# RE-ESTIMATING THE ABUNDANCE OF THE DAVIS STRAIT POLAR BEAR SUBPOPULATION BY GENETIC MARK-RECAPTURE 

FINAL REPORT-amended

May 9, 2022

Dyck, M., Dunham, K.D., Ware, J.V., Koons, D.N., Regehr, E.V., Hosmer, D.W., Derocher, A.E., Dale, A., Pisapio, J., and Szor, G. Prepared for: Department of Environment Box 209, Igloolik, NU, Canada XOA OLO

| M. Dyck* <br> Department of Environment <br> Government of Nunavut <br> Box 209 <br> Iglulik, NU <br> XOA OLO Canada <br> *deceased | K. Dunham, Ph.D. <br> Postdoctoral Fellow <br> Nunavut Wildlife Cooperative Research <br> Unit (NuWCRU) <br> Department of Biological Sciences <br> University of Alberta <br> kdunham@ualberta.ca |
| :---: | :---: |
| J. V. Ware, Ph.D. <br> Department of Environment <br> Government of Nunavut <br> Box 209 <br> Iglulik, NU <br> XOA OLO Canada <br> jware@gov.nu.ca | D. N. Koons, Ph.D. <br> James C. Kennedy Endowed Chair <br> Wetland \& Waterfowl Conservation <br> Dept. of Fish, Wildlife, and <br> Conservation Biology <br> Colorado State University <br> Fort Collins, CO 80523-1474 <br> david.koons@colostate.edu |
| E. V. Regehr, Ph.D. <br> Polar Science Center - Applied Physics <br> Laboratory <br> Box 355640 <br> University of Washington <br> 1013 NE 40th Street <br> Seattle, WA 98105-6698 <br> eregehr@uw.edu | D. W. Hosmer, Ph.D. <br> Adjunct Professor of Statistics Department of <br> Mathematics and Statistics <br> University of Vermont <br> Adjunct Professor of Biostatistics <br> Menzies Institute for Medical Research University <br> of Tasmania <br> Professor of Biostatistics (Emeritus) Department of <br> Biostatistics <br> University of Massachusetts <br> 128 Worcester Road <br> Stowe, VT 05672 <br> dhosmer@umass.edu |
| A. E. Derocher, Ph.D. Department of Biological Sciences University of Alberta <br> Edmonton, AB T6G 2E9 <br> Phone: (780) 492-5570 <br> derocher@ualberta.ca | A. Dale <br> Torngat Wildlife, Plants \& Fisheries Secretariat Box 2050, Station B Happy Valley-Goose Bay, NL, A0P 1E0 aaron.dale@torngatsecretariat.ca |
| S. McCarthy, (formerly J. Pisapio) <br> Forestry and Wildlife Branch <br> Department of Fisheries, Forestry and <br> Agriculture; Government of <br> Newfoundland and Labrador <br> Happy Valley- Goose Bay, NL, AOP <br> 1E0 <br> *current contact- <br> saramccarthy@gov.nl.ca | G. Szor <br> Biologiste MSc <br> Direction de la gestion de la faune du Nord-duQuébec <br> Ministère des Forêts, de la Faune et des Parcs <br> 951 boul. Hamel,Chibougamau, QC, G8P 2 Z3 <br> Guillaume.szor@mffp.gouv.qc.ca |

Any views expressed in this report are solely the views of the authors. Mention of any type of gear and equipment does not mean that it is endorsed by the representative institutions of the authors.

## Citation:

Dyck, M., Dunham, K.D., Ware, J.V., Koons, D.N., Regehr, E.V., Hosmer, D.W., Derocher, A.E., Dale, A., Pisapio, J., and Szor, G. 2021. Re-estimating the abundance of the Davis Strait polar bear subpopulation by genetic markrecapture. Final Report, Government of Nunavut, Department of Environment, Iglulik.

## Table of Contents

1. EXECUTIVE SUMMARY (ALL LANGUAGES) ..... 9
 ..... 9
RÉSUMÉ. ..... 11
 ..... 13
AULATSIJILLAGET NAILLITITAUSIMANNINGA ..... 15
EXECUTIVE SUMMARY ..... 18
2. INTRODUCTION ..... 20
Study Area ..... 25
3. METHODS ..... 26
Samples ..... 26
Field collections ..... 26
Recovering previously marked bears through harvest ..... 29
Recaptured bears from past subpopulation study ..... 30
Sample preparations ..... 30
Genetic analysis ..... 30
Survival analysis ..... 31
Data Collection. ..... 31
Hierarchical model structure ..... 32
Parameterization ..... 35
Environmental conditions ..... 38
Model implementation, fit, and evaluation ..... 40
Supplementary survival analyses ..... 41
Reproduction ..... 41
Abundance ..... 42
Body Condition. ..... 43
4. RESULTS ..... 45
General overview ..... 45
Samples examined ..... 46
Survival ..... 47
Abundance ..... 48
Reproduction ..... 49
Body condition ..... 49
5. DISCUSSION ..... 50
General ..... 50
Abundance ..... 50
Survival ..... 51
Reproduction ..... 56
Body condition ..... 58
6. MANAGEMENT IMPLICATIONS ..... 58
7. ACKNOWLEDGEMENTS ..... 60
8. LITERATURE CITED ..... 62
9. FIGURES AND TABLES ..... 73
Figure 1. The Davis Strait polar bear subpopulation (blue outline) with different jurisdictionsin shades of gray (Newfoundland and Labrador [Nunatsiavut], light gray; Nunavut, dark gray;Québec [Nunavik], medium gray).73
Figure 2. Sampling (blue triangles) and harvest (red circles) locations for Davis Strait polarbears where coordinates for both events for the same individual bear were available ( $\mathrm{n}=$163). Green lines indicate subpopulation boundaries74
Figure 3. Sampling locations by field season (blue = 2017; purple = 2018) within the DavisStrait polar bear study area (Note: the sampling stratification for the coastline shown byblack lines, the 10 km and 30 km strata are also indicated). Inset: Davis Strait subpopulationarea in context of Canada75Figure 4. Overview of bear observations and helicopter paths flown in search for polar bearsin Davis Strait during August - October 2017 and 2018. Inset: Davis Strait subpopulation area(red) in context of Canada.76
Figure 5. Estimates of annual survival rates for Davis Strait polar bears by age class. Light gray squares and dashed lines are the annual means and $95 \%$ Bayesian credible intervals for offspring (cubs-of-the-year and yearlings). Dark gray triangles and dotted lines are the annual means and $95 \%$ credible intervals for subadult polar bears (males: 2-7 years, females: 2-4 years). Black circles and solid black lines are the annual means and $95 \%$ Bayesian credible intervals for adult polar bears (males: 8+ years, females: $5+$ years). Using combined capture-recapture-recovery data, we estimated survival in all years for adult polar bears; however, estimates of survival for younger age classes were limited to years following releases.77
Figure 6. Estimates of annual recapture probability of Davis Strait polar bears by age and sex class. Capture-mark-recapture data were collected intermittently, and recapture probabilities were estimable for only four years across two sampling periods. Light gray squares and
dashed lines are the annual means and 95\% Bayesian credible intervals for subadult polar bears (males: 2-7 years old, females 2-4 years old). Dark gray triangles and dotted lines are the annual means and 95\% Bayesian credible intervals for adult females ( $5+$ years old) and offspring (cubs-of-the-year and yearlings). Black circles and solid lines are the annual means and 95\% Bayesian credible intervals for adult male polar bears 78

Figure 7. Estimates of abundance for the Davis Strait subpopulation of polar bears. Black circles and dashed lines represent the mean and 95\% CRI derived from recapture probabilities using multistate live-capture dead-recovery models. Point estimates and credible intervals are shown for $2006,2007,2017$, and 2018 only because those were the only years in which recapture probability were estimable due to intermittent sampling. The red circle and dashed lines represent the mean and 95\% confidence interval of abundance estimated for the period of 2005-2007 and reported by Peacock et al. (2013) for comparison.

Figure 8. Predicted probability $\pm$ SD of bears being classified in poor body condition in the early sampling period (2005-2007) or the later sampling period (2017-2018).

Figure 9. Predicted probability $\pm$ SEM of bears being classified in good body condition for each reproductive age class as a function of the number of days between sea-ice retreat and when the bear was sampled. 81

Table 1. Number of live observations (black, captures \& recaptures) and dead recoveries (gray, in parentheses) of individually identified polar bears in the Davis Strait subpopulation used in survival estimation. No marked cubs of the year (COY) were harvested in our data set. However, there were a total of 9 marked bears harvested as yearlings (1.5 years old) prior to becoming subadults (at 2.5 years old).82

Table 2. Sequential model selection for Davis Strait polar bear survival and encounter probabilities based on information criterion (WAIC) to address our primary objective of identifying temporal patterns in survival.83

Table 3. Parameter estimates from the top model for Davis Strait polar bears with data from 2005-2018 (model M2; Table 2). Demographic parameters are reported as the mean, standard deviation, and 95\% Bayesian credible intervals (CRI) on the probability scale. Temporal variance is reported on the logit scale.85

Table 4. Recapture probability metrics for each year and each recapture age-sex class. (LCRI = lower Bayesian credible interval, UCRI = upper Bayesian credible interval). 86

Table 5. Abundance estimates from our model (2006-2018) and average estimate over 20052007 from Peacock et al. (2013). In 2017, surveys were not conducted on Edgell and Resolution Islands. In 2018, surveys were not conducted on Edgell and Resolution islands or in an area around Loksland. Abundance estimates were subsequently adjusted for these incomplete surveys (see Methods for details; CRI = Bayesian credible interval).87

Table 6. Annual numbers of litters and mean litter sizes (LS) of cub-of-the year (COY) and yearling (YRL) litters encountered during the capture-recapture studies in Davis Strait. 88

Table 7. Ratio of the number of cubs-of-the-year (COY) to adult females (ADF), the number of yearlings (YRL) to adult females, and the number of adult females with cubs-of-the-year (ADF_COY) to adult females in the subpopulation. 89

Table 8. Number of polar bears classified in each category of body condition index ( BCI ) in the Davis Strait subpopulation 2005-2007 and 2017-2018. Poor BCI corresponds to a thin bear ( BCl of 1 or 2 ) and Good BCl corresponds to a fat/obese bear ( BCl of 4 or 5). Age classes are adult ( $\geq 5$ years) and subadult ( $2-4$ years).

Table 9. Fitted multinomial regression model parameter estimates (reference level =
"poor"/BCI = 1 or 2 , intercept represents adult independent females in 2005-2007 sampling
period) for body condition index analysis of the Davis Strait subpopulation. See Methods for
variable definitions.
91

Table 10. Reported mean harvest for the Davis Strait (DS) polar bear subpopulation by
jurisdiction between 1999-2008 and 2009-2019 [Numbers represent mean $\pm$ standard
deviation (range); NU = Nunavut, NL = Newfoundland and Labrador, GL = Greenland]. ........ 92
10. SUPPLEMENTARY MATERIALS ....................................................................................................... 93

Supplementary Methods .......................................................................................................... 93
Table SM1. Parameters, their definitions, and prior distributions used in a multistate model
for Davis Strait polar bears. ...................................................................................................... 93
Table SM2. Point estimates of total survival (includes natural and harvest mortality) from capture-recapture studies for polar bears. These values were used to generate informative priors for survival in a multi-state capture-recapture-recovery model for polar bears in Davis Strait. Further details on their use in the main text (Methods - Model implementation, fit, selection). Table adapted from supplementary table S3 in Regehr et al. (2018). ..................... 94

Supplementary Results .............................................................................................................. 96
Table SR1. Results of a prior sensitivity analysis comparing parameter estimates from Model M2 initialized with informative priors for adult and subadult survival compared with estimates from Model M2U initialized with uninformative (uniform) priors for adult and subadult survival. Model M2 includes the best fit model structure for survival, recovery, and recapture probabilities without environmental covariates. Demographic parameters are reported as the posterior mean, standard deviation, and 95\% Bayesian credible intervals (CRI) on the probability scale for averages over time. Temporal variance estimates are reported on the logit scale.

Figure SR1. Density plots of uniform (uninformative; gray line) and Beta (informative; blue line) prior distributions for subadult and adult polar bear survival developed using the mean and standard deviation of the mean across previous polar bear survival studies following the approach of Regehr et al. 2018 (see also Table SM1 and Table SM2). 98

Figure SR2. Posterior distributions of subadult and adult survival from multistate model (M2) initialized with either uninformative (Uniform (0,1); gray line) or informative (Table SM1; blue line) priors for Davis Strait polar bear capture-recapture-recovery data99
Additional analysis - time constant and fixed effect models ..... 100

Table SR2. Parameter estimates from the top model for Davis Strait polar bears with data from 2005-2018. Demographic parameters are reported as the posterior mean, standard deviation, and 95\% Bayesian credible intervals (CRI) on the probability scale for averages over time. Temporal variances are reported on the logit scale. 100

## EXECUTIVE SUMMARY（ALL LANGUAGES）



 ব $\sigma \Omega$ ロ مـ
 ${ }^{\text { }}$








 1，833－2，542］．ヘィऽ

















 $\dot{\alpha} h D \cap^{q} \rho^{c}{ }^{\text {a }}$





 ${ }^{\text {a }}$






















## RÉSUMÉ

Au cours des dernières décennies, les changements climatiques dans l'ensemble de l'Arctique ont modifié l'habitat de l'ours polaire (Ursus maritimus) à un rythme sans précédent et d'autres changements sont attendus. Pour aider à conserver les souspopulations viables d'ours polaires en tant que partie intégrante de l'écosystème et pour assurer la disponibilité continue d'une ressource de subsistance pour les Inuits, des recherches scientifiques et des études de surveillance sont effectuées pour évaluer l'état des sous-populations et déterminer si les objectifs de gestion sont atteints. Nous présentons ici les résultats de la récente étude des sous-populations d'ours polaires pour la sous-population du détroit de Davis. Nos analyses ont porté sur les échantillons de biopsies génétiques prélevés en 2017 et 2018, les données de captures vivantes recueillies de 2005 à 2007 et les données de récupération des prises obtenues chaque année de 2005 à 2018. L'abondance estimée pour la période 2017-2018 était de 2015 ours (écart-type [ET] = 251; intervalle de crédibilité bayésien [ICR] à $95 \% 1603$ 2 588). L'abondance estimée pour la période 2006-2007 était de 2250 [ET = 133; ICR 1989 - 2 512]. À titre de comparaison, Peacock et autres ont estimé en 2013 l'abondance pour la période 2005-2007 à 2158 [intervalle de confiance (IC) à $95 \%=$ 1833 - 2 542]. Il est important de noter que nos estimations pour la période 2006-2007 se situaient dans les intervalles de confiance rapportés par Peacock et autres (2013) pour la période de 2005 à 2007. De 2006 à 2018, la moyenne géométrique de
croissance des sous-populations était de 0,989 (ICR à $95 \% 0,974-1,010$ ), ce qui correspond à une probabilité de 0,896 que la croissance de la sous-population ait été de $<1$ et, par conséquent, que la sous-population a très probablement diminué (d'au moins un ours) au cours de cette période. Au cours de cette même période, le gouvernement du Nunavut a modifié l'objectif de gestion afin de réduire l'abondance de la sous-population. Ainsi, la prise annuelle moyenne déclarée par l'ensemble des administrations est passée de $64,1 \pm 10,1$ (ET) ours/année de 1999 à 2008 à $86,8 \pm$ 23,6 de 2009 à 2019. Nous notons également que le quota a été augmenté à Terre-Neuve-et-Labrador, passant de six à 12 ours au cours de notre période d'étude. II n'existe aucune exigence de déclaration des prises dans la section québécoise de l'aire de répartition du détroit de Davis; cela suscite des incertitudes quant aux niveaux de prise totale pour la sous-population du détroit de Davis. Le recrutement moyen d'oursons de l'année (nombre d'oursons par femelle adulte) varie de 0,23 à 0,45 et le recrutement moyen de petits d'un an (nombre de petits d'un an par femelle adulte) varie de 0,23 à 0,41 , ce qui semble suffisant pour soutenir la sous-population. Nous n'avons pas trouvé de preuves de différences de taux de survie entre les oursons de l'année et les petits d'un an ou de taux de survie spécifiques au sexe pour aucun groupe d'âge. Nos taux de survie moyens étaient de 0,794 (ICR à $95 \% 0,723-0,861$ ) pour les jeunes dépendants, de 0,873 (ICR à $95 \% 0,826-0,914$ ) pour les jeunes adultes indépendants et de 0,871 (ICR à $95 \% 0,853-0,892$ ) pour les adultes; ces taux sont inférieurs aux taux rapportés par Peacock et autres (2013) mais se situent dans leurs intervalles de confiance. Nous n'avons trouvé aucune preuve de relations entre la survie et des variables environnementales (p. ex., paramètres de la glace de mer, indice climatique, abondance des phoques). Notre analyse de l'état corporel a indiqué que les ours étaient moins susceptibles d'être en mauvaise condition physique pendant la période 2017-2018 comparativement à la période 2005-2007. En 2017 et 2018, les mâles adultes et les femelles adultes indépendantes étaient en meilleure condition que les jeunes adultes et les femelles avec des rejetons dépendants. Étant donné que le marquage-recapture génétique par fléchette biopsique a été la seule méthodologie employée pour le recensement et que la télémétrie par satellite n'a pas été effectuée,
nous n'avons pas été en mesure de déterminer s'il y a eu des changements de l'utilisation de l'habitat ou de la distribution au fil du temps.

Cette étude représente la deuxième évaluation structurée des sous-populations de 2005 à 2018 pour la sous-population du détroit de Davis. D'importantes lacunes dans les données (c.-à-d. les intervalles de temps entre les études successives) peuvent contribuer à de plus grandes incertitudes et à un biais possible dans les estimations des indices vitaux tels que la survie, et certains paramètres ne peuvent pas être estimés lorsque l'âge des ours n'est pas enregistré lors de l'échantillonnage sur le terrain. Néanmoins, la disponibilité d'un vaste ensemble de données provenant d'une étude antérieure et les renseignements obtenus des prises d'ours et des marqueurs de biopsie génétique nous ont permis de faire des prévisions pour les taux démographiques de base. Les évaluations des risques liés à la prise qui tiennent compte de la précision des données disponibles sur les sous-populations et des effets possibles de la transformation de l'habitat sont un outil analytique relativement récent qui peut fournir des renseignements concernant les effets démographiques d'une gamme de stratégies de prise possibles. À l'avenir, une évaluation des risques liés à la prise pourrait être effectuée pour la sous-population du détroit de Davis à l'aide des estimations des indices vitaux et de l'abondance fournies par la présente étude.

