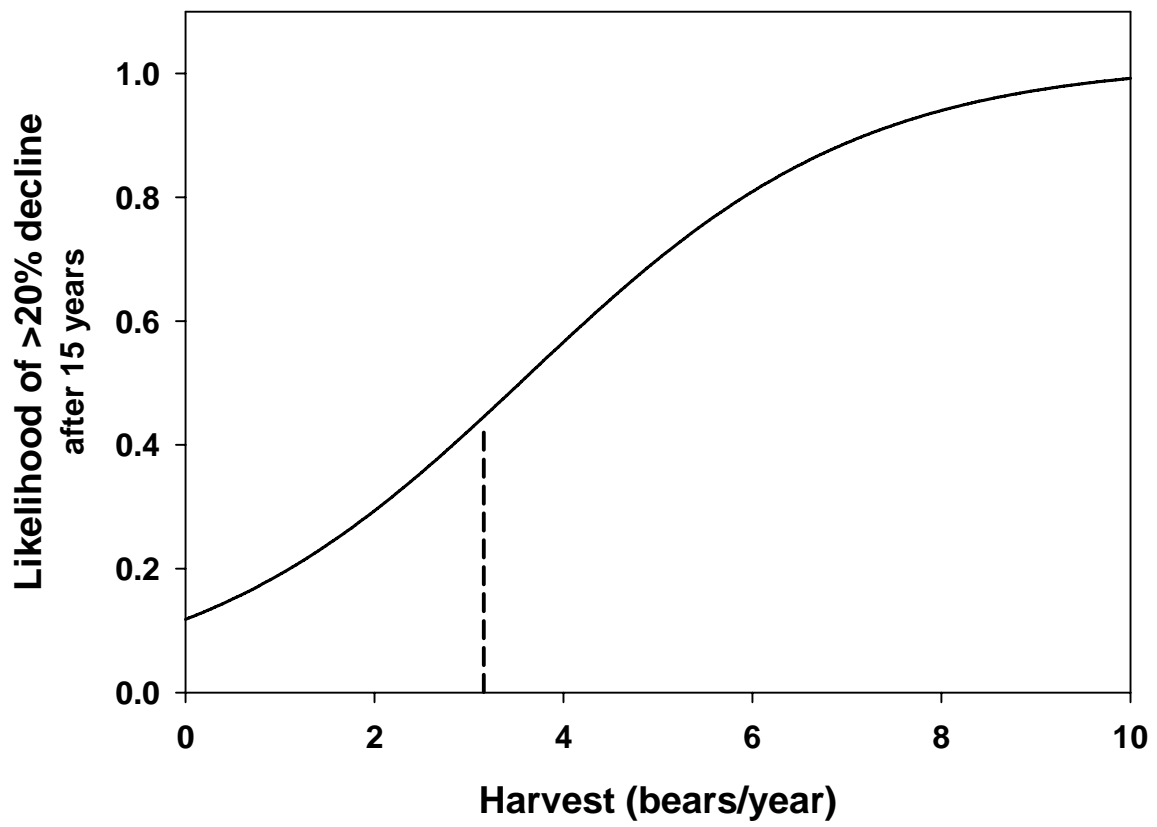
Fig. 1.

Fig. 2

Fig. 3