## 





```
\DeltaCD\L\Gammab}\mp@subsup{\sigma}{}{\mathrm{ cqabbb}
```















 Q.
 2009 - 2019. ${ }^{\text {¢ }}$ b


































## AULATSIJILLAGET NAILLITITAUSIMANNINGA

MânnaKammik jârini, silak asianguvallianinga nanituinnak Ukiuttattumi asiangutitsisimavuk nanunik (Ursus maritimus) inigiKattajanginnik nigiunangitunik sukkanigijanginnik ammalu suligok asianguvallialangajuk. Ikajugasuagiamut tigumiagiamullu nanunik ilangagijaulluni avatimmik ammalu atuinnaunginnaniammata niKitsagijaulluni piviannatolluni ilingajunut Inutuinnanut, Kaujisattilagijet Kaujisannik ammalu kamagigiangit Kaujisannink suliagijauKattavut Kimiggugiamut omajungita nanekkomangâmmik ammalu aulatsigunnagiamut tugâgutiliuttaujut kamagijaugaluammangâmmilonnet. Tapvani, Kaujititsivugut allaKutimmik Kaujijausimajunut mânnaKammik suliagijausimajunut omajunut Kaujisattausimajunut nanunik iniKajunut Davis Ikâgiapvingani (DI) nanuKutigijanginnik. Kaujisimajavut
ilautitsivuk timinnint tigusisimavugut ottugattaugajattunut tigujaulauttunut jâringinni 2017 ammalu 2018, omatlutik-tigujausimajut Kaujigatsait katitsutausimavut 2005-2007, ammalu katitsutausimajut Kaujigatsait katitsutauKattasimavut jâri tamât 2005-2018. kititangit unuttotigijunut ilingajunut 2017-2018 imailingasimavut 2,015 nanuit (Ajunnangitumik Avittutausimajunut $(A A)=251 ; 95 \%$ Bayesian Credible Interval [CRI] 1,603-2,588). kititangit unuttoningit ilingajumut 2006-2007 imalingasimavut 2,250 [SD = 133; CRI 1,989-2,512]. Atjigengitonnik, Peacock et al. 2013 kititangit unuttoningit ilingajumut 2005-2007 omani 2,158 [95\% Confidence Interval (CI) = 1,833-2,542]. IkKanaluattumut, uvagut kitisimajavut ilingajumut 2006-2007 jâringinni katasimavut iluani Kaujimajautsiatunut kitijausimajunut allaKutingatigut tâpsumunga Peacock et al. 2013 ilingajumut 2005-2007 jâringinni. Una taijaujuk Geometric tukiKajuk omajungita piguvallianingit akungani 2006 ammalu 2018 imailingasimajuk 0.989 ( $95 \%$ CRI 0.974 1.010) tamanna malitsiajuk ominga 0.896 piguvalliaKosimajunut ununningit imailingasimajumut <1 ammalu omajugijangit ikilliumisimakKotut Kângivalliasimanninganik. Jâringita 2006-2018, tainna kavamakkut Nunavummi asiangutitsilauttut aulatsijigijanginnik tugâgutinginnik ikilliumittisigiamut unuttoninginnik omajunik ammalu tukigijangita jâri tamât allaKutingit katitsutauKattajunik ilonnanginnik pitsatuniKajunut katiutigillugit puttusimavuk pisimajumit $64.1 \pm 10.1$ (AA) nanuit/jâringa akungani $1999-2008$ tikijumut $86.8 \pm 23.6$ akungani $2009-2019$. KaujimakKujigivugut taikkua tigujausot puttugiasimammijut Newfalâmi ammalu Labradorimi pisimajumit 6 nanunnik omunga12 nanunnut iluani Kaujisasimaniagatta. MaligatsaKalungilak katitsuigunnagiamut ilingajumut Quebec ininganik iniKajunut DI iningini, sakKititsijumik nalunattumik ilinganiKajumut ilonnanginnik kititanik pijausonik iniKajunut Davis Ikâgiapvingani nanugijanginnik iluingajunut. TukiKajuk piagait jârimi tigujausimajut (PT) (numarangit PT atunik anâlunnut pisimajumajunit 0.23 tikijumut 0.45 ammalu tukiKajuk piaganik tigujauKattajut (numarangit piagausimajut atunik annâlunnut) pisimajuk 0.23 tikijumut 0.41, sollu nâmmalungituk omajugijauKatigijaujunut. Kaujisimavugut ikajutsitaulungituk atjigengitojunut omajunut akungani PT ammalu piagausimajunut upvalu Kanuittoningit omaluasimajunut ammalu Katsinituinnak jâriKajunut. Tamanna tukiKattisijuk ununnigijangit omaKattajunut imalingasimavut 0.795 (95\% CRI; 0.723, 0.861 ) piaganut, $0.873(95 \% \mathrm{CRI} ; 0.826,0.914)$ taikkununga immigolingajunut
pigugesimajunut, ammalu piguKataugiallasimajunut, ammalu 0.871 ( $95 \% \mathrm{CRI} ; 0.853$, 0.892 ) pigugesimajunut, taikkua ikinnisausimajut sivunganinit Kaujititauniammat allaKutimmi iluanit Peacock et al. (2013) tâvatuak iluanettitauvut Kaujimajautsiatunut kitijausimajunut. Ammalugiallak, sukkaninga sikuk nunguvallianinga piujogunnaininga malitsiatigivuk taikkununga pigugesimajunut omagunnagiamut () iluani omajunut ikilliumiliaKijunut jârini Kangatuinnak sikuk nunguvallialimmat (upvalu auvallialimmat) tapvainauluatlatumik., ilautillugit tamapsuminga kamagijausimajunut kititausimavut $50 \%$ taikkununga Kangaulimmat atjigengitoKattajunut (jârimit jârimut atjigengitonnningit) pigugesimajut omaKattaningit. Tamakkua kititangit attuininga sukkajonninganik sikumit nunguvallianinganik taikkununga pigugeKatausimajunullu piungitosimammijuk tâvatuak ikinnisamik malitsialugani (). Timigijavut piusinga Kimiggutausimajunut nalunaitsilaukKuk taikkua nanuit piungitualosimajut timingit jâringinni 2017-2018 atjigengitojunut taipsumaniusimajumut 2005 - 2007. Jâringani 2017 ammalu 2018, angutialuit ammalu immigolingajut pigugesimajut annâluit piunitsaulauttut timingit taikkunangat annanut piagaKajunut. Silak asianguvallianinga akunin ulugianattumettisivuk taikkununga nanunnut ammalu iluani DI omagiamut attutaulaukKut iinganiKajumut sukkajonninga sikuk auvalliajumut nalunaitsijumik nanuKutet piungitumik attutaulâttut kajusiutigijaumut sikumik asiujivalliagatta. Tigusitluta Kanuittoningit-tigusigiallagatta petsitluta timinginnit kapputinnik atutluta tainnatuak atulauttavut Kaujisagiamut ammalu sâtilaittikut Kaujisalaunginatta, Kaujigunnalaungilagut inigijauKattajut atuttauKattajut asianguvalliasimagalaummangâllonet Kângivalliatillugu.

Tamanna Kaujisannik kiggatuvuk aippanganik tungavigijausimajumut nunannik omajunginnik Kaujisannimik akunganit 2005 ammalu 2018 ilingajumut DI omajunginnik. Aulatsijet ammalu asigiallait sivukkatet Kaujimagialet angijualuk Kaujigatsait amigagijauvut (sollu., Kangaulimmat akungani kajusiutigijautsiaKattajunut Kaujisannet) tunitsigajattuk Kaujimajaugengitunik pimmagittunik sukkajoningit, sollu omaKattajunut, ammalu inigijangita Kaujijaugunnangitut taikkua nanuit jâringit Kaujijaungimata nunami Kaujisagasualimmata. Tamannaugaluatluni, atuinnauningit anginitsait Kaujigatsait pisimajumit sivunganit Kaujisattausimajunut, katiutigillugit taikkununga katitsutausimagettunut nanusimajunut ammalu timinginnit tigujausimajunut
pivitsaKattisisimavuk uvattinik kititsigiamut ajunnangitunik inigijauKattajunut. Katitsuigiamut ulugianattuk Kimiggutaunninga (KUK) mânnaKammiuvuk Kaujijausimajut atuttausongutluni siumagijautitsijumik atjigengitunik katitsuigunnagiamut atâgut atjigengitojunik avatimit piusigijanginnik ammalu Katset katitsuiKattajut ulugianattojunut. Sivuppiagasualluta, taikkua Kaujisagiamut atuttausot atuinnauvut taikani DI omajugijanginnik aulataugiaKakKotunik pitsatunigijaulluni ippiniappata

## EXECUTIVE SUMMARY

In recent decades, climatic changes across the Arctic have altered polar bear (Ursus maritimus) habitat at unprecedented rates and further changes are expected. To help retain viable polar bear subpopulations as part of the ecosystem and to ensure continued availability of a subsistence resource for Inuit, scientific research and monitoring studies are conducted to evaluate subpopulation status and whether management objectives are being met. Here, we report the results of the recently conducted subpopulation study for polar bears of the Davis Strait (DS) subpopulation. Our analyses included genetic biopsy samples collected in 2017 and 2018, live-capture data collected 2005-2007, and harvest recovery data collected annually 2005-2018. Estimated abundance for the 2017-2018 period was 2,015 bears (Standard Deviation [SD] = 251; 95\% Bayesian Credible Interval [CRI] 1,603-2,588). Estimated abundance for the 2006-2007 period was 2,250 [SD = 133; CRI 1,989-2,512]. For comparison, Peacock et al. 2013 estimated abundance for the period 2005-2007 at 2,158 [95\% Confidence Interval (CI) = 1,833-2,542]. Importantly, our estimates for the 2006-2007 period fell within the confidence intervals reported by Peacock et al. 2013 for the 2005 2007 period. Geometric mean subpopulation growth between 2006 and 2018 was 0.989 ( $95 \%$ CRI $0.974-1.010$ ) which corresponds to a 0.896 probability that subpopulation growth was $<1$ and thus the subpopulation most likely declined (by at least one bear) over this period. Through 2006-2018, the Government of Nunavut modified the management objective to reduce abundance of the subpopulation and mean annual reported harvest from all jurisdictions combined increased from $64.1 \pm 10.1$ (SD) bears/year between 1999 - 2008 to $86.8 \pm 23.6$ between $2009-2019$. We also note
that the quota was increased in Newfoundland and Labrador from 6 bears to 12 bears within our study period. There is no mandatory harvest reporting requirement for the Québec portion of the DS range, creating uncertainty related to total harvest levels for the Davis Strait subpopulation. Mean cub-of-the-year (COY) recruitment (number of COYs per adult females) ranged from 0.23 to 0.45 and mean yearling recruitment (number of yearlings per adult female) ranged from 0.23 to 0.41 , which appear to be sufficient to sustain the subpopulation. We found no support for differences in survival between COYs and yearlings or for sex-specific survival rates for any age class. Our mean survival rates were 0.794 ( $95 \%$ CRI; $0.723,0.861$ ) for dependent young, 0.873 ( $95 \%$ CRI; $0.826,0.914$ ) for independent subadults, and 0.871 ( $95 \%$ CRI; $0.853,0.892$ ) for adults, which are lower than previously reported in Peacock et al. (2013) but fall within their confidence intervals. We did not find evidence for a relationship between survival and any environmental variables (e.g. sea ice parameters, climate index, seal abundance). Our body condition analysis indicated that bears were less likely to be in poor body condition during 2017-2018 compared to 2005-2007. In 2017 and 2018, adult males and independent adult females were in better condition than subadults and females with dependent offspring. As genetic mark-recapture via biopsy darting was the sole methodology used for the survey and because satellite telemetry was not conducted, we were unable to determine whether habitat use, or distribution has changed over time.

This study represents the second structured subpopulation assessment between 2005 and 2018 for the DS subpopulation. Large data gaps (i.e., time intervals between successive studies) can contribute to higher uncertainty and potential bias in estimates of vital rates, such as survival, and some parameters cannot be estimated when ages of bears are not recorded during field sampling. Nevertheless, the availability of a large dataset from a previous study, combined with information collected from harvested bears and genetic biopsy markers allowed us to estimate basic demographic rates. Harvest risk assessments that consider the precision of available subpopulation data and the potential effects of habitat change are a relatively recent analytical tool that can provide information on the demographic effects of a range of potential harvest strategies. Moving forward, a harvest risk assessment could be performed for the DS
subpopulation using estimates of vital rates and abundance provided by the current study.

## INTRODUCTION

Wildlife managers face complex decisions when seeking to address conservation challenges against other societal priorities. Decisions and outcomes must be evaluated periodically so that new information can be fed back into an adaptive management framework (Holling 1978, Johnson 1999, Lancia et al. 1996). Accurate and up-to-date estimates of subpopulation abundance are often a key component of informed management decisions (Nichols and Williams 2006). Typically, new estimates of abundance are acquired periodically according to a monitoring interval that is determined by management objectives and species biology (Gibbs 2008). As climatic changes affect many areas around the globe, shortened monitoring intervals may be required to understand the concurrent effects of management interventions and environmental change. Broadly, more frequent monitoring increases the probability of meeting management objectives and reduces the severity of potential negative outcomes (Taylor et al. 2007, Regehr et al. 2017a).

One species that has received significant monitoring attention is the polar bear (Ursus maritimus Phipps 1774). Polar bears are characterized by having delayed maturation, small litter sizes, and high adult survival rates (Bunnell and Tait 1981). They are at the top of the Arctic food chain and as such may bioaccumulate environmental contaminants (e.g., McKinney et al. 2009, 2011; Letcher et al. 2010, Fisk et al. 2009, Derocher et al. 2003). As a circumpolar species that depends on the sea ice for hunting, travel, mating, and in some instances denning (Amstrup 2003), sea-ice loss resulting from climate change is predicted to impact polar bear subpopulations severely in the future (Derocher et al. 2004, Amstrup et al. 2008, Stirling and Parkinson 2006, Stirling and Derocher 2012, Durner et al. 2009, Atwood et al. 2016, Regehr et al. 2016). The global polar bear population, consisting of 19 subpopulation units, is estimated to be approximately 26,000 polar bears (Regehr et al. 2016, Wiig et al. 2015). Currently there
is no empirical evidence for declines in global abundance due to sea-ice loss (Regehr et al. 2016). However, accurate assessment of such changes is complicated by insufficient data for many polar bear subpopulations (Durner et al. 2018), spatial and temporal variation in the effects of ice loss, and the fact that some subpopulations have likely recovered in recent decades from overexploitation prior to the 1973 Agreement on the Conservation of Polar Bears (Larsen and Stirling 2009).

Despite the various on-going research and monitoring efforts on polar bears, reliable and updated abundance and demographic information for some subpopulations are still lacking (Obbard et al. 2010, Vongraven et al. 2012). Polar bear research is expensive and logistically challenging, especially for management jurisdictions that oversee more than just one subpopulation. Nunavut, Canada, is home to 12 subpopulations ( 8 shared with other jurisdictions, 4 entirely within Nunavut; Obbard et al. 2010) and as such carries the major responsibility of polar bear research in Canada. To maintain healthy and viable polar bear populations, subpopulation studies in Nunavut are scheduled to follow a 10 to 15 -year rotational cycle, which can vary depending on research needs and priorities. Here we present findings from a 2017 2018 monitoring study to develop an updated estimate of the abundance of the Davis Strait (DS) polar bear subpopulation, and to compare demographic data from this study to the results of the previously (2005-2007) conducted subpopulation study (Peacock et al. 2013).

Within Canada, the DS polar bear subpopulation is shared by Nunavut, Québec (Nunavik), and Newfoundland and Labrador (NL; Nunatsiavut) [Durner et al. 2018; Figure 1]. The subpopulation was first inventoried in the 1970s (Stirling and Kiliaan 1980; Stirling et al. 1980). Although that study did not cover the entire area, and likely underestimated the subpopulation size, it estimated the subpopulation to be around 900 bears. Subsequent work conducted on the Labrador coast in the early 1990s located approximately twice the numbers of bears per hour of search compared to observations during the 1970s (Stirling, unpubl.data in Stirling and Parkinson, 2006). During that same period (1970s to 1990s), abundance of harp seals (Phagophilus groenlandicus), the primary food source for DS polar bears (Iverson et al. 2006), as well as hooded seals increased significantly in the Northwest Atlantic (Bowen et al., 1987; Stenson et
al.,1997; Healey and Stenson, 2000). This high abundance of food resources for DS polar bears during that period was suggested as a primary factor in the likely increase of their abundance during those two to three decades (Stirling and Parkinson, 2006). In early 2000, Nunavut Inuit inhabiting the Davis Strait region reported seeing more bears during all seasons (Kotierk 2009), also supporting the probable increasing abundance of DS polar bears. However, since the 1980s, a declining trend in sea-ice duration (forming later and breaking up earlier [Stirling and Parkinson 2006, Stern and Laidre 2016; Regehr et al. 2016]) has raised the question of how polar bears and seals are affected by climate warming, which has been identified as the primary threat to polar bears throughout their range (Polar Bear Range States 2015).

Because of the uncertainties surrounding the DS subpopulation status, the Government of Nunavut (GN) conducted another population survey from 2005-2007, with funding and logistic support from the governments of NL and Nunatsiavut, Makivik Corporation, Polar Continental Shelf Project, Parks Canada and the Nunavut Wildlife Management Board. That study resulted in an abundance estimate of 2,158 (95\% CI: 1833 - 2542) bears (Peacock et al. 2013). The results suggested that the subpopulation had grown substantially between the 1970s and 2007 but was at that point experiencing a decline in both productivity and growth rate, possibly through density-dependent mechanisms. In addition, the observed declining trend in sea-ice duration might also have played a role in that productivity decline through reduced access to seals. If productivity remained low in subsequent years, bear abundance may have continued to decline in the region.

In recent years, Inuit have broadly expressed the view that increasing numbers of bears are causing increases in human-bear conflicts and generally creating elevated public safety concerns, especially for people going out on the land (Kotierk 2009; Henri 2012; NMRWB 2019). Inuit also report that the bears are increasingly impacting other wildlife by eating large numbers of young seals and eggs in bird colonies. (York et al. 2015; NMRWB 2019). Some corroborating science exists for these observations, particularly with respect to plasticity of bear foraging behaviour (Barnas et al. 2020, Rode et al. 2015). Although there is a logical relationship between increased abundance and increased human-bear conflicts, and such a relationship has been demonstrated for
black bears (Garshelis et al. 2020), increases in the frequency of human-bear conflicts and any cause-and-effect relationships are not limited to considerations of bear abundance. There is also a substantial body of evidence that sea-ice declines have resulted in longer periods of bears being seasonally restricted to land (Bromaghin et al. 2015, Lunn et al. 2016, Obbard et al. 2016, Regehr et al. 2010, Stirling and Derocher 2012, among others). In some cases, this has resulted in further changes in seasonal distribution, migration, and concentration patterns of bears in relation to communities and other areas of high human use. These behavioural and movement pattern changes are also relevant to monitoring and assessing changes in frequency of human-bear conflicts and are not necessarily based on any change (increase or decrease) in abundance of bears.

Following the results from the 2005-2007 study, the co-management partners within Nunavut decided to increase the total allowable harvest (TAH) from 46 to 61 bears annually for the 2012/2013 harvest season in an effort to reach a managed decline of the DS subpopulation. Despite this change in TAH, Nunavut Inuit annual harvest only increased from an average of 39.4 bears during the 1999-2008 period to 44.2 bears during the 2009-2019 period. Inuit reported harvest in Nunavik (Québec) however increased significantly between those two same time periods from an average of 16.5 bears to 30.2 bears per year while Nunatsiavut (Newfoundland and Labrador) reported harvest increased from an average of 5.9 bears to 10.9 bears per year (Table 10). Given the increased harvest, Inuit observations, and continued sea-ice decline, there was uncertainty surrounding the current status of the DS subpopulation.

Polar bears in Nunavut have been managed through a complex co-management system that includes community-level (Hunters and Trappers Organizations, HTOs), regional-level (Regional Wildlife Organizations, RWOs), and territorial-level (Nunavut Wildlife Management Board, NWMB, and the GN) participants. Through consultation and discussion, memoranda of understanding (MOU) ${ }^{1}$ between each community's HTO and the GN were developed. These MOUs lay out harvest, management, and research aspects for each polar bear subpopulation. Under the existing 2004 MOU, the GN committed to a new subpopulation study for DS. To address uncertainty in the DS

[^0]status and to fulfill its obligations under the 2004 MOU, the co-management partners, including jurisdictions that share this subpopulation, planned to conduct a new subpopulation study between 2017 and 2018. Consultations on the proposed study design and methodology were conducted with each Nunavut community that harvests from DS and all supported the less-invasive genetic mark-recapture methodology. Local HTO members participated in field research.

In Newfoundland and Labrador responsibilities for polar bear conservation and management are shared between the Government of Newfoundland and Labrador, the Nunatsiavut Government, and the Torngat Wildlife and Plants Co-Management Board, in accordance with the Labrador Inuit Land Claims Agreement (and its associated Act) and the Newfoundland and Labrador Wild Life Act. All three entities prioritized the 2017-2018 genetic mark-recapture methodology, led the field collection of data in the Labrador portion of the range and adjacent areas in Nunavut and Québec, and have engaged in the analysis. Co-management partners in Newfoundland and Labrador and Québec, as in Nunavut, have invested in this research to better understand various aspects of polar bear ecology and inform co-management decision-making.

Similarly, in Québec, the management of polar bears is complex and relies on a collaboration between the Québec government, wildlife management boards as well as local Inuit and Cree hunter organizations. Consultations were conducted in Québec with Local Nunavimmi Umajulivijiit Katujiqatigininga (LNUK) as well as with the Hunting, Fishing and Trapping Coordinating Committee who supported the 2017-2018 survey using the genetic mark-recapture approach. Representatives from the Québec government and from Nunavik communities participated in the collection of data in the Québec portion of the range and adjacent areas in Nunavut.

The new study had the objective to estimate the current subpopulation size and composition and compare those results to the 2005-2007 study to inform responsible management authorities for decision-making. In addition, we sought to obtain data that would provide estimates of survival and reproductive parameters for future subpopulation viability analyses and harvest risk assessments. Based on available methodologies and community-level feedback, the supported method was the lessinvasive genetic mark-recapture method, which can be a useful alternative to physical
mark-recapture in subpopulation monitoring (Vongraven et al. 2012; Vongraven and Peacock 2011). To address these objectives, we conducted a genetic mark-recapture study from 2017-2018.

## Study Area

The Davis Strait demographic unit (Figure 1) has been previously delineated based on the movements of collared adult female bears (Taylor et al. 2001), the locations of bears marked and subsequently recaptured or harvested (Taylor and Lee 1995), and DNA analysis (Paetkau et al. 1999, Malenfant et al. 2016). The full range of polar bears in the DS subpopulation unit covers approximately $420,000 \mathrm{~km}^{2}$ between Canada and Greenland, including the Davis Strait, Labrador Sea, Ungava Bay, Frobisher Bay and Cumberland Sound (Taylor et al. 2001, Taylor and Lee 1995). Davis Strait is generally ice free during summer and early fall (July - October; Stern and Laidre 2016) and polar bears are distributed and concentrated along the shoreline and on off-shore islands on the Canadian side of their distributional range, from Cape Dyer on eastern Baffin Island down to northern Labrador (Taylor et al. 2001, Peacock et al. 2013) during this time.

Using cluster analysis of polar bear movements from satellite telemetry, Taylor et al. (2001) identified a generally strong boundary between the DS and Baffin Bay (BB) subpopulations, and movements between DS and Foxe Basin (FB) were infrequent causing demographic discontinuity between the two subpopulations. Genetic clustering methods (Obbard et al. 2010) suggested that mating fidelity of polar bears to southern DS (i.e., south of Hudson Strait); central DS (i.e., south of Cumberland Sound on Baffin Island); and northern DS on Baffin Island (i.e., north of Cumberland Sound) exist. Peacock et al. (2013) suggested from their analysis that the sub-regions differed where a) harp seals constituted a significantly larger part of polar bear diet in southern DS compared to the more northerly sub-regions (Iverson et al. 2006); b) harvest levels in southern DS differed from those in central and northern DS; and c) exchange between polar bears in DS and BB was more likely to occur in northern DS than in other subregions (Figure 2; also see methods and results sections).

## METHODS

## Samples

## Field collections

We conducted our survey across the entire DS subpopulation summer and fall range, including Nunavut, Québec and Labrador, during 2017 and 2018. Our study design followed that of the previous physical mark-recapture study conducted in DS between 2005-2007 (Peacock et al. 2013), however, it did not involve the immobilization and physical handling of bears (Figure 3 and 4). Inuit co-management partners in Nunavut and Nunavik frequently expressed their concern over wildlife capture and handling (Department of Environment 2013, Lunn et al. 2010) and as a result, the responsible government management agencies explored alternative research methods. After discussions with the affected communities and co-management partners in neighbouring jurisdictions, genetic mark-recapture was chosen as the method since it is less-invasive (Garshelis 2006) and has been successfully applied on various species, including bears (Brown et al. 1991, Palsbøll et al. 1997, Boulanger et al. 2004, Lukacs and Burnham 2005, Schwartz et al. 2006, Paetkau 2003). The survey team selected this methodology recognizing that certain aspects of habitat use, age structure and spatiotemporal comparisons with the previous study, Peacock et al. (2013), would not be available.

We constrained our study to August - October, like the 2005 - 2007 study, in order to search for bears along their summer and fall range, which consists of coastline and on near-shore islands. While on land, bears can be found further inland, and at higher elevations, which could make them undetectable if search effort is only concentrated along the coast (e.g., Ferguson et al. 1997, 2000; Taylor et al. 2001; Escajeda et al. 2018). In addition, bears frequently segregate by age class and reproductive status where adult females with cubs tend to select fjords, avoiding offshore islands and coastal regions where densities of adult males are usually greater. Pregnant bears select inland and upland denning habitats where they are less available for sampling (Ferguson et al. 1997, Escajeda et al. 2018). Therefore, we adopted a similar method as the 2011-2013 BB polar bear survey (SWG 2016). We applied the

BB study stratification to our study area with a high-density stratum, including the coastline and offshore islands, extending to 5 km inland; a moderate-density stratum including inland regions $5-10 \mathrm{~km}$ from the coastline; and a low-density stratum from 10 to 30 km inland (Figure 3). During the BB study, bears were reportedly found on glaciers, high-elevation snow patches, and plateaus along the coast and on islands (SWG 2016). For this study, we included all elevations within our strata to ensure the greatest opportunity for bears to be observed and sampled. Search efforts were allocated according to the anticipated bear densities with roughly $65 \%, 25 \%$, and $10 \%$ of helicopter search effort spent in the high-, moderate-, and low- density strata, respectively. We set a priori guidelines to systematically distribute inland search effort along the entirety of the islands (SWG 2016). All offshore islands were surveyed as completely as possible, while accommodating weather and safety concerns. In both 2017 and 2018, portions of the Nunavut coastline as well as Resolution and Edgell Islands along with Loks Land could not be surveyed because of inclement weather, though this represented a small fraction of the overall study area (Figure 4).

This study combined genetic mark-recapture data collected during the 2017 and 2018 field seasons, data from earlier physical mark-recapture research conducted 2005 - 2007 in DS (Peacock et al. 2013), and information on harvest recoveries of marked bears. Genetic samples were collected from every bear that was encountered when operating and darting conditions were safe. The east coast of Baffin Island (including offshore islands), parts of the Ungava peninsula and Labrador, are very steep and sampling bears is challenging, especially when the field crews attempted to sample offspring of family groups. In such instances, attempts were made to collect a skin sample of the mother only, rather than all members of the family group, to minimize chase times and to avoid separation of family group members. Regardless of terrain or sampling, all offspring were recorded in the dataset to estimate reproductive parameters.

We obtained genetic material for individual bears from a small sample of skin and hair ( $<5 \mathrm{~mm}$ diameter) collected via a remote biopsy dart (Pneudart Type C - Polar Bear, Williamsport, PA) fired from a dart gun (Capchur Model 196) from inside a
helicopter ${ }^{2}$ approximately $3-7 \mathrm{~m}$ above the ground and targeted at the rump (Pagano et al., 2014; SWG, 2016). Remote marking biopsy darts (Pneudart Type C - Polar Bear, Williamsport, PA) were also occasionally used when multiple bears were present at a given site (e.g., family group). Those darts were identical to the regular biopsy darts except they left a dye mark on the bear upon impact. The biopsy dart automatically falls off the bear after extracting the skin and hair sample via small barbs, thus eliminating the need to physically handle bears to obtain a DNA sample. The darts have relatively low velocity which means that risk of injury to a bear is minimal. Typically, bears show no or little response to the impact of the dart and are left with no obvious mark. In order to facilitate easy spotting of darts on the ground, a $10-15 \mathrm{~cm}$ long and $\sim 2 \mathrm{~cm}$ wide strip of brightly colored flagging tape (C.H. Hanson, Naperville, IL; or Johnson, Montreal, PQ) was tied and wrapped around the distal end of the dart. Alternatively, darts were spray painted bright orange to maximize detection and recovery. Every bear that was encountered and biopsied received a unique field identification number so that the genetic results and our field data could be cross-referenced and linked.

Additional field information included the date, time and location where each bear (or group of bears) was sampled, body condition based on visual assessment using a standardized subjective fat index (e.g., Stirling et al. 2008; a scale from 1-5 with 1 being skinny, 3 average and 5 obese), specific markings or characteristics, group size or litter size, the estimated field age class (e.g., cub-of-the-year [COY], yearling, 2 -year-old, subadult, adult) and sex classification. Field age class and sex were both recorded with a confidence qualifier (e.g., high and low confidence). Dependent offspring were distinguished as COYs, yearlings, and 2 -yr olds based on their size relative to their mother. Cues such as body size of the individual bear in relation to its surroundings or group members, body shape and proportions, presence of scars, secondary sexual characteristics, observation of urination, and gait were all used to determine field sex and age class (SWG, 2016; Laidre et al., 2020a, 2020b). When field age class and sex of a bear were initially assessed with low confidence, additional field notes were taken. For example, notes may suggest an alternative field age class and sex if observers were unsure, particularly for difficult-to-discern solitary young subadult male bears and

[^1]younger adult females. These field observations, together with genetic microsatellite results, allowed us to confirm field-estimated sex and age class. Lastly, we recorded factors that may have influenced detection probability during sightings, including weather conditions (e.g., cloudy, clear, sun glare), bear activity when first observed, and simple habitat characteristics in general, and within, the immediate vicinity ( $\sim 30 \mathrm{~m}$ ) of an individual bear that may make detection more difficult (e.g., boulders).

## Recovering previously marked bears through harvest

Recoveries occurred when a previously sampled bear was recovered through the harvest monitoring program. Both Nunavut and Nunatsiavut polar bear harvest monitoring programs record detailed information about every human-caused bearmortality and collect a variety of tissue samples (Lee and Taylor 1994, GNL tech reports) while Québec harvest reporting and sampling remains fragmentary. Polar bear harvest data from 2005 to 2018 were included in this study and compiled where possible from Nunavut, Greenland, Québec, and Newfoundland and Labrador. We assumed that the detection and reporting of previously marked bears would vary throughout this period. The detection rate of previously marked bears, through ear tag and tattoo recovery, drops to about 8-10\% seven to eight years after a physical markrecapture study has been concluded (Government of Nunavut, unpublished data). This is likely because ear tags are ripped out by conspecifics and tattoos fade, becoming harder to detect by hunters and officers. We assumed that returns of tag and tattoos for bears marked in DS was 100\% between 2005 and 2011 and relied on hunter-reports to identify recoveries. After 2011, we used available harvest-collected tissue samples and genotyped those from DS, the neighbouring FB, and BB polar bear subpopulations. Logistical and financial constraints prevented us from using all available harvest samples from the neighbouring BB subpopulation to detect potential DS-marked bears that had been harvested there. Therefore, we restricted our BB harvest sample collection to bears that were harvested within 0-400 km north of the DS/BB subpopulation boundary. Sampling of harvested bears in Québec was low between 2005 and 2017 but a sampling program was implemented in in 2017 and 2018 to increase the detection of biopsied bears in the harvest. Sampling of harvested bears in

Newfoundland and Labrador began in 2011 and all samples were made available for this study. For the analyses in this report, we used all available harvest recoveries of bears marked in DS, including those that were recovered in neighbouring subpopulations (Burnham 1993).

## Recaptured bears from past subpopulation study

Recaptures represent bears that were previously sampled and subsequently sampled in a later year. All available individuals of the 2005-2007 DS study were genotyped. These results $(\mathrm{n}=1549)$ allowed us to determine, through DNA, whether a marked bear from the previous study was also encountered during the 2017-2018 genetic markrecapture sessions.

## Sample preparations

We used the same method to prepare all field and laboratory tissues. A small piece of skin (~ 1-1.5 mm thick) or tissue was cut from the biopsy sample, the ear plug (e.g., a small tissue core that was obtained when applying ear tags during the 2005-2007 study), or the muscle tissue with a new scalpel blade (\# 20), transferred onto a shipping card (Avery, $70 \times 35 \mathrm{~mm}$ ), and attached with scotch tape. Each sample card was labelled with the unique bear identification number, placed into a coin envelope (57x 89 mm ), and left to dry at room temperature for up to three days. The dried specimens were then sent to Wildlife Genetics International Inc. (Nelson, British Columbia) for individual genotyping and sex determination.

## Genetic analysis

The tissue samples had DNA extracted using QIAGEN DNeasy Blood and Tissue Kits (Qiagen Inc.) and were genotyped at eight previously published dinucleotide microsatellite loci (REN145P07, CXX20, MU50, G10B, G10P, G10X, MU59, G10H; Paetkau and Strobeck 1994, Paetkau et al. 1995, 1998; Taberlet et al. 1997, Breen et al., 2001, Ostrander et al 1993). Analysis of individual identity followed a 3-phase protocol previously validated for bears (Paetkau 2003; Kendall et al. 2009).

To select markers for the analysis of individual identity, we used allele frequency data from approximately 1700 polar bears for which complete 20-locus genotypes existed before the genetic mark-recapture study began (Government of Nunavut, unpublished data). We ranked the 20 microsatellite markers in the dataset by expected heterozygosity. The eight most variable markers that could be analyzed together in a single sequencer lane were selected for use. These surpassed the required standard for marker variability (Paetkau 2003). In addition to the eight microsatellite markers, we analyzed sex on every sample, using a ZFXIZFY marker. We searched the dataset for genotype matches that seemed unlikely based on our field data. In each case, three extra markers were added to the genotypes to lower the probability of chance matches between individuals. The extra loci confirmed all matches. Once the genotyping and error-checking was complete, we defined an individual for each unique eight-locus genotype.

## Survival analysis

## Data Collection

In the early study period (2005-2007), polar bears were physically captured following standard chemical immobilization techniques (Stirling et al. 1989). Bears captured during this period were given a unique identification number using an ear tag and upper lip tattoo. Information on the location of the capture along with sex and field age class were recorded. Additionally, genetic samples were collected, and most bears had a premolar tooth extracted for more accurate age determination (Calvert and Ramsay 1998). For the 2017-2018 study period, genetic capture-recapture techniques were employed, "marking" the bears using biopsy darts to collect small tissue samples which were later genetically analyzed to determine sex and to assign a genetic individual identification to each bear (Dyck 2017, Dyck and Ware 2018). For all captures in 2017 and 2018, exact age past the yearling classification could not be determined as bears were not physically handled. During surveys conducted in both study periods, bears were assigned a field age class (e.g., subadult, adult). We assigned a numeric age to the unknown-age bears in 2017-2018 based on the mean age of known-age bears within the same field age class from 2005-2007.

Our analysis also included bears marked in DS that were subsequently shot and reported in DS or adjacent subpopulations, including BB, FB, and Lancaster Sound (LS; Figure 2). Unlike live captures which were constrained to the survey period (August October), dead recoveries could occur year-round between the live-capture sampling study periods. For the DS data, there was minimal temporal overlap of live-recapture and dead-recovery periods. To ensure that there were no instances of bears being coded as harvested before being observed alive during the sampling period in year $t$, we set harvests recorded before August in year $t$ as occurring after the live recapture sampling period in year $t-1$, whereas harvests after August 1 were assumed to have occurred after live-recapture sampling in year $t$.

## Hierarchical model structure

We analyzed the capture-recapture-recovery data using a multistate survival model with a marginalized likelihood (Williams et al. 2002, Kéry and Schaub 2012, Yackulic et al. 2020). We developed different multistate model structures for females and males to accommodate the dynamic processes of aging and reaching sexual maturity in addition to transitions between live and dead states. For each sex, the multistate model structure included multiple live states determined by the aging process in addition to two dead states. For females, we considered eight possible states at time $t$ that included cub-of-the-year ( $\sim 9$ months old and dependent on their mother; COY, state 1), yearlings (state 2), states 3-5 included independent subadults between ages 2 and 4, state 6 included adult females $>4$ years old, state 7 included female bears shot and reported dead between time $t-1$ and $t$ (hereafter, "recently dead"), and state 8 was an absorbing dead state (e.g., "dead"). Because we had 9 years with dead recoveries only, we were unable to model survival of adult females with offspring as separate states because these states were unobservable and thus survival would be inestimable during this time (see Lunn et al. 2016). We set the adult female class to be $>4$ years old as most females were first observed with COYs were $\geq 5$ years old in the 2005-2007 data set. For males, we considered 11 possible states at time $t$ that included COY (state 1), yearling (state 2), independent subadults between ages 2 and 7 (states 3-8), adults > 7 years old (state 9 ), bears shot and reported dead between time $t-1$ and $t$ ("recently dead", state 10), and
an absorbing dead state ("dead", state 11). For the males, we included an extended subadult stage because most males begin breeding at ca. 8 years old (Rosing-Asvid et al. 2002, Richardson et al. 2020), at which time they exhibit different behaviours than subadults that could affect survival.

Here, we include the female state transition matrix representing probabilities of transitioning from a true state at time $t$ (rows) to a true state at time $t+1$ (columns).
COY
YRL
2
2
3
4
Recently dead
ARL
0 $\left[\begin{array}{cccccccc}\text { Dead } \\ 0 & S_{C O Y} & 0 & 0 & 0 & 0 & 4 & \text { AD } \\ 0 & S_{Y R L} & 0 & 0 & 0 & \left(1-S_{Y R L}\right) * r_{F} & \left(1-S_{Y R L}\right) *\left(1-r_{F}\right) \\ 0 & 0 & 0 & S_{S A} & 0 & 0 & \left(1-S_{S A}\right) * r_{F} & \left(1-S_{S A}\right) *\left(1-r_{F}\right) \\ 0 & 0 & 0 & 0 & S_{S A} & 0 & \left(1-S_{S A}\right) * r_{F} & \left(1-S_{S A}\right) *\left(1-r_{F}\right) \\ 0 & 0 & 0 & 0 & 0 & S_{S A} & \left(1-S_{S A}\right) * r_{F} & \left(1-S_{S A}\right) *\left(1-r_{F}\right) \\ 0 & 0 & 0 & 0 & 0 & S_{A D} & \left(1-S_{A D}\right) * r_{F} & \left(1-S_{A D}\right) *\left(1-r_{F}\right) \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1\end{array}\right]$

Parameters in the state transition matrix included state-specific probabilities of survival $(S)$ and recovery $(r)$ (i.e., probability of reporting conditioned on mortality). This parameterization refers to the most general model (M1, see Table 2). Classes for survival included cubs-of-the-year (COY), yearlings (YRL), subadults (SA, ages 2-4), and adult females (AD, ages 5+). For recovery, class ' $F$ ' includes all females $\geq 2$ years old. In our dataset, several yearlings (males and females) were recovered just before their second birthday and were also assigned the recovery probability for females. The state transition matrix for males is largely the same with an extended subadult stage (27 years old) and male-specific recovery probabilities. Transitions between live states were conditional on survival probability, $S_{x, t}$, defined as the probability that an individual
in class $x$ survives from year $t$ to year $t+1$. Survival probabilities were affected by all sources of mortality, including harvest mortality and natural mortality, and are thus a measure of 'total' annual survival. In this framework, the first dead state ("recently dead") was observable and could be entered at time $t$ conditional on the probability of being shot (i.e., $1-S_{x, t}$ ) * $r_{x, t}$ ) and being reported dead (i.e., recovery, $r_{x, t}$ ) since time $t$ 1. Here, the recovery probability $r_{x, t}$ is equivalent to Seber's conditional probability of detection for dead individuals (Otis and White 2004). This state could be entered from all but the COY live state because harvest of dependent young is prohibited and no marked COYs were reported as being harvested in our data set. The second dead state ("dead") was an unobservable absorbing dead state that could be entered from the COY live state with probability $1-S_{C O Y}$, entered from the remaining live states conditional on mortality ( $1-S_{x, t}$ ) and not being recovered and reported ( $1-r_{x, t}$ ), or entered from the recently dead state with probability of 1 . Because we included dead recoveries of bears marked in DS and later shot and reported from anywhere in DS or the adjacent BB, FB, and LS subpopulations, we were able to estimate true probabilities of $S_{x, t}$ decoupled from permanent emigration outside of the capture-recapture survey area (Burnham 1993, Schaub and Pradel 2004).

Our observation model linked the true and observed states. Here, we include the female observation matrix representing the link between true (rows) and observed (columns) states at time $t$ after release (COY are 'recaptured' for the first time as YRL). Parameters included class-specific recapture probability ( $p$ ). Classes include adult females and offspring (FO) and subadults (SA) as denoted in the matrix below.

|  | Seen alive | Seen alive | Seen alive | Seen alive | Seen alive | Seen alive | Recovered | Not seen o |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | as COY | as YRL | as 2 | as 3 | as 4 | as AD | dead | recovered |
| COY | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YRL | 0 | $p_{\text {FO }}$ | 0 | 0 | 0 | 0 | 0 | 1- $p_{F O}$ |


| 2 |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 3 |  |  |  |  |  |  |  |
| 4 |  |  |  |  |  |  |  |
| AD |  |  |  |  |  |  |  |
| Recently Dead |  |  |  |  |  |  |  |
| 0 | 0 | $p_{S A}$ | 0 | 0 | 0 | 0 | $1-p_{S A}$ |
| Dead | 0 | 0 | $p_{S A}$ | 0 | 0 | 0 | $1-p_{S A}$ |
| 0 | 0 | 0 | 0 | $p_{S A}$ | 0 | 0 | $1-p_{S A}$ |
| 0 | 0 | 0 | 0 | 0 | $p_{F O}$ | 0 | $1-p_{F O}$ |
|  | 0 | 0 | 0 | 0 | 0 | 1 | 0 |

Specifically, this matrix included the probability of being seen alive in class $x$ (e.g., adult females and offspring (FO) or subadults (SA)) at time $t$, the probability of being recovered dead in class $x$ at time $t$, and the probability of not being seen or recovered in class $x$ at time $t$. The observation matrix for males was largely the same but again included the extended subadult stage (2 to 7 years old). We included $r_{x}$ in the state transition matrix (Figure 2) instead of the observation matrix to overcome an update problem as described in Kéry and Schaub (2012).

Because the live capture-recapture surveys were conducted intermittently, several years of survival estimates for certain age classes were inestimable when there were no marked bears in the sample because they had aged out of the relevant states. For example, we could not estimate COY survival past 2008 because there were none in the sample (Table 1). In years when survival probabilities were inestimable due to the lack of data, we fixed the parameters to 1 . Similarly, we fixed recapture probability ( $p$ ), to 0 in years without live capture-recapture surveys. These parameter constraints had no bearing on the mean or on the estimates of recapture or survival probabilities in other years.

## Parameterization

We constructed a series of candidate models for survival, recovery, and recapture probability with the initial state structure outlined above (see Hierarchical model structure). We conducted model selection for each parameter in a stepped fashion (Table 2). We used this approach to select the top-ranked model structure for each
parameter ( $S, r, p$ ) based on the selected structure for any previously evaluated parameters and a general structure for parameters not yet evaluated. When applicable, each parameter may include the subscript $x$ to indicate the estimates are class specific (defined therein) and may include the subscript $t$ to indicate year-specific estimates.

The parameterization of the most general model (M1) included 4 age classes for survival (COY, yearlings, subadults, adults). For offspring (COY and yearlings), survival was kept constant across time in all models because we lacked the data to model temporal variation. For the subadult and adult classes, we were specifically interested in evaluating temporal variation and modeled survival around a central mean (logit [ $S_{x, t}$ ]) using independent Gaussian random effects for each class on the logit scale: $\varepsilon_{x, t} \sim \operatorname{Norm}\left(0, \sigma_{x}^{2}\right)$. The general model included time-constant estimates of recovery, $r_{x}$, for 2 sex classes (females $\geq$ age 2 , males $\geq$ age 2 ), and a separate mean recapture probability for 3 age-sex classes (adult females and offspring, subadults, and adult males) with an additive fixed effect $\beta_{\text {year }}$ coefficients for each capture-recapture period to adjust the mean $p$ up or down in a non-random fashion with the fixed effect of year to capture temporal variation, resulting in estimates $p_{x, t}$. The parameterization of the initial model (M1) was based on previous studies of polar bears (e.g., Regehr et al. 2010, Lunn et al. 2016), especially the previous DS study by Peacock et al. (2013).

Steps $1-3$ in the model selection process were focused on identifying the best structure for survival probabilities. First, we compared models for age (Step 1, models M1 and M2) and sex (Step 2, models M3 and M4) structure, followed by alternative models for temporal variation (Step 3, models M5-M6) while using the best age and sex structure from steps 1 and 2 (Table 2). Using the top model from steps $1-3$, we then assessed alternative models for temporal variation in recovery probability (Step 4, models M7 and M8) and age-sex structure in recapture probability (Step 5, model M9). Finally, using the best model from steps 1 through 5, we tested alternative models for the effects of environmental covariates on annual survival rates (step 6, models M11 M17). We describe these steps and models in detail below.

Our first step was aimed at identifying the best model for age structure in survival probabilities. Model M1 included 4 age classes (as described above). The second model (M2) included three age classes: a single class for dependent young (COY and
yearlings), subadults, and adults. We note Peacock et al. (2013) found that point estimates of survival for old senescent bears (> age 20) were lower than those for prime-aged adults, however, bears marked or captured in 2017-2018 could not be assigned to an adult versus senescent age class and therefore we estimated a common $S_{x, t}$ for all adults (e.g., Regehr et al. 2010, Lunn et al. 2016). Following determination of the best age structure for survival probability, we assessed alternative models to identify the best model for sex-structured survival probabilities (Step 2). These models included either sex-specific survival for the adult and subadult age classes (e.g., 5 age-sex classes, M 3 ) or sex-specific survival for the adult class only (e.g., 4 age-sex classes, M4).

Next, we assessed alternative models of temporal variation in survival using the best model for age and sex structure identified in steps 1 and 2 . These models encompassed temporal variation parameterizations for the adult and subadult age classes $\left(S_{x, t}\right)$ including a mixed effects model with linear time trends and year random effects (M5) and a year fixed effects model (M6). The year fixed effects model (M6) assumes survival is different at each occasion and estimates are independent of one another. We included the year fixed effects model given its common application in the literature and to compare the results to our year random effects general model structure. The use of random effects "shrinks" annual estimates towards the overall mean or trend for a given category of individuals, with greater shrinkage as parameter precision decreases (Royle and Link 2002). This property avoids the fitting of sampling noise as opposed to signal and analogously keeps probability estimates from converging on the boundaries of 0 or 1 . Although correlated random effects would also allow for the sharing of information among age classes, we could not consider these because the intermittent capture-recapture sampling resulted in the absence of COY, yearling, and subadult individuals in the sample at different times. We considered the mixed-effects model with linear time trends in logit ( $S_{x, t}$ ) for subadults and adults including stochastic departures $\left(\varepsilon_{x, t}\right)$ around each trend (M5) according to the randomeffects approach described above. The linear predictor for a given age class and the linear trend appeared as $\operatorname{logit}\left(S_{x, t}\right)=\beta_{0, \chi}+\beta_{1, x} Y_{t}+\varepsilon_{x, t}$, where each $\beta_{0, x}$ is equivalent to
logit $\left(S_{x}\right), Y_{t}$ denotes the year of study scaled to mean 0 and standard deviation of 1 , and $\beta_{1, x}$ is the linear trend coefficient for each class, $x$.

Following steps 1 through 3 which focused on modeling survival, we assessed alternative models for temporal variation in recovery probability (Step 4) and age-sex structure in recapture probability (Step 5). Here, we compared the initial recovery model structure with time-constant, sex-specific recovery rates $\left(r_{x}\right)$ to two alternative models. These models included class specific (M7) temporal random effects (e.g., $\varepsilon_{x, t} \sim \operatorname{Norm}\left(0, \sigma_{x}^{2}\right)$ ) added to the mean of each $r_{x}$ on the logit scale or (M8) temporal random effects shared between classes e.g., $\varepsilon_{t} \sim \operatorname{Norm}\left(0, \sigma^{2}\right)$. Next, we compared the initial recapture parameterization with 3 age classes (subadults, adult females and offspring, adult males) and year fixed effects to a model with 4 age-sex classes (subadult males, subadult females, females with offspring, adult males) and year fixed effects (M9) to estimate $p_{x, t}$.

Using the best fit model from steps 1 through 5 , we sought to identify the best fit model for explicit measurements of environmental effects on survival. We considered covariates describing sea-ice dynamics, climatic conditions, and prey abundance that could affect survival based on demographic analyses for other polar bear subpopulations (e.g., Lunn et al. 2016). These covariates included the ice-free period length, summer sea-ice concentration, the rate of within-year sea-ice decay, the North Atlantic Oscillation (NAO), the Arctic Oscillation (AO), and harp seal abundance (see below). We assessed models including only single covariates (M10 - M15) and tested two additional models that included multiple covariates (M16 and M17). Specifically, we modeled additive effects of the rate of sea-ice decay and harp seal abundance (M16) and additive effects of the rate of sea-ice decay, the NAO, and the ice-free period length (M17). We did not run additional models with other combinations of covariates primarily because most of the covariates were highly correlated and because the single covariate models had little support. All covariates were $Z$-scored.

## Environmental conditions

We calculated sea-ice metrics within the DS subpopulation boundary following the methods employed by Stern and Laidre (2016) using daily sea-ice concentration data
from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data available from the National Snow and Ice Data Center (NSIDC, Boulder, CO). These data include daily sea-ice concentrations, or the percentage of the ocean area covered by sea ice within the DS subpopulation boundary. We included two metrics common to polar bear studies: the length of the ice-free period and the mean summer sea-ice concentration. We define and calculate the length of the ice-free period as the number of days between the $50 \%$ threshold of sea-ice breakup and freeze-up over the continental shelf (water $<300 \mathrm{~m}$ deep). Mean sea-ice concentration represents the ice available during the summer period between June 1 and October 31. Because polar bears rely on sea ice to access their prey in addition to other critical life-history events, when sea-ice concentration is low and when the length of the ice-free period is extended, polar bears are subjected to dietary fasting with potential deleterious effects on body conditions and subsequently, survival. We also calculated the rate of sea-ice decay following Lunn et al. (2016), which describes how fast the ice disappears every spring and summer. In years when ice disappears rapidly, bears may become stranded and need to travel considerable distances to find suitable habitat. We used the absolute value of the slope of an ordinary least squares regression of sea-ice extent from May 1 until the date when ice concentration reached a threshold low of $16,000 \mathrm{~km}^{2}$. We set the lower threshold to $16,000 \mathrm{~km}^{2}$ to accommodate the noise associated with the sea ice data that may indicate sea ice is present when it is not. During the month of September, we expect there to be no sea ice in the DS region, yet, between 2005 and 2018 the sea ice concentration data indicated between 11,000 and $16,000 \mathrm{~km}^{2}$ of sea ice in the area. The noise in the sea ice data is a product of the scale (satellite imagery grid size) and associated land contamination of ocean grid cells.

The North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) influence regional climate variability and may impact sea-ice dynamics (Heide-Jorgensen et al. 2007) and abundance of prey species for polar bears (Stenson et al. 2016). We extracted the winter (December - March) indices for both the NAO and AO from the National Oceanographic and Atmospheric Administration (NOAA, College Park, Maryland, USA). Further, harp seals are an important prey species for DS polar bears (Iverson et al. 2006, Peacock et al. 2013). Thus, we also included annual estimates of the total
population size of harp seals in the Northwest Atlantic as an index of prey availability (Hammill et al. 2021).

## Model implementation, fit, and evaluation

We embraced the philosophy of Bayesian statistics and used informative priors where possible (Supplementary Table SM1). Specifically, we used informative Beta priors for subadult and adult survival based on point estimates of total survival probabilities (e.g., includes harvest and natural mortality) from 13 polar bear subpopulations, following the approach of Regehr et al. (2018) (Supplementary Table SM2). Because the prior distributions were based on survival estimates for subpopulations with differing demographic statuses and across the species' range, they corresponded to a range of biologically plausible survival probabilities for polar bear.
When relevant for a given model, we included separate prior distributions by sex within the subadult and adult age classes. We used moment-matching to convert the informative means and standard deviations to shape and scale parameters for the respective Beta prior distributions (Hobbs and Hooten 2015). We used vague priors for all other parameters (Table SM1). Further details regarding the sensitivity of estimated parameters to the choice of priors are provided in the supplement.

To estimate all parameters in our multistate models, we multiplied the marginalized likelihood for the capture-recapture-recovery data ( $\mathbf{m}$ ) and prior probability distributions using Bayes' theorem to attain the joint posterior distribution, for example:

$$
\operatorname{Pr}(\mathbf{S}, \mathbf{p}, \mathbf{r}, \boldsymbol{\beta} \mid \mathbf{m})
$$

where bold font denotes matrix notation that encapsulates age, sex, and time parameterizations. We sampled posterior distributions of the capture-recapture-recovery parameters using a Markov chain Monte Carlo algorithm (MCMC, Gelfand and Smith 1990) in JAGS 4.3 .0 (Plummer 2017), run from the jagsUl package (Kellner 2015) in program $R$ ( $R$ Core Team 2019). We ran three MCMC chains for 20,000 iterations in JAGS and discarded the first 16,000 as burn-in. We then thinned the samples to retain a total of 6,000 posterior samples for each parameter. The multiple MCMC chains allowed us to use the Gelman and Rubin (1992) $\hat{R}$ statistic (we sought $\hat{R}$ values $<1.10$ ) along with trace plots to monitor chain convergence.

To score the relative within-sample predictive abilities of our multistate capture-recapture-recovery models with different parameterizations, we used the WatanabeAkaike information criterion (WAIC; Watanabe 2010). In practice, we monitored the loglikelihood for each $\mathbf{m}$, combined them into a joint likelihood, and then applied the waic function in the loo package for R (Vehtari et al. 2020).

Unlike other studies (see Lunn et al. 2016), we modeled the survival of adult females and offspring independently due to the extended period between capturerecapture surveys where the 'state' (with or without offspring) of adult females was unobservable and therefore unknown. Because the survival of offspring is dependent on the survival of their mothers, we calculated an overdispersion factor $(\hat{c})$ following methods employed by Taylor et al. (2009). We calculated $\hat{c}$ as the ratio of live observations of offspring ( $n c$ ) to total live observations $(n)$ where $\hat{c}=n /(n-n c)$ to serve as a rudimentary measure of goodness of fit due to a lack of independence.

## Supplementary survival analyses

Finally, we wanted to assess the effects of prior choice and explore an additional model that is more commonly employed in the polar bear literature. Full methodological descriptions and results are included in the Supplementary Materials. The model included the same general structure as model M2 but did not include year random effects on subadult or adult survival (i.e., constant survival). We did not use this model for inference but report the results in the supplementary material and compare these results to those from model M 2 in the discussion below. This model was fit using the same methods described above.

## Reproduction

We calculated reproductive indices for polar bears in DS using data from physical and genetic mark-recapture surveys in 2005-2007 and 2017-2018, respectively. We summarized metrics identified as important for monitoring polar bear populations as outlined in Vongraven et al. (2012) and subsequently reported as indices of productivity in other studies (Peacock et al. 2015, Regehr et al. 2015). Specifically, we tallied the
annual number of litters and mean litter sizes of COYs and yearlings, the ratio of the number of COYs and yearlings to adult females, the ratio of the number of females with COYs to the number of adult females in the subpopulation and summarized COY litter size by study period to compare to estimates from earlier analyses (Peacock et al. 2013). Because the data were collected intermittently, in our multistate model for survival we could not parse out the differences in recapture rates between females with and without offspring. Therefore, we calculate the reproductive metrics using the raw capture-recapture data and report only point estimates. Further, we did not consider the effects of environmental covariates on reproduction metrics because the final study period included only two years of data.


#### Abstract

Abundance

As in other polar bear studies (McDonald and Amstrup 2001, Taylor et al. 2002, Peacock et al. 2013), we estimated annual abundance using the Horvitz-Thompson estimator: $\widehat{N}_{t}=c_{x, t} / \hat{p}_{x, t}$, where $c_{x, t}$ refers to the number of bears captured in class $x$ (inclusive of recaptures) within a year $t$ and $\hat{p}_{x, t}$ is the estimated probability of detection for class $x$ in year $t$ based on recapture probabilities according to age and sex class (Steinhorst and Samuel 1989, Williams et al. 2002). An advantage of the Bayesian analysis was our ability to use posterior distributions for the estimated $\hat{p}_{x, t}$ from our multistate capture-recapture-recovery model that best predicted the data (see Table 2) to 'derive' exact posterior distributions for $\widehat{N}_{t}$ with no need to approximate sampling variance with the delta method (e.g., Huggins 1989, Borchers et al. 1998). We define abundance here as the actual realized number of bears within this subpopulation (e.g., expected number of bears within the DS boundaries at these time periods).

Due to weather and logistical challenges during 2017 and 2018, sampling was not completed on Edgell or Resolution Islands. In 2018, a region around Loks Land in addition to Edgell and Resolution Islands could not be sampled due to inclement weather (Figure 4). During the 2005-2007 sampling period all these regions were comprehensively sampled with a considerable number of bear encounters. To determine the effects of differences in sampling on estimates of abundance, we subset


the 2005-2007 live-capture data to remove captures that occurred within the areas that were not sampled in later years. We produced two geographic data subsets, one that removed just Edgell and Resolution Island samples, and another that also removed samples from the unsampled area around Loks Land to adjust for the year-specific unsampled areas. We fit our top model without covariates on survival (M8) to these two data sets. Following methods employed for similar issues with the Baffin Bay abundance estimate (SWG 2016), we compared estimates of abundance from using the full data set versus the geographic subset data to inform potential biases from incomplete sampling. Thus, we assumed that $\widehat{N}_{2006-2007}^{\text {subset data } / \widehat{N}_{2006-2007}^{\text {full data }} \approx}$ $\widehat{N}_{\text {2017-2018 }}^{\text {subset data }} / \widehat{N}_{2017-2018}^{\text {full data }}$, where the ratio of abundance estimates from the subset data in the early period $\widehat{N}_{2006-2007}^{\text {subset data }}$ to the full data in the early period $\widehat{N}_{2006-2007}^{\text {full data }}$ would provide an inflation factor that we could use to adjust the estimates of abundance for the later period $\widehat{N}_{2017}^{\text {subset datata }}$ for what we expect would have been obtained if the complete sampling area had been covered $\widehat{N}_{2017-2018}^{\text {full data }}$. We completed this using the two geographic subsets and adjusted the estimate in 2017 for missing Edgell and Resolution Islands and adjusted 2018 for missing Loksland in addition to Edgell and Resolution Islands. We calculated the geometric mean subpopulation growth rate ( $\lambda$ ) between 2006 and 2018 as $\lambda=\left(N_{2018} / N_{2006}\right)^{1 / 12}$ to generate the finite growth rate over this time period.

## Body Condition

We compiled body condition index ( BCI ) data from the two distinct time periods of markrecapture sampling in DS to allow inference on trends. Bears were assigned a BCI on a scale of $1-5$ with 1 being skinny and 5 being obese (Stirling et al. 2008) through physical handling and capture (2005-2007) or aerial observation during biopsy sampling (2017-2018). All BCI observations occurred in fall (August through October) during the ice-free period in DS. Sex, age, and reproductive classes were assigned during physical handing during 2005-2007 and ages were determined based on previous capture history, known birth year, or from tooth analysis (Calvert and Ramsay
1998). During the biopsy sampling period, classification was done at approximately 3-7 $m$ above the ground with sex verified by subsequent genetic analysis (Atkinson et al. 2021, Dyck et al. 2020a, Dyck et al. 2021). Observers who participated in classifying age class and sex during biopsy sampling had either participated in both sampling periods or were experienced in physical capture-mark-recapture studies.

The BCl data were summarized into 3 classes: 'poor' (1-2), 'average’ (3), and 'good' (4-5) to facilitate comparison with other studies (Laidre et al. 2020a, b; Dyck et al. 2020a, Dyck et al. 2021). We did not include dependent offspring in the BCI analyses because their body condition is dependent on maternal condition (SWG, 2016). We excluded within-year observations of the same individual but retained observations of the same individual in different years. Observations collected during the 2005-2007 study and the 2017 - 2018 study were combined into their respective sampling periods (period $_{\text {early }}$ and period ${ }_{l a t e r)}$ ) to facilitate comparison over time. We combined reproductive status (i.e., with or without offspring), age, and sex into a four-level categorical variable reproclass (ADM = adult male, ADFI = independent adult female, ADFWO = adult female with offspring, and SUB = subadults of both sexes). Body condition varies among sex and age classes, most notably for females with dependent offspring generally being in poorer body condition that single bears of either sex (Rode et al., 2012; Laidre et al., 2020a, Dyck et al., 2021). To evaluate potential effects of ice availability on body condition, we included the covariate ts.springtran, which represented the length of time, in days, between sea-ice retreat and when we observed the animal, similar to previous studies (Laidre et al. 2020a, Obbard et al. 2016). Longer durations with reduced ice and open water were predicted to be negatively associated with body condition. Sea-ice retreat date was calculated as described above (See Data Analysis: Environmental conditions).

The first decision that had to be made before statistical analysis could begin was how to model the three-category ordinal scaled outcome variable, BCI . The primary criteria were that any resulting analysis be not only statistically correct in the sense of adhering to statistical model assumptions, not be overly simplistic at the expense of foregoing useful descriptions of the results and would yield interpretable results for managers. We identified three possible approaches. The first was to fit an ordinal
logistic regression as described in detail in Section 8.2 Hosmer, D.W., Lemeshow, S. and Sturdivant, R.X. (2013). The second approach used a binary classification that recoded $B C I$ into two categories: $Y=1$ if $B C I$ was good or average and $Y=0$ if $B C I$ was poor. The third approach was to use the multinomial logistic regression model.

We rejected the ordinal logistic regression model as the data did not satisfy a key assumption, the parallel regression assumption, which states that the coefficients are the same for relationships between categories of the response variable. In this case, that would mean the relationship between being average to good body condition would be equal to comparing good to poor body condition. We rejected the binary logistic regression model, as it would not allow separate results for the good versus poor and average versus poor, which may be of interest to managers. Thus, the model we used was a full 3 category multinomial logistic regression model which yielded probabilities of inclusion in the poor, average, and good classes.

Multinomial logistic model development followed the methods described in Chapter 4 of Hosmer et al. (2013). Key steps in this process addressed the need for interactions between model covariates that made sense biologically. A second modeling issue addressed was to check the linearity on the logit assumption for continuous covariates in the model (ts.springtran); no fractional polynomial transformation was significantly better than linear, indicating that a linear term was the best fit (Hosmer et al. 2013). The final model: $B C l_{i t}=\beta_{0}+\beta_{1}$ period $_{t}+\beta_{2}$ ts.springtran ${ }_{i t}+\beta_{3} A D F W 0_{i t}+\beta_{5}$ ADMit $^{+} \beta_{6}$ SAF $_{i t}+\beta_{7}$ SAMit $^{2} \beta 8$ periodt:ADFWO $_{i t}+\beta_{9}$ periodt:ADMit $+\beta 10$ periodt:SAFit $^{\text {it }}$ $+\beta 11$ periodt:SAM it, was evaluated for its goodness of fit using the multinomial model extension of the Hosmer-Lemeshow test (Fagerland and Hosmer, 2012). Results are presented by inverting the logit model, using predict function within package nnet in R, to calculate predicted probabilities (package nnet; Venables and Ripley, 2002).

## RESULTS

## General overview

We spent an average of 350 hours flying within the study area in search of bears during each of the 2017 and 2018 field seasons. Search operations were conducted between August and early October each year (i.e., when the sea ice is at its minimum in DS and most bears are onshore) along coastlines, inside fiords, over land and across nearshore islands, with an average distance flown of about $35,300 \mathrm{~km}$ per field season. The number of bears encountered during each survey season was similar, with a mean of 670 observed bears per field season.

## Samples examined

During the 2017-2018 study periods, we encountered 1,343 polar bears, of which 1,139 were biopsied. The overall genotyping success rate from these samples was ~ $98 \%(n=1,116)$. Field crews identified 493 male and 442 female solitary polar bears. The sex was correctly determined for 407 males and 368 females (or roughly between $82-84 \%$ ) by aerial inspection based on verification via genetics. Subadult males were commonly misidentified as adult females (e.g., up to 70\%; Government of Nunavut, unpublished data), and young adult females were often mis-classified in the field as subadult males (M. Dyck, personal obs). Field notes and sex identification through genetics aided in assigning age classes with high confidence.

From our field biopsy samples, we identified 34 individuals that were previously sampled in BB between 2011-2013, 177 individuals that were handled during the 2005 - 2007 DS study, and 669 new individuals that we sampled during 2017 and 2018. Of all biopsied bears in 2017, 110 were re-sampled during the 2018 field season. Resampling of bears within the same field season was relatively low with approximately 29 bears and 50 bears in 2017 and 2018, respectively, sampled more than once. Biopsy sampling leaves no visible marks on the individual animal unlike traditional markrecapture studies (e.g., Peacock et al. 2013); thus, it is impossible to avoid some resampling, unless every sampled bear receives a dye mark.

Through the harvest sampling program, we submitted 1,623 tissue samples for genetic analysis, representing kills between 2006-2018 from DS and neighboring subpopulations ( $n=445 \mathrm{BB}, \mathrm{n}=460 \mathrm{DS}, \mathrm{n}=718 \mathrm{FB}$ ). Sixty-four of these samples were
unfit for genetic testing. The genotyping success rate of harvest samples was approximately $96.0 \%$.

## Survival

Our live-capture dataset consisted of 2,513 individuals (1,201 females, 1,312 males) collected in 2005-2007 and 2017-2018. We included 233 harvested bears (42 females, 191 males) as dead recoveries reported between 2005 and 2018 (Table 1). Of these dead recoveries, 22 bears were harvested in BB, 11 in FB, 1 in Lancaster Sound, and 199 in DS (Figure 2). A total of 681 individuals in our data set were of unknown age and were assigned the mean numeric age of known age bears within a field age class. The post-hoc test for overdispersion related to the lack of independence between females and offspring resulted in a $\hat{c}=1.30$. Convergence was attained for all estimated parameters in all models ( $\hat{R}<1.02$ ) and trace plots indicated mixing among stationary chains.

We report results from the best fit model, M2, which we used for inference (Table 2). The best fit model included 3 age-sex classes and year fixed effects for recapture probability. Further, accounting for differences in recovery by sex (independent males, independent females) and constraining the estimates to remain time constant provided the best fit of the models we tested. The best model for survival included a timeconstant estimate for offspring (COY and Yearlings), and separate means for subadults and adults with separate year random effects. No environmental covariates investigated for their effects on variation in survival were included in the top model, suggesting that interannual variation in survival was not related to the environmental covariates consider in our analyses.

Using combined capture-recapture-recovery data, we were able to estimate survival in all years (2005-2017) for adult bears (Figure 5). Estimates of survival for younger age classes were limited to years following releases based on the number of years individuals could remain within that age/sex class and be recaptured or recovered through harvest (Table 1, Figure 5). Mean survival rates were 0.794 ( $95 \%$ Credible interval (CRI); 0.723, 0.861) for offspring, 0.873 ( $95 \%$ CRI; $0.826,0.914$ ) for
independent subadults, and 0.871 ( $95 \%$ CRI; $0.853,0.892$ ) for adults (Table 3). Mean estimates of survival for adults and subadults represent the long-term average or "global" mean survival for individuals in these age classes for this subpopulation. Annual departures are modeled as temporal random effects around this mean thereby producing annual estimates of survival for adults and subadults.

Mean recapture rates in the first year (e.g., 2006) were 0.383 ( $95 \%$ CRI; 0.327, 0.443 ) for subadults, 0.489 ( $95 \%$ CRI; $0.434,0.544$ ) for adult males, and 0.338 ( $95 \%$ CRI; 0.291, 0.390) for adult females and offspring (Table 4). The fixed effects of year indicated a negligible difference between recapture rates in 2006 and 2007 ( $\beta_{2007}=$ $-0.026 ; 95 \%$ CRI -0.248, 0.19) (Figure 6). However, the fixed effects of year indicated recapture rates were lower in 2017 ( $\beta_{2017}=-0.456 ; 95 \%$ CRI $-0.810,-0.108$ ) and 2018 $\left(\beta_{2018}=-0.189 ; 95 \%\right.$ CRI -0.469, 0.089) than in 2006 (Figure 6). Annual estimates of recapture probability are available in Table 4. Mean recovery rates (i.e., probability of reporting conditioned on mortality) were 0.072 ( $95 \%$ CRI; 0.053, 0.093) for females and 0.248 ( $95 \%$ CRI; 0.215, 0.282 ) for males (Table 3).


#### Abstract

Abundance

The comprehensive data set used to estimate abundance in 2006, 2007, 2017, and 2018 included 2,226 individuals. The geographic subset data used to adjust abundance in 2017 included 2,163 individuals. The geographic subset of data used to adjust abundance for 2018 included 1,995 individuals. Parameter estimates (survival, recovery, and recapture) from the models fit with the geographic subsets of data were consistent with the comprehensive data set.

Annual estimates of abundance for the DS subpopulation were 2,190 (95\% CRI $1,954-2,454$ ) in 2006, and 2,311 ( $95 \%$ CRI $2,111-2,536$ ) in 2007. After accounting for the incomplete sampling adjustment, estimates were 2,085 (95\% CRI 1,613-2,699) in 2017 and 1,944 ( $95 \%$ CRI 1,593-2,366) in 2018 (Figure 7, Table 5). Geometric mean subpopulation growth between 2006 and 2018 was 0.989 ( $95 \%$ CRI 0.974 1.010 ) and the probability that subpopulation growth was $<1$ (e.g., declining) was 0.896 indicating the subpopulation likely declined by at least one bear over this period but


stability could not be ruled out. The mean estimate for the first sampling period (2006 2007) was $2,250(S D=$ standard deviation $=133 ; 95 \%$ CRI $1,989-2,512)$. The mean estimate for the second period (2017 and 2018) was 2,015 bears (SD $=251 ; 95 \%$ CRI $1,603-2,588$ ). Our estimate of abundance for the first study period (2006-2007) fell within the estimated confidence intervals of abundance between 2005 and 2007 reported by Peacock et al. (2013) (Table 5, Figure 7).

## Reproduction

We observed a total of 231 adult females with COYs and 215 adult females with yearlings across all sampling years (2005-2007 and 2017-2018) (Table 6). Here, we report the overall and sampling period means and standard errors as the mean of the annual estimates and the standard error of the mean annual estimates. The overall mean COY litter size across all years was 1.43 (standard error of the mean [SE] = 0.039 ) and varied between 1.44 (SE 0.05) in the first study period (2005-2007) to 1.42 (SE 0.03) in the second study period (2017-2018) (Table 6). The overall mean yearling litter size was 1.53 (SE 0.088) and varied between 1.52 (SE 0.037) in the first study period and 1.54 (SE 0.17). Mean COY recruitment (e.g., number of COYs per adult females) ranged from 0.23 to 0.45 and mean yearling recruitment (e.g., number of yearlings per adult female) ranged from 0.23 to 0.41 (Table 7). The ratio of the number of females with COY litters to the number of total adult females varied annually and ranged from 0.16 in 2007 to 0.32 in 2017 (Table 7).

## Body condition

Observations of BCl were taken on 1911 bears from 2005-2007 and 895 bears from 2017-2018 from early August to early October (Table 8). Bears were less likely (Wald z test $P<0.001$ ) to be in poor body condition in the $2015-2017$ sampling period. On average, bears observed in $2005-2007$ had a $25 \%$ chance of being in poor body condition and 8\% chance during 2017-2018. (Figure 8, Table 9). Adult males and adult independent females were more likely to be in better body condition than subadults or
females with offspring. On average, adult males and independent adult females had a $40 \%$ probability of being in good condition while subadults had $12 \%$ probability and females with offspring had a $5 \%$ chance of being scored as good condition, regardless of when they were observed (Figure 9). Overall, bears sampled later in the season were less likely to be in good body condition for a given year (Wald z test $P<0.05$; Figure 9).

## DISCUSSION

## General

This study reports subpopulation abundance, survival, subpopulation growth, reproductive indices and body condition using the data from surveys conducted in the DS polar bear subpopulation between 2005-2007 and 2017-2018 along with dead recoveries of harvested bears from 2005-2018. Moreover, we evaluate the effects of environmental covariates on DS polar bear survival and body condition. We provide updated estimates of abundance, survival, reproduction, and body condition that can be used to inform harvest management.


#### Abstract

Abundance

We estimated abundance in 2006, 2007, 2017, and 2018 to compare to estimates from previous analyses (Peacock et al. 2013) and provide updated estimates for use in harvest management. Again, we define abundance here as the actual realized number of bears within this subpopulation (e.g., expected number of bears within the DS boundaries at these time periods). Peacock et al. (2013) estimated abundance for the combined period of $2005-2007$ at $2,158(95 \%$ CI 1,833-2,542). Our annual estimates and early study period estimate fell within the confidence limits of these estimates even with major differences between our datasets (more years of data) and minor differences in analytical methods (Table 3, Figure 7). We estimated abundance in the most recent sampling period (2017-2018) by adjusting for incomplete sampling following an approach used to adjust for sampling differences in Baffin Bay (SWG 2016, Atkinson et


al. 2021). Fortunately, the unsampled area included a relatively small portion of the total bears encountered in the DS and represented, at maximum, a difference of $7 \%$ between the adjusted and unadjusted estimates. The geometric mean growth rate between 2006 and 2018 indicates the subpopulation has most likely declined (mean $=0.989 ; 95 \% \mathrm{CRI}$ $0.974-1.010$ ), which suggests that the Nunavut management objective to decrease the subpopulation over this period was met to some degree. Harvest management varies across jurisdictions. The total allowable harvest in Nunavut was increased in 2013 from 46 to 61 bears per year based on traditional knowledge of increased abundance. However, the reported removal only increased by $13 \%$, to 44.2 bears per year. Newfoundland and Labrador also increased the total allowable harvest from 6 to 12 bears annually over a similar period. While there are no quotas or mandatory reporting in Québec, of the bears reported removed, there was an increase over this time. The DS harvest quota was 73 (NL, NU) +3 (Greenland) + QC with a reported annual mean removal of 86.8 bears in 2009-2019 compared to 64.1 during 1998-2008 (Table 10). Thus, it is possible that harvesting impacted abundance between our two study periods (2005-2007 and 2017-2018). However, the upper 95\% credible interval of geometric mean growth rate overlaps 1 , indicating there is a 0.104 probability that the subpopulation remained stable or increased over this period and a 0.896 probability that the subpopulation declined. These estimates currently represent the best-available science and are suitable for informing management.

## Survival

Capture-recapture data were collected intermittently, and recapture probabilities were estimable for a total of 4 years across two sampling periods. In our top model (M11), recapture probability varied annually and across three age-sex classes which was consistent with the age-sex class structure used in previous analyses (Peacock et al. 2013). However, we note that Peacock et al. (2013) included a geographic component to model variation in survival $(S)$, recovery $(r)$, and recapture $(p)$ probability as a function of a bear's initial capture location (e.g., North, Central, and South Davis Strait). We did not incorporate a geographic component in our models because we did not believe
there was sufficient evidence to support 3 distinct subpopulations within the DS region, and furthermore, did not want to reduce sample sizes which would limit the scope of inference. Recapture rates of adult males were, on average, higher than those estimated for subadults or females and offspring, a finding consistent with previous analyses (Peacock et al. 2013). Recapture rates may vary by sex due to sex-based habitat segregation. Overall, recapture rates were higher in the first sampling period (2006 and 2007) than in the most recent sampling period (2017 and 2018). These results may reflect the change in capture methods (e.g., physical versus genetic) and/or a decline in survey effort. Estimates of recapture probabilities in the 2017/2018 period were less precise than those in the 2006/2007 period which is consistent with the extended interval between capture-recapture surveys. Recapture rates for Davis Strait polar bears are high compared to other subpopulation surveys (e.g., Lunn et al 2016). We suspect this is related to the particularly large number of individuals marked over a relatively short period of time ( $n=2,513$ ) and known late summer / fall concentration of bears on the northernmost portion of the Labrador Peninsula and Button Islands (Government of NL, unpublished data).

Our top model for recovery probability included 2 sex classes and was time constant. In contrast, Peacock et al. (2013) included a time period effect and an additional class to account for females harvested along with their offspring. Here, we did not consider an additional class for females with offspring because management systems preclude harvesting of family groups and during this period no marked females with COY were harvested. Several yearlings were harvested; however, they were likely independent at the time of harvest because they would have been > 1.5 years old and exhibited behaviours more like subadults than offspring. Furthermore, recovery rates were considerably higher for independent males than for independent females, consistent with male-biased harvest and estimates from earlier analyses (Peacock et al. 2013).

Our top model for survival and estimates therein differed from those in the previous analysis. In contrast to previous work, we found no support for differences in survival between COY and yearling or for sex-specific survival rates for any age class. Further, we did not explore geographic variation in survival rates. However, the point
estimates of survival by geographic region were similar (Table SM2 and see Peacock et al. 2013) and we do not expect this to be a significant source of variation in survival. Though our point estimates of survival fall within the $95 \%$ confidence levels reported in Peacock et al. (2013), they are generally lower than those estimated for the overlapping period between these two studies (2005-2008) and we expect there are two possible explanations. The use of fixed effects to model full temporal variation in survival can bias estimates towards the boundaries (e.g., 0 or 1 ) when data are sparse (Kéry and Schaub 2012). The use of "time-binning", or averaging, estimates over a subjective time length is commonly implemented to overcome this issue while still accounting for some temporal variation (e.g., Peacock et al. 2013). However, because years with more data can have a strong influence on the mean estimate over the defined period, relative to true temporal variation, this approach can induce further bias (Koons et al. 2019). Considering Peacock et al. (2013) had separated the data into geographic regions, thus limiting sample size, and then used a time-binning approach, it is possible that the resulting point estimates of survival were biased high. Second, Peacock et al. (2013) included only known-age bears, and thus they were able to model adults (<20 years old) separately from senescent bears ( $\geq 20$ years old). Survival estimates of senescent bears ( $\geq 20$ years old) from DS and other subpopulations (e.g., Lunn et al. 2016, Peacock et al. 2013) are generally lower than those of prime-age adult bears (5-20 years old). Because the final two years of this data set are from non-invasive genetic captures only, we no longer have the information necessary to age-classify bears with that resolution. Thus, including the senescent bears with prime age adults likely reduced the overall estimate of adult survival. Finally, negative bias in survival estimates may occur at the end of a time series due to temporary emigration from the study area. Though we expect high site fidelity to the management region during the ice-free period, it is certainly possible that individuals had moved temporarily outside of the study area inducing negative bias on survival estimates. However, if this were the case, we would expect to see a decline in the annual estimates for adult bears in the final years of the study which did not occur.

Posterior estimates of survival for subadults were less precise and more variable than those for adults. While we expect subadult survival to be more variable than that of
adults, the sample sizes of subadult bears were generally lower than adults, and without physical recapture to age the bears misclassification could have further contributed to the level of uncertainty in our estimates (e.g., some adult bears classified as subadults) (Figure 8, Table 4). The effects of sample size and the time between study periods were reflected by the imprecision or lack of subadult survival estimates in the years right before the second study period (Figure 5). Our survival estimates of offspring (COY and yearlings) were lower than estimates from the neighboring BB subpopulation (Atkinson et al. 2021) and those produced in the previous DS analysis (Peacock et al. 2013). Due to the intermittent surveys, we were unable to estimate annual survival rates for offspring and subsequently could not explore the effects of environmental factors on this sensitive life stage.

We tested a series of survival models including environmental covariates that have been evaluated across other polar bear studies. Previous research identified harp seal abundance and mean summer sea-ice concentration to be important predictors of DS polar bear survival (Peacock et al. 2013). In contrast to findings from Peacock et al. (2013), we were unable to detect a relationship between harp seal abundance or summer sea-ice concentration and survival. We should note that Peacock et al. (2013) analyzed data between 1974 and 2008, over which time harp seal abundance increased considerably (Hammill et al. 2021). While harp seal abundance increased between 2005 and 2018, numbers remained consistently high (> 5 million seals) (Hammill et al., 2021). Thus, we expect that when harp seal abundance was increasing over time this may have contributed to an increase in DS polar bear survival; however, now that harp seal abundance has stabilized, it likely has a less detectable influence on changes in polar bear survival. Peacock et al. (2013) identified support for a positive effect of mean summer sea-ice concentration on survival when the concentration was between 17\% and $29 \%$, however, mean summer sea-ice concentration did not exceed $8 \%$ within our study period. We investigated the relationship between sea-ice decay rate and survival following Lunn et al. (2016). Similarly, we found no relationship between DS polar bear survival and rate of sea-ice decay. Furthermore, we found no effect of the number of ice-free days on survival. The NAO and AO winter indices are strong indicators of seaice extent during the spring to summer period (Stern and Heide-Jorgensen 2003, Heide-

Jorgensen et al. 2007) though neither index had any detectable effect on polar bear survival in our independent or additive models.

For polar bears, modeling patterns of temporal variation in survival is a key step towards understanding how harvest and environmental change can affect subpopulation dynamics. For the DS subpopulation, we used sparse data to make inferences about temporal variation in survival and investigate relationships between survival and environmental conditions. Large sample sizes of marked and recovered bears allowed us to explore temporal variation in a more explicit manner than previous analyses (e.g., Baffin Bay [SWG 2016]). Specifically, within our modeling framework we were able to incorporate year-specific random effects on survival and were not limited to time constant or time binned estimates. Treating year effects as random variables generates estimates influenced primarily by the long-term mean and annual variance. Estimates deviate only when data support it, which is particularly advantageous in sparse data situations (Royle and Link 2002, Koons et al. 2019). The main benefit of using a random effects approach for modeling survival was the opportunity to estimate the percent of temporal variation explained by the addition of covariates (Kery and Schaub 2012). However, our analysis did not find a significant relationship between survival and any of the environmental covariates we tested. To contrast with our random effects approach, we ran an additional model (supplementary material, Table SR2) similar to model M2, but without year random effects for survival. The model was more parsimonious in that the WAIC values was substantially lower than those reported for our top model likely due to the reduction in the number of parameters (i.e., no year random effects). Despite the structural differences, the results from the time-constant model were consistent with its counterpart (M2). Specifically, there was considerable overlap between the posteriors for comparable parameters (Table SR2). There are several advantages to using random effects and mixed effects models; however, we note that the timeconstant and fixed effects covariate models delivered comparable results and were more parsimonious.

Here, we present an improved analytical approach assessing a series of models that built upon previous analyses. The duration of the surveys and time between surveys ultimately limited our ability to make complete inference about temporal
patterns in survival of all age-sex classes. Specifically, we were unable to model temporal variation in offspring survival and could not estimate survival for subadult polar bears in 2015 and 2016. We had a large sample of known-age bears from the initial capture period which was conducted with physical capture techniques and included marking COY. However, we could no longer estimate survival separately for adults and senescent bears. Moving forward with genetic mark-recapture only, we will lose more critical age-specific information and will not be able to estimate age-specific survival rates with the same degree of resolution that is possible during physical capturerecapture studies that provided numeric ages based on counts of cementum annuli. Future analyses may need to rely on field classifications, which are prone to error (Nunavut unpublished data) and may require more complex models to accommodate such uncertainty (e.g., multievent models [Pradel 2005]). Alternatively, we will need to further reduce model complexity and limit the age/sex classes to dependent and independent (e.g., <2 and >2 years old) which has been required for other polar bear subpopulations). While genetic mark-recapture has significant benefits, most notably lower intrusiveness and less stress on the bears, the implications of forgoing agespecific survival estimations needs to be acknowledged and carefully considered as part of study design and methodological processes. Integrating auxiliary data sets (e.g., sexspecific age-at-harvest data, harvest counts, satellite telemetry) may offer a considerable opportunity to estimate demographic rates more precisely when other data are sparse or intermittently collected.

## Reproduction

We calculated reproductive metrics annually and by study period where possible. Drawing conclusions about how reproductive metrics differ between the two study periods is challenging because of the change in survey methods and sample sizes. Here, capture-recapture surveys were conducted during autumn and thus reproductive metrics cannot be compared to those estimated for populations surveyed in the spring because we do not have information on COY mortality between 0 and 9 months. Though it is difficult to compare reproductive metrics across subpopulations due to differences in sampling and analytical methods, estimates of COY litter size in DS in the
previous study were the lowest of any other subpopulation studied during the autumn (Peacock et al. 2013). We calculated COY litter size to compare to previous estimates as the number of COYS divided by the number of adult females with COYS where our sample size reflects the number of adult females with COYS in our sample. Peacock et al. (2013) estimated COY litter size for the period between 2005-2007 as 1.49 (SE $0.14, n=116$ ). Over the same study period, we estimated COY litter size to be 1.43 (SE $0.05, n=130$ ) (Table 6). Our estimate of COY litter size for the 2017-2018 period was 1.42 (SE 0.03, $n=102$ ), which is very similar to our estimate in the previous period. Overall COY litter sizes for the DS subpopulation remained lower than estimates for other subpopulations including Baffin Bay and Western Hudson Bay, both seasonal ice populations (Laidre et al. 2020a, Lunn et al. 2016). Peacock et al. (2013) did not report yearling litter size; thus, we cannot compare our estimates to previous estimates for the DS subpopulation. However, our estimates of yearling litter size (Table 6) are generally consistent with those estimated for Baffin Bay between 1993 and 2013 (Laidre et al. 2020a).

Recruitment of COY (e.g., ratio of COY to adult females) is considered an important reproductive metric to monitor for polar bear populations (Vongraven et al. 2012). Our estimates of COY recruitment ranged between 0.23 and 0.45 and are substantially lower than those estimated for Baffin Bay across the time period 1993 2013 where values ranged between 0.55 and 0.83 (Laidre et al. 2020a). However, low rates of COY recruitment are consistent with low COY litter size in DS. Yearling recruitment (e.g., the ratio of yearlings to adult females) can be used as an indicator of population persistence (Regehr et al. 2017a). Studies indicate that yearling recruitment rates between 0.1 and 0.3 are sufficient for subpopulation persistence provided sufficiently high survival probability (Regehr et al. 2017a). Our estimates of yearling recruitment varied between 0.23 and 0.41 across our study period (2005-2018). These values are less variable but generally consistent with estimates from BB for the period between 1993 and 2013 (Laidre et al. 2020a). Despite low COY litter size, the recruitment of yearlings is seemingly adequate to sustain a viable DS subpopulation, although further demographic analyses are necessary to assess the subpopulation growth rates that would follow from the estimates of reproduction and survival in this
study (Regehr et al. 2017a, Laidre et al. 2020a). Insight into reproductive dynamics for the DS are limited due to intermittent capture-recapture surveys. Increasing the duration of the survey periods may help provide further insight into annual variation in productivity, effects of environmental conditions on productivity, and how reproduction affects overall subpopulation dynamics.

## Body condition

Observations collected during 2017-2018 reveal bears in DS were in better body condition than during surveys in 2005-2007. Similar improvements in body condition for polar bear subpopulations have been noted during studies in the last 10 years (e.g., 2011-2018), including Kane Basin (Laidre et al. 2020b), Gulf of Boothia (Dyck et al. 2020a), and M'Clintock Channel (Dyck et al. 2021). These subpopulations represent a range of ecosystems, though all have some amount of ice that persists through the summer and fall, whereas DS experiences a mostly ice-free summer (Stern and Laidre 2016).

Like other subpopulations, females with offspring were most likely to be in poorer body condition while adult males and independent females had the highest probabilities of being in good body condition (Laidre et al. 2020b, Rode et al. 2014, Dyck et al. 2020a, Dyck et al. 2021), though this relationship may vary seasonally or by ecosystem (Laidre et al. 2020a). Over the past 10-15 years, harp seal numbers in Davis Strait remained abundant (Hammill et al. 2021) and their availability likely contributed to improved polar bear body condition. Moreover, the annual DS harvest rate after 2008 increased from 64 to 86.8 bears and may have indirectly affected body condition of bears by reducing subpopulation density.

## MANAGEMENT IMPLICATIONS

Through this study we demonstrated that sample sizes were sufficiently large for estimating annual survival rates for adult polar bears given the number of dead recoveries between the two capture-recapture periods. However, the duration of time
between capture-recapture surveys (10 years for this subpopulation) ultimately limited our ability to make complete inference about annual changes in survival (e.g., inestimable for offspring and subadults in certain years) and resulted in less precise, estimates of recapture probability in the later survey period following an extended interval without capture surveys and therefore a diminished sample size of marked bears available for recapture. Subsequently, estimates of abundance in the later survey period, particularly in the first sampling year, are imprecise, limiting our ability to estimate trends in abundance over the time series. The negative effect of long periods between sampling efforts on obtaining more precise parameters and subpopulation demographics to inform management has also been noted recently for other subpopulations (Dyck et al. 2020a, Dyck et al. 2021). Sampling efforts, either capture-mark-recapture surveys or intermittent sampling to increase the number of marked individuals in the subpopulation, could be conducted with fewer years between them to provide a more detailed and accurate picture of how the subpopulation is changing over time. Analyses to determine the optimal survey frequency and sample size for DS are forthcoming in separate independent analyses.

Ideal wildlife management includes not only obtaining census data but also information about wildlife distributions and habitat use. This is particularly important in the Arctic where reports of human-bear interactions are increasing, and habitat is rapidly changing. Recent studies of long-term movement data for polar bear studies in the BB and Kane Basin subpopulations documented changes in denning habitat, habitat use and distribution (Escajeda et al. 2018, Laidre et al. 2018a, b) in response to longterm changes in sea-ice patterns and environmental changes. In addition, movement data can assist in determining the degree of temporal emigration, improve survival estimates, and can be used to determine whether an abundance estimate relates to a superpopulation (see Dyck et al. 2020a, b for details). Like recent studies in the Gulf of Boothia and M'Clintock Channel polar bear subpopulations (Dyck et al. 2020a, Dyck et al. 2021), use of satellite telemetry in DS was not supported by Inuit co-management partners given the option of utilizing less-intrusive biopsy darting and this was accepted by the study team. This decision limited our ability to make inferences about distribution and habitat use. From dead recovery data, however, it appears that the boundary for
the DS subpopulation is still valid since over $85 \%$ of harvested bears were recovered within the DS management unit. Additionally, satellite telemetry from the northern neighboring subpopulation BB, supports the delineation between the two subpopulations (Laidre et al., 2018a).

Davis Strait is a subpopulation that is shared between Greenland and Canada (Nunavut, Newfoundland and Labrador, Québec), and is harvested by hunters in portions of their range in each of these jurisdictions (Peacock et al. 2013, Rode et al. 2012). This survey, inclusive to 2018, provides managers and responsible jurisdictions with an updated subpopulation estimate to inform respective jurisdictional harvest management objectives. Objectives among jurisdictions may not always be aligned and to ensure the sustainability and health of this subpopulation, communication on management objectives are required. Any such efforts are now informed by the updated survey findings presented in this report. Harvest risk assessment (HRA) is a relatively recent analytical tool that considers various harvest options under varying environmental conditions and levels of harvest risks (Regehr et al. 2017a, b; 2019). Moving forward, such analytical tools may be an appropriate for the multi-jurisdictional DS subpopulation should management authorities feel it warranted to pursue.

## ACKNOWLEDGEMENTS

This project was logistically and financially supported by the Government of Nunavut Department of Environment, Environment and Climate Change Canada, the Nunavut Wildlife Management Board, the Nunavut General Monitoring Program, Polar Continental Shelf Project, the Government of Newfoundland and Labrador- Department of Fisheries, Forestry and Agriculture, the Government of Québec - Ministère des Forêts, de la Faune et des Parcs, Nunatsiavut Government, Nunavik Marine Region Wildlife Board, Makivik Corporation, Parks Canada, the Torngats Wildlife and Plants Co-Management Board, Greenland Institute of Natural Resources, and the World Wildlife Fund - Canada Arctic Species Conservation Fund. We thank the pilots L. Pike, G. Hartery, N. Rose, S. Lodge, J.-Y. Lacasse and S. Sandi for safe flight operations, and the engineers Brian, Alex, Mark, and Jason for keeping the helicopters in the air. Field support and data collection was conducted by R. Akulukjuk, J. Aliqatuqtuq, W.

Angutinguaq, D. Annanack, W. Annanack, N. Armstrong, R. Arsenault, S. Atkinson, G. Baike, M. Carrier, A. Dale, D. Dyck, M. Dyck, W. Flaherty, J. Goudie, J. Joyce, C. Jutras, B. Kovic, J. Kulula, P. Kulula, M. Lougheed, J. Neely, S. Noble, B. Pirie, J. Pisapio, G. Szor, M. Taylor, T. Uyarak, J. Ware, D. White. We are grateful to the Mayukalik Hunters and Trappers Organization (HTO), the Amaruq HTO and the Pangnirtung HTO who provided support or this project and provided input during study design. We thank E. Richardson and D. McGeachy (Environment and Climate Change Canada) and Harry Stern (University of Washington) for the use of up-dated sea-ice data. We thank Garry Stenson and Mike Hammill (Department of Fisheries and Oceans Canada) for providing updated harp seal abundance data for our analyses. We also thank J. Bromaghin and S. Converse whose reviews and suggestions helped improve and clarify this report.

This research was carried out under Nunavut Wildlife Research Permits (WRP 2017011, WRP 2018-002), animal care approvals (NWTWCC 2017-003, NWTWCC 2018006), Inuit Owned Land land-use permits (Q17X005), a Third Party-Support licence (17003), a Parks Canada Agency Research and Collection Permit (TMNP-2017-25357), Quebec Scientific Research Permit (2017-06-22-121-10-S-F), NL Scientific Research Permit (WLR2017-38, WLR2018-22) and a Nunavik Parks Licence.

Finally, we would like to pay our gratitude and our respects to the project organizer, our colleague, and our friend, Markus Dyck. He died in a helicopter crash along with the pilot, Steven Page, and engineer, Benton Davie, in April 2021, while surveying polar bears in Lancaster Sound. We hope that the research contained here, and in future manuscripts, will honor his immense legacy in Arctic wildlife management.

## LITERATURE CITED

Atkinson, S.N., Laidre, K.L., Arnold, T.W., Stapleton, S., Regehr, E.V., Born, E.W., Wiig, Ø., Dyck, M., Lunn, N.J., Stern, H.L. and Paetkau, D. 2021. A novel mark-recapture-recovery survey using genetic sampling for polar bears Ursus maritimus in Baffin Bay. Endangered Species Research, 46, 105-120.

Atwood, T.C., Peacock, E., McKinney, M.A., Lillie, K., Wilson, R., Douglas, D.C., Miller, S., and Terletzky, P. 2016. Rapid environmental change drives increased land use by an Arctic marine predator. PLoS One 11:e0155932.

Amstrup, S.C. 2003. Polar bear, Ursus maritimus. In: G.A. Feldhamer, B.C. Thomson and J.A. Chapman (eds), Wild Mammals of North America: Biology, Management, and Conservation, pp. 587-610. John Hopkins University Press, Baltimore, MD, USA.

Amstrup, S.C., Marcot, B.G., and Douglas, D.C. 2008. A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. Pages $213-268$ in E. T. DeWeaver, C. M. Bitz, and L.-B. Tremblay. editors. Arctic sea ice decline: observations, projections, mechanisms, and implications. Geophysical Monograph Series 180. American Geophysical Union, Washington, DC, USA.

Barnas, A.F., Iles, D.T., Stechmann, T.J., Wampole, E.M., Koons, D.N., Rockwell, R.F., and Ellis-Felege, S.N. 2020. A phenological comparison of grizzly (Ursus arctos) and polar bears (Ursus maritimus) as waterfowl nest predators in Wapusk National Park. Polar Biology 43:457-465.

Borchers, D. L., Buckland, S.T., Goedhart, P.W., Clarke, E.D., and Hedley, S.L. 1998. Horvitz-Thompson estimators for double-platform line transect surveys. Biometrics 54:122-1237.

Bowen, W.D., Myers, R.A., and Hay, K. 1987. Abundance estimation of a dispersed, dynamic population: Hooded seals (Cystophora cristata) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 44:28

Breen, M., Jouquand, S., Renier, C., Mellersh, C.S., Hitte, C., Holmes, N.G., Cheron, A., Suter, N., Vignaux, F., Bristow, A.E., Priat, C., McCann, E., Andre, C., Boundy, S., Gitsham, P., Thomas, R., Bridge, W.L., Spriggs, H.F., Ryder, E.J., Curson, A., Sampson, J., Ostrander, E.A., Binns, M.M., and Galibert, F. 2001. Chromosomespecific single-locus FISH probes allow anchorage of an 1800marker integrated radiation-hybrid/linkage map of the domestic dog genome to all chromosomes. Genome Research 11:1784-1795.

Bromaghin, J.F., McDonald, T.L., Stirling, I., Derocher, A.E., Richardson, E.S., Regehr, E.V., Douglas, D.C., Durner, G.M., Atwood, T., and Amstrup, S.C. 2015. Polar
bear population dynamics in the Southern Beaufort Sea during a period of sea ice decline. Ecological Applications 25: 634-651. doi: 10.1890/14-1129.1.

Brown, M.W., S.D. Kraus and Gaskin, D.E. 1991. Reaction of North Atlantic right whales (Eubalaena glacialis) to skin biopsy sampling for genetic and pollutant analysis. Report of the International Whaling Commission (Special Issue 13):81-89.

Boulanger, J., S. Himmer, and Swan C. 2004. Monitoring of grizzly bear population trends and demography using DNA mark-recapture methods in the Owikeno Lake area of British Columbia. Canadian Journal of Zoology 82:1267-1277.

Bunnell, F.L. and Tait, D.E.N. 1981. Population dynamics of bears-implications. In C. W. Fowler and T. D. Smith (eds.), Dynamics of large mammal populations, pp. 75-98. John Wiley and Sons, New York.

Burnham, K.P. 1993. A theory for combined analysis of ring recovery and recapture data. In Marked Individuals in Bird Population Studies (Edited by J.-D. Lebreton and P. North), pp. 199-213. Birkhauser Verlag, Basel.

Calvert, W. and Ramsay, M.A. 1998. Evaluation of age determination of polar bears by counts of cementum growth layer groups. Ursus 10:449-453.

Department of Environment. 2013. Statutory Report on Wildlife to the Nunavut Legislative Assembly. 75 pp. Available at: http://assembly.nu.ca/library/ GNedocs/2013/001029-e.pdf. Accessed 24 December 2015.

Derocher, A.E., Wolkers, H., Colborn, T., Schlabach, M., Larsen, T.S., and Wiig, $\varnothing$. 2003. Contaminants in Svalbard polar bear samples archived since 1967 and possible population level effects. The Science of the Total Environment 301:163174.

Derocher, A.E., Lunn, N.J., and Stirling, I. 2004. Polar bears in a warming climate. Integrative and Comparative Biology 44:163-176.

Durner, G.M., Laidre, K.L., and York, G.S. (eds.) 2018. Polar Bears: Proceedings of the 18th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 7-11 June 2016, Anchorage, Alaska. Gland, Switzerland and Cambridge, UK: IUCN. 207 pp.

Durner, G.M., Douglas, D.C., Nielson, R.M., Amstrup, S.C., McDonald, T.L., Stirling, I., Mauritzen, M., Born, E.W.,Wiig, Ø., DeWeaver, E., Serreze, M.C., Belikov, S.E., Holland, M.M., Maslanik, J., Aars, J., Bailey, D.A. and Derocher, A.E. 2009. Predicting 21st-century polar bear habitat distribution from global climate models. Ecological Monographs 79:25-58.

Dyck, M. 2017. Re-estimating the abundance of the Davis Strait polar bear subpopulation via genetic mark-recapture sampling. 2017 Interim Field Report, Government of Nunavut, Iglulik, NU, 8 pages.

Dyck, M. and Ware, J.V. 2018. Re-estimating the abundance of the Davis Strait polar bear subpopulation via genetic mark-recapture sampling. 2018 Interim Field Report, Government of Nunavut, Iglulik, NU, 9 pages.

Dyck, M., E.V. Regehr, and J.V. Ware. 2020a. Re-assessment of abundance for the Gulf of Boothia polar bear subpopulation using genetic mark-recapture. Final Report, Government of Nunavut, Department of Environment, Iglulik, NU, 75pp.

Dyck, M., Lukacs, P. and Ware. J. 2021. Demographic indices suggest recovery from reduction: The M'Clintock Channel polar bear subpopulation, Nunavut, Canada. Arctic 74:509-524.

Escajeda, E., Laidre, K.L., Born, E.W., Wiig, Ø., Atkinson, S., Dyck, M., Ferguson, S.H., and Lunn, N.J. 2018. Identifying shifts in maternity den phenology and habitat characteristics of polar bears (Ursus maritimus) in Baffin Bay and Kane Basin. Polar Biology 41:87-100.

Fagerland, M.W. and Hosmer, D.W. 2012. A generalized Hosmer-Lemeshow Goodness-of-Fit Test for multinomial logistic regression models. The Stata Journal 12(3):447-453.

Ferguson, S.H., Taylor, M.K., and Messier F. 1997. Space use of polar bears in and around Auyuittuq National Park, Northwest Territories, during the ice-free period. Canadian Journal of Zoology 75:1585-1594.

Ferguson, S.H., Taylor, M.K., and Messier, F. 2000. The influence of sea ice dynamics on habitat selection by polar bears. Ecology 81:761-772.

Fisk, A.T., de Wit, C.A., Wayland, M., Kuzyk, Z.Z., Burgess, N., Letcher, R.J., Braune, B., Norstrom, R.J., Polischuk Blum, S., Sandau, C., et al. 2009. An assessment of the toxicological significance of anthropogenic contaminants in Canadian Arctic wildlife. The Science of the Total Environment 351-352:57-93.

Garshelis, D.L. 2006. On the allure of noninvasive genetic sampling - putting a face to the name. Ursus 17:109-123.

Garshelis, D. L., K. V. Noyce, and V. St-Louis. 2020. Population reduction by hunting helps control human-wildlife conflicts for a species that is a conservation success story. PLoS ONE 15:20.

Gelman, A., and Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457-511.

Gibbs, J.P. 2008. Monitoring for Adaptive Management in Conservation Biology. Synthesis. American Museum of Natural History, Lessons in Conservation. Available at http:// ncep.amnh.org/linc

Hammill, M.O., Stenson, G.B., Mosnier, A. and Doniol-Valcroze, T. 2021. Trends in abundance of harp seals, Pagophilus groenlandicus, in the Northwest Atlantic, 1952-2019. DFO Can. Sci. Advis. Sec. Res. Doc. 2021/006

Healey, B.P., and Stenson, G.B. 2000. Estimating pup production and population size of the northwest Atlantic harp seal (Phoca groenlandicus). Canadian Stock Assessment Secretariat Research Document 2000/081. Ottawa: Canadian Science Advisory Secretariat, Fisheries and Oceans Canada. 27 p

Heide-Jorgensen, M.P., Stern, H.L., and Laidre, K.L. 2007. Dynamics of the sea ice edge in Davis Strait. Journal of Marine Systems 67:170-178.

Henri, D. 2012. Managing nature, producing cultures: Inuit participation, science and policy in wildlife governance in the Nunavut Territory, Canada. D.Phil. thesis. University of Oxford

Holling, C.S. 1978. Adaptive environmental assessment and management. Willey \& Sons

Hosmer, D.W., Lemeshow, S., and Sturdivant, R.X. 2013. Applied logistic regression. Vol. 398. John Wiley \& Sons, New York, USA

Huggins, R.M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133-140.

Iverson, S.J., I. Stirling, and S.L.C. Lang. 2006. Spatial and temporal variation in the diets of polar bears across the Canadian Arctic: ndicators of changes in prey populations and environment. Pages 98-117 in I. L. Body, S. Wanless, and C. J. Camphyuysen, editors. Top predators in marine ecosystems. Cambridge University Press, Cambridge, United Kingdom.

Johnson, B.L. 1999. The role of adaptive management as an operational approach for resource management agencies. Conservation Ecology 3:8. URL: http://www.consecol.org/vol3/iss2/art8.

Kellner, K. 2015. jagsUI: A wrapper around "rjags" to streamline "JAGS" analyses. R package version 1.3.7. http://CRAN. R-project.org/package=jagsUI

Kendall, K.C., J.B. Stetz, J.B. Boulanger, A.C. Macleod, D. Paetkau, and G.C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. Journal of Wildlife Management 73:3-14.

Kéry, M. and Schaub, M., 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.

Koons, D.N., Aubry, L.M., and Rockwell, R.F. 2019. Liberalized harvest regulations have not affected overabundant Snow Geese in Northern Manitoba. The Condor: Ornithological Applications pp 1-13 DOI: 10.1093/condor/duz006

Kotierk, M. 2009. The documentation of Inuit and public knowledge of Davis Strait polar bears, climate change, Inuit knowledge and environmental management using public opinion polls. Department of Environment, Government of Nunavut, Igloolik, Nunavut, Canada.

Laidre, K.L., Born, E.W., Atkinson, S.N., Wiig, Ø., Andersen, L.W., Lunn, N.J., Dyck, M., Regehr, E.V., McGovern, R. and Heagerty, P. 2018a. Range contraction and increasing isolation of a polar bear subpopulation in an era of sea-ice loss. Ecology and Evolution 8(4), pp.2062-2075.

Laidre, K.L., Stern, H., Born, E.W., Heagerty, P., Atkinson, S., Wiig, Ø., Lunn, N.J., Regehr, E.V., McGovern, R. and Dyck, M. 2018b. Changes in winter and spring resource selection by polar bears Ursus maritimus in Baffin Bay over two decades of sea-ice loss. Endangered Species Research 36, pp.1-14.

Laidre, K.L., Atkinson, S., Regehr, E.V., Stern, H.L., Born, E.W., Wiig, Ø., Lunn, N.J. and Dyck, M. 2020a. Interrelated ecological impacts of climate change on an apex predator. Ecological Applications 30(4):e02071.

Laidre, K.L., Atkinson, S.N., Regehr, E.V., Stern, H.L., Born, E.W., Wiig, Ø., Lunn, N.J., Dyck, M., Heagerty, P. and Cohen, B.R. 2020b. Transient benefits of climate change for a high-Arctic polar bear (Ursus maritimus) subpopulation. Global Change Biology 26(11):6251-6265.

Lancia, R.A., Braun, C.E., Collopy, M.W., Dueser, R.D., Kie, J.G. et al. 1996. ARM! For the future: adaptive resource management in the wildlife profession. Wildlife Society Bulletin 24:436-442.

Larsen, T., \& Stirling, I. 2009. The agreement on the conservation of polar bears: its history and future. Norwegian Polar Institute. 17pp.

Lee, J., and M. Taylor. 1994. Aspects of the polar bear harvest in the Northwest Territories, Canada, in Ninth International Conference on Bear Research and Management. 9:237-243.

Letcher, R.J., Bustnes, J.O., Dietz, R., Jenssen, B.M., Jorgensen, E.H., Sonne, C., Verreault, J., Vijayan, M.M., and Gabrielsen, G.W. 2010. Exposure and effects assessment of persistent organohalogen contaminants in Arctic wildlife and fish. The Science of the Total Environment 408:2995-3043.

Lukacs, P.M. and Burnham, K.P. 2005 Review of capture-recapture methods applicable to noninvasive genetic sampling. Molecular Ecology 14:3909-3919.

Lunn, N.J. et al. 2010. Polar bear management in Canada, 2005-2008. Pages 87-114 in M.E. Obbard, G.W. Thiemann, E. Peacock, and T.D. DeBruyn (eds.) Polar Bears: Proceedings of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, Copenhagen, Denmark, 29 June-3 July 2009. Gland, Switzerland and Cambridge, UK: IUCN.

Lunn, N.J., Servanty, S., Regehr, E.V., Converse, S.J., Richardson, E., and Stirling, I. 2016. Demography of an apex predator at the edge of its range: impacts of changing sea ice on polar bears in Hudson Bay. Ecological Applications 26: 1302-1320.

Malenfant, R.M., Davis, C.S., Cullingham, C.I., Coltman, D.W. 2016 Circumpolar genetic structure and recent gene flow of polar bears: a reanalysis. PLoS ONE 11(3): e0148967.

McDonald, T. L., and Amstrup, S. C. 2001. Estimation of population size using open capture-recapture models. Journal of Agricultural, Biological, and Environmental Statistics 6206-220.

McKinney, M. A., Peacock, E. and Letcher, R.J. 2009. Sea ice-associated diet change increases the level of chlorinated and brominated contaminants in polar bears. Environmental Science and Technology 43:4334-4339.

McKinney, M.A., Letcher, R.J., Aars, J., Born, E.W., Branigan, M., Dietz, R., Evans, T.J., Gabrielsen, G.W., Peacock, E. and Sonne, C. 2011. Flame retardants and legacy contaminants in polar bears from Alaska, Canada, East Greenland and Svalbard, 2005-2008. Environment International 37:265-274.

McLoughlin, P. D., Taylor, M.K., and Messier, F. 2005. Conservation risks of maleselective harvest for mammals with low reproductive potential. Journal of Wildlife Management 69:1592-1600.

Molnár, P.K., Bitz, C.M., Holland, M.M., Kay, J.E., Penk, S.R., and Amstrup, S.C. 2020. Fasting season length sets temporal limits for global polar bear persistence. Nature Climate Change 10:732-738.

Nichols, J.D., and Williams, B.K. 2006. Monitoring for conservation. Trends in Ecology and Evolution 21:668-673.

Nunavik Marine Regional Wildlife Board (NMRWB). 2019. Nunavik Inuit knowledge and observations of polar bears: Polar bears of the Davis Strait sub-population. Project conducted and report prepared for the NMRWB by Basterfield, M., Furgal, C., Breton, Honeyman, K., Rae, J, and O'Connor, M. 111 pp.

Obbard, M.E., Thiemann, G.W., Peacock, E. and DeBruyn, T.D (eds). 2010. Polar Bears: Proceedings of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, Copenhagen, Denmark, 29 June-3 July 2009. pp. 235. IUCN, Gland, Switzerland and Cambridge, UK.

Obbard, M.E., M.R.L. Cattet, E.J. Howe, K.R. Middel, E.J. Newton, G.B. Kolenosky, K.F. Abraham, and Greenwood, C.J. 2016. Trends in body condition in polar bears (Ursus maritimus) from the Southern Hudson Bay subpopulation in relation to changes in sea ice. Arctic Science 2:15-32.

Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. Wildlife monographs 62: 3-135.

Ostrander, E.A., Sprague, G.F.J., and Rine, J. 1993. Identification and characterization of dinucleotide repeat (CA)n markers for genetic mapping in dog. Genomics 16:207-213.

Paetkau, D. and Strobeck C. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489-495.

Paetkau, D. W., Calvert, C., Stirling, I. and Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347-354.

Paetkau D, Shields GF, and Strobeck C. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. Molecular Ecology 7:1283-1292.

Paetkau, D., Amstrup, S.C., Born, E.W., Calvert, W., Derocher, A.E., Garner, G.W., Messier, F., Stirling, I., Taylor, M.K., Wiig, Ø., Strobeck, C., 1999. Genetic structure of the world's polar bear populations. Molecular Ecology 8:1571-1584.

Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology 12:1375-1387.

Pagano, A.M., Peacock, E., and McKinney, M.A. 2014. Remote biopsy darting and marking of polar bears. Marine Mammal Science 30:169-183.

Palsbøll, P. J., Allen, J., Berube, M., et al. 1997. Genetic tagging of humpback whales. Nature 388:767-769.

Peacock, E., Taylor, M.K., Laake, J., and Stirling, I. 2013. Population ecology of polar bears in Davis Strait, Canada and Greenland. Journal of Wildlife Management, Doi:10.1002/jwm. 489.

Polar Bear Range States. 2015. Circumpolar Action Plan: Conservation Strategy for Polar Bears. A product of the representatives of the parties to the 1973 Agreement on the Conservation of Polar Bears.

Pradel, R. (2005). Multievent: an extension of multistate capture - recapture models to uncertain states. Biometrics, 61, 442-447.

R Core Team. 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. www.r-project.org.

Regehr, E.V., Hunter, C.M., Caswell, H., Amstrup, S.C., and Stirling, I. 2010. Survival and breeding of polar bear in the southern Beaufort Sea in relation to sea ice. Journal of Animal Ecology 79:117-127.

Regehr, E.V., Wilson, R.R., Rode, K.D., and Runge, M.C. 2015. Resilience and risk—A demographic model to inform conservation planning for polar bears. U.S. Geological Survey Open-File Report 2015-1029:56.

Regehr, E.V., Laidre, K.L., Akcakaya, H.R., Amstrup, S.C., Atwood, T.C., Lunn, N.J., Obbard, M., Stern, H., Thiemann, G.W., and Wiig, Ø. 2016. Conservation status of polar bears (Ursus maritimus) in relation to projected sea ice declines. Biology Letters 12:1-5.

Regehr, E.V., Wilson, R.R., Rode, K.D., Runge, M.C., and Stern, H.L. 2017a. Harvesting wildlife affected by climate change: a modelling and management approach for polar bears. Journal of Applied Ecology 54:1534-1543.

Regehr, E.V., S. Atkinson, E.W. Born, K.L. Laidre, N.J. Lunn, and Ø. Wiig. 2017b. Harvest assessment for the Baffin Bay and Kane Basin polar bear subpopulations: Final report to the Canada-Greenland Joint Commission on Polar Bear, 31 July 2017: iii + 107 pp.

Regehr, E.V., Hostetter, N.J., Wilson, R.R., Rode, K.D., Martin, M.S., and Converse, S.J. 2018. Integrated population modeling provides the first empirical estimates of vital rates and abundance for polar bears in the Chukchi Sea. Scientific Reports 8:16780.

Regehr, E., M. Dyck, G. Gilbert, S. Iverson, D. Lee, N. Lunn, J. Northrup, A. Penn, M.C. Richer and Szor, G. 2019. Provisional harvest risk assessment for the Southern Hudson Bay polar bear subpopulation. Report to the Southern Hudson Bay Polar Bear Subpopulation Advisory Committee, 07 June 2019. Unpublished report. 75 pp

Rode, K.D., Regehr, E.V., Douglas, D., Durner, G., Derocher, A.E., Thiemann, G.W., and Budge, S.M. 2014. Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. Global Change Biology 20:76-88.

Rode, K.D., Peacock, L., Taylor, M., Stirling, I., Børn, E.W., Laidre, K.L., and Wiig, O. 2012. A tale of two polar bear populations: ice habitat, harvest, and body condition. Population Ecology 54:3-18.

Rode K.D., Robbins C.T., Nelson L., and Amstrup S.C. 2015 Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities? Frontiers Ecology and Environment 13:138-145.

Rosing-Asvid, A., Born, E.W., Kingsley, M.C.S. 2002.Age at sexual maturity of males and timing of the mating season of polar bears (Ursus maritimus) in Greenland. Polar Biology 25:878-883.

Royle, J.A. and Link, W.A. 2002. Random effect and shrinkage estimation in capturerecapture models. Journal of Applied Statistics 29:329-351.

Schaub, M., and Pradel, R. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. Ecology 85:930-938.

Schwartz, M.K., Luikart, G., and Waples, R.S. 2006. Genetic monitoring as a promising tool for conservation and management. Trends in Ecology and Evolution 22, DOI: 10.1016/ j.tree.2006.08.009.

Stenson, G.B., Myers, R.A., Ni, I.-H., and Warren, W.G. 1997. Pup production and population growth of hooded seals (Cystophora cristata) near Newfoundland, Canada. Canadian Journal of Fisheries and Aquatic Sciences 54:209-216.

Stenson, G.B., Buren, A.D., and Koen-Alonso, M. 2016. The impact of changing climate and abundance on reproduction in an ice-dependent species, the Northwest Atlantic harp seal, Pagophilus groenlandicus. ICES Journal of Marine Science: Journal du Conseil 73:250-262.

Stern, H.L. and Heide-Jorgensen, M.P. 2003. Trends and variability of sea ice in Baffin Bay and Davis Strait, 1953-2001. Polar Research 22:11-18.

Stern, H.L. and Laidre, K.L. 2016. Sea-ice indicators of polar bear habitat. The Cryosphere 10:1-15.

Stirling, I., and Kiliaan, H.P.L. 1980. Population ecology studies of the polar bear in northern Labrador. Canadian Wildlife Service Occasional Paper 42. Edmonton, Alberta, Canada.
Stirling, I., W. Calvert, and Andriashek, D. 1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. Canadian Wildlife Service Occasional Paper 44, Edmonton, Alberta, Canada.

Stirling, I., Spencer, C., and Andriashek, D. 1989. Immobilization of polar bears (Ursus maritimus) with Telazol in the Canadian Arctic. Journal of Wildlife Diseases 25:159-168.

Stirling, I., and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (Ursus maritimus) in the Canadian Arctic. Arctic 59:261-275.

Stirling, I., Thiemann, G., and Richardson, E. 2008. Quantitative support for a subjective fatness index for immobilized polar bears. Journal of Wildlife Management 72:568-574.

Stirling, I., and Derocher, A.E. 2012. Effects of climate warming on polar bears: a review of the evidence. Global Change Biology 18:2694-2706

SWG [Scientific Working Group to the Canada-Greenland Joint Commission on Polar Bear]. 2016. Re-Assessment of the Baffin Bay and Kane Basin Polar Bear Subpopulations: Final Report to the Canada-Greenland Joint Commission on Polar Bear. 31 July 2016: $x+636$ pp.

Taberlet, P., Camarra, J.J., Griffin, S., Uhres, E., Hanotte, O., Waits, L.P., DuboisPaganon, C., Burke, T., and Bouvet, J. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. Molecular Ecology 6:869-876.

Taylor, M.K. and Lee, J. 1995. Distribution and abundance of Canadian polar bear populations: A management perspective. Arctic 48:147-154.

Taylor, M.K., Akeeagok, S., Andriashek, D., Barbour, W., Born, E.W., Calvert, W., Cluff, H.D., Ferguson, S., Laake, J., Rosing-Asvid, A., Stirling, I., and Messier, F. 2001. Delineating Canadian and Greenland polar bear (Ursus maritimus) populations by cluster analysis of movements. Canadian Journal of Zoology 79:690-709.

Taylor, B.L., Martinez, M., Gerrodette, T., Barlow, J., and Hrovat, Y.N. 2007. Lessons from monitoring trends in abundance of marine mammals. Marine Mammal Science 23:157-175.

Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P., Paananen, T., Gelman, A. 2020. "loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models." R package version 2.4.1, https://mc-stan.org/loo/.

Venables W.N. and Ripley B.D. 2002. Modern Applied Statistics with S, Fourth edition. Springer, New York. https://www.stats.ox.ac.uk/pub/MASS4/.

Vongraven, D. and Peacock, E. 2011. Development of a pan-Arctic monitoring plan for polar bears: a background paper. Circumpolar Biodiversity Monitoring

Programme, CAFF Monitoring Series Report No. 1. CAFF International Secretariat, Akureyri, Iceland.

Vongraven, D., Aars, J., Amstrup, S., Atkinson, S.N., Belikov, S., Born, E.W., DeBruyn, T.D., Derocher, A.E., Durner, G., Gill, M., Lunn, N., Obbard, M.E., Omelak, J., Ovsyanikov, N., Peacock, E., Richardson, E., Sahanatien, V., Stirling, I., and Wiig, $\varnothing$. 2012. A circumpolar monitoring framework for polar bears. Ursus 5:166.

Watanabe, S. 2010. Asymptotic Equivalence of Bayes Cross Validation and Widely Applicable Information Criterion in Singular Learning Theory. Journal of Machine Learning Research 11: 3571-3594.

Wiig, Ø., Amstrup, S., Atwood, T., Laidre, K., Lunn, N., Obbard, M., Regehr, E. and Thiemann, G. 2015. Ursus maritimus. The IUCN Red List of Threatened Species 2015: e.T22823A14871490.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of wildlife populations. Academic Press, San Diego, CA.

Yackulic, C. B., Dodrill, M., Dzul, M., Sanderlin, J.S., and Reid, J.A. 2020. A need for speed in Bayesian population models: a practical guide to marginalizing and recovering discrete latent states. Ecological Applications 30:e02112.

York, J., Dale, A., Mitchell, J., Nash, T., Snook, J., Felt, L., Dowsley, M. and Taylor, M. 2015. Labrador polar bear traditional ecological knowledge final report. Torngat Wildlife Plants and Fisheries Secretariat Ser. 2015/03 + 118 + iv p

## FIGURES AND TABLES



Figure 1. The Davis Strait polar bear subpopulation (blue outline) with different jurisdictions in shades of gray (Newfoundland and Labrador [Nunatsiavut], light gray; Nunavut, dark gray; Québec [Nunavik], medium gray).


Figure 2. Sampling (blue triangles) and harvest (red circles) locations for Davis Strait polar bears where coordinates for both events for the same individual bear were available ( $n=163$ ). Green lines indicate subpopulation boundaries.


Figure 3. Sampling locations by field season (blue = 2017; purple =2018) within the Davis Strait polar bear study area (Note: the sampling stratification for the coastline shown by black lines, the 10 km and 30 km strata are also indicated). Inset: Davis Strait subpopulation area in context of Canada.


Figure 4. Overview of bear observations and helicopter paths flown in search for polar bears in Davis Strait during August - October 2017 and 2018. Inset: Davis Strait subpopulation area (red) in context of Canada.


Figure 5. Estimates of annual survival rates for Davis Strait polar bears by age class. Light gray squares and dashed lines are the annual means and 95\% Bayesian credible intervals for offspring (cubs-of-the-year and yearlings). Dark gray triangles and dotted lines are the annual means and $95 \%$ credible intervals for subadult polar bears (males: 2-7 years, females: 2-4 years). Black circles and solid black lines are the annual means and $95 \%$ Bayesian credible intervals for adult polar bears (males: $8+$ years, females: $5+$ years). Using combined capture-recapture-recovery data, we estimated survival in all years for adult polar bears; however, estimates of survival for younger age classes were limited to years following releases.


Figure 6. Estimates of annual recapture probability of Davis Strait polar bears by age and sex class. Capture-mark-recapture data were collected intermittently, and recapture probabilities were estimable for only four years across two sampling periods. Light gray squares and dashed lines are the annual means and $95 \%$ Bayesian credible intervals for subadult polar bears (males: 2-7 years old, females 2-4 years old). Dark gray triangles and dotted lines are the annual means and 95\% Bayesian credible intervals for adult females ( $5+$ years old) and offspring (cubs-of-the-year and yearlings). Black circles and solid lines are the annual means and $95 \%$ Bayesian credible intervals for adult male polar bears.


Figure 7. Estimates of abundance for the Davis Strait subpopulation of polar bears. Black circles and dashed lines represent the mean and 95\% CRI derived from recapture probabilities using multistate live-capture dead-recovery models. Point estimates and credible intervals are shown for 2006, 2007, 2017, and 2018 only because those were the only years in which recapture probability were estimable due to intermittent sampling. The red circle and dashed lines represent the mean and 95\% confidence interval of abundance estimated for the period of 2005-2007 and reported by Peacock et al. (2013) for comparison.


Figure 8. Predicted probability $\pm$ SD of bears being classified in poor body condition in the early sampling period (2005-2007) or the later sampling period (20172018).


Figure 9. Predicted probability $\pm$ SEM of bears being classified in good body condition for each reproductive age class as a function of the number of days between sea-ice retreat and when the bear was sampled.

Table 1. Number of live observations (black, captures \& recaptures) and dead recoveries (gray, in parentheses) of individually identified polar bears in the Davis Strait subpopulation used in survival estimation. No marked cubs of the year (COY) were harvested in our data set. However, there were a total of 9 marked bears harvested as yearlings (1.5 years old) prior to becoming subadults (at 2.5 years old).

| Year | Adult Males | Adult Females | Subadult Males | Subadult Females | Yearlings | COY |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 2005 | 207 | 175 | 115 | 32 | 40 | 51 |
| 2006 | 263 (3) | 206 (3) | 160 (3) | 64 (0) | 70 (1) | 76 |
| 2007 | 269 (4) | 251 (2) | 152 (5) | 54 (0) | 102 (1) | 57 |
| 2008 | (17) | (4) | (9) | (2) | (2) |  |
| 2009 | (12) | (3) | (12) | (4) | (2) |  |
| 2010 | (12) | (1) | (8) | (1) |  |  |
| 2011 | (17) | (3) | (3) |  |  |  |
| 2012 | (9) | (2) | (1) |  |  |  |
| 2013 | (16) | (3) | (2) |  |  |  |
| 2014 | (11) | (4) | (2) |  |  |  |
| 2015 | (10) | (3) | (1) |  |  |  |
| 2016 | (9) | (0) |  |  |  |  |
| 2017 | 156 (6) | 172 (0) | 48 (0) | 40 (0) | 46 (0) | 76 |
| 2018 | 153 (13) | 191 (2) | 93 (1) | 51 (1) | 54 (3) | 66 |

Table 2. Sequential model selection for Davis Strait polar bear survival and encounter probabilities based on information criterion (WAIC) to address our primary objective of identifying temporal patterns in survival.

| Model | Parameterization | WAIC | $\Delta$ WAIC |
| :---: | :---: | :---: | :---: |
| Step 1. Best model for age structure in survival; includes random effects |  |  |  |
| M2 | 3 age classes; Dependent young, Subadults, Adults | 6883.6 |  |
| M1 | 4 age classes; COYS, Yearlings, Subadults, Adults | 6891.6 | 8.0 |
| Step 2. Best model for sex structure in survival using the best model for age structure in survival (Model M2); includes random effects |  |  |  |
| M2 | 3 age classes; Dependent young, Subadults, Adults | 6883.6 |  |
| M4 | 4 age-sex classes; Dependent young, subadults, adult males, adult females | 6899.4 | 15.8 |
| M3 | 5 age-sex classes; Dependent young, subadult males, subadult females, adult males, adult females | 6910.3 | 26.7 |
| Step 3. Best model for temporal variation in survival using the best model for age/sex structure in survival (Model M2) |  |  |  |
| M2 | Subadult and Adult class year random effects | 6883.6 |  |
| M5 | Subadult and Adult class linear trend with year random effects | 6888.0 | 4.4 |
| M6 | Subadult and Adult class year fixed effects | 6903.8 | 20.2 |
| Step 4. Best model for temporal variation in recovery using the best age/sex structure for survival (Model M2) |  |  |  |
| M2 | 2 sex classes; constant | 6883.6 |  |

M8 2 sex classes; shared year random effects ..... 6890.1 ..... 6.5
M7 2 sex classes; year random effects ..... 6894.2 ..... 10.6
Step 5. Best model for age/sex structure in recapture probability using the best structure for survival and recovery (Model M2)M2 3 age-sex classes and year fixed effects; Subadults, Females and Dependent young, Adult6883.6males
M9 4 age-sex classes and year fixed effects; Subadult Male, Subadult Female, Females and ..... 6886.6 ..... 3.0 Dependent Young, Adult males
Step 6. Quantify effects of environmental covariates on adult and subadult survival
M2 Year random effect ..... 6883.6
M10 Ice decay + year random effect ..... 6884.2 ..... 0.6
M11 Ice-free days + year random effect ..... 6884.8 ..... 1.2
M14 NAOw + year random effect ..... 6885.1 ..... 1.5
M13 Mean summer ice concentration + year random effect ..... 6885.92 .3
M12 Harp seals + year random effect ..... $6893.3 \quad 9.7$
M15 AOw + year random effect ..... 6893.7 ..... 10.1
M16 Ice decay + harp seals + year random effect ..... 6893.9 ..... 10.3
M17 Ice decay + NAOw + ice-free days + year random effect ..... 6894.5 ..... 10.9

Table 3. Parameter estimates from the top model for Davis Strait polar bears with data from 2005-2018 (model M2; Table 2). Demographic parameters are reported as the mean, standard deviation, and 95\% Bayesian credible intervals (CRI) on the probability scale. Temporal variance is reported on the logit scale.

| Parameter | Mean | SD | $95 \%$ CRI |
| :--- | :---: | :---: | :---: |
| Offspring survival | 0.794 | 0.0353 | $(0.723,0.861)$ |
| Subadult survival | 0.873 | 0.0230 | $(0.826,0.914)$ |
| Adult survival | 0.871 | 0.009 | $(0.853,0.892)$ |
| Male recovery | 0.248 | 0.017 | $(0.215,0.282)$ |
| Female recovery | 0.072 | 0.010 | $(0.053,0.093)$ |
| Temporal variance: subadult survival | 0.236 | 0.336 | $(0.0019,1.093)$ |
| Temporal variance: adult survival | 0.048 | 0.059 | $(0.000007,0.215)$ |

Table 4. Recapture probability metrics for each year and each recapture age-sex class. (LCRI = lower Bayesian credible interval, UCRI = upper Bayesian credible interval)

| Recapture Class | Year | Mean | SD | $95 \%$ LCRI | $95 \%$ UCRI |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Females \& Offspring |  |  |  |  |  |
|  | 2006 | 0.338 | 0.025 | 0.291 | 0.390 |
|  | 2007 | 0.332 | 0.020 | 0.294 | 0.373 |
|  | 2017 | 0.246 | 0.030 | 0.191 | 0.308 |
|  | 2018 | 0.298 | 0.025 | 0.252 | 0.349 |
|  | 2006 | 0.383 | 0.029 | 0.327 | 0.443 |
|  | 2007 | 0.377 | 0.025 | 0.329 | 0.427 |
|  | 2017 | 0.284 | 0.037 | 0.218 | 0.360 |
| Subadults | 2018 | 0.340 | 0.031 | 0.284 | 0.402 |
|  | 2006 | 0.489 | 0.028 | 0.434 | 0.508 |
|  | 2007 | 0.482 | 0.024 | 0.437 | 0.528 |
|  | 2017 | 0.378 | 0.039 | 0.305 | 0.459 |
|  | 2018 | 0.442 | 0.032 | 0.380 | 0.506 |

Table 5. Abundance estimates from our model (2006-2018) and average estimate over 2005-2007 from Peacock et al. (2013). In 2017, surveys were not conducted on Edgell and Resolution Islands. In 2018, surveys were not conducted on Edgell and Resolution islands or in an area around Loksland. Abundance estimates were subsequently adjusted for these incomplete surveys (see Methods for details; CRI = Bayesian credible interval).

| Year | Annual estimate <br> $(95 \%$ CRI) | Study period <br> estimate <br> (95\% CRI) | Peacock et al. estimate <br> Average over 2005-2007 <br> (95\% Confidence Interval) |
| :--- | :---: | :---: | :---: |
| 2006 | 2,190 | 2,250 | 2,158 |
| 2007 | $(1,954-2,454)$ | $(1,989-2,512)$ | $(1,833-2,542)$ |
|  | $(2,111-2,536)$ |  | NA |
| 2017 | 2,085 | 2,015 |  |
| 2018 | $(1,613-2,699)$ | $(1,603-2,588)$ |  |
|  | $(1,593-2,366)$ |  |  |

Table 6. Annual numbers of litters and mean litter sizes (LS) of cub-of-the year (COY) and yearling (YRL) litters encountered during the capture-recapture studies in Davis Strait.

|  | $\mathbf{2 0 0 5}$ | $\mathbf{2 0 0 6}$ | $\mathbf{2 0 0 7}$ | $\mathbf{2 0 1 7}$ | $\mathbf{2 0 1 8}$ |
| :--- | :---: | :---: | :---: | :---: | :---: |
| No. COY litters | 38 | 51 | 41 | 55 | 47 |
| Mean COY LS | 1.39 | 1.49 | 1.41 | 1.40 | 1.45 |
| No. YRL litters | 27 | 45 | 67 | 38 | 38 |
| Mean YRL LS | 1.48 | 1.56 | 1.52 | 1.66 | 1.42 |

Table 7. Ratio of the number of cubs-of-the-year (COY) to adult females (ADF), the number of yearlings (YRL) to adult females, and the number of adult females with cubs-of-the-year (ADF_COY) to adult females in the subpopulation.

|  | $\mathbf{2 0 0 5}$ | $\mathbf{2 0 0 6}$ | $\mathbf{2 0 0 7}$ | $\mathbf{2 0 1 7}$ | $\mathbf{2 0 1 8}$ |
| :--- | :---: | :---: | :---: | :---: | :---: |
| COY: ADF | 0.30 | 0.37 | 0.23 | 0.45 | 0.36 |
| YRL: ADF | 0.23 | 0.34 | 0.41 | 0.37 | 0.28 |
| ADF_COY: ADF | 0.21 | 0.25 | 0.16 | 0.32 | 0.25 |

Table 8. Number of polar bears classified in each category of body condition index (BCI) in the Davis Strait subpopulation 2005-2007 and 2017-2018. Poor BCI corresponds to a thin bear ( BCl of 1 or 2 ) and Good BCl corresponds to a fat/obese bear ( BCl of 4 or 5 ). Age classes are adult ( $\geq 5$ years) and subadult (2-4 years).

|  | 2005-2007 |  |  |  | 2017-2018 |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Poor | Average | Good |  | Poor | Average | Good |
| Adult female <br> without <br> offspring | 66 | 157 | 135 |  | 5 | 87 | 74 |
| Adult female <br> with offspring | 113 | 146 | 13 |  | 17 | 176 | 10 |
| Adult male | 97 | 292 | 343 |  | 31 | 180 | 101 |
| Subadult male | 102 | 240 | 67 |  | 15 | 99 | 13 |
| Subadult female | 38 | 90 | 12 |  | 6 | 67 | 14 |
| Total | $\mathbf{4 1 6}$ | 925 | 570 |  |  |  |  |

Table 9. Fitted multinomial regression model parameter estimates (reference level = "poor"/ $\mathrm{BCl}=1$ or 2 , intercept represents adult independent females in 2005-2007 sampling period) for body condition index analysis of the Davis Strait subpopulation. See Methods for variable definitions.

|  | Parameter estimate $\pm$ SE |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| BCI | Intercept | Time since spring transition | Period | Adult female with offpsring | Adult male | Subadult female | Sub- <br> adult <br> male | Period x <br> adult <br> female <br> with <br> offspring |  | Period x Subadult female | Period x <br> Sub- <br> adult <br> male |
| Average | $\begin{aligned} & 0.98 \pm \\ & 0.307 \end{aligned}$ | $\begin{gathered} -0.001 \pm \\ 0.002 \end{gathered}$ | $\begin{aligned} & 1.97 \pm \\ & 0.486 \end{aligned}$ | $\begin{array}{r} -0.61 \pm \\ 0.193 \end{array}$ | $\begin{gathered} 0.24 \pm \\ 0.188 \end{gathered}$ | $\begin{array}{r} -0.009 \\ \pm 0.243 \end{array}$ | $\begin{array}{r} -0.013 \\ \pm 0.188 \end{array}$ | $\begin{aligned} & 0.09 \pm \\ & 0.560 \end{aligned}$ | $\begin{gathered} -1.33 \pm \\ 0.533 \end{gathered}$ | $\begin{gathered} -0.44 \pm \\ 0.672 \end{gathered}$ | $\begin{gathered} -0.96 \pm \\ 0.569 \end{gathered}$ |
| Good | $\begin{aligned} & 1.40 \pm \\ & 0.343 \end{aligned}$ | $\begin{gathered} -0.006 \pm \\ 0.003 \end{gathered}$ | $\begin{aligned} & 1.85 \pm \\ & 0.490 \end{aligned}$ | $\begin{array}{r} -2.89 \pm \\ 0.329 \end{array}$ | $\begin{gathered} 0.56 \pm \\ 0.190 \end{gathered}$ | $\begin{array}{r} -1.90 \pm \\ 0.364 \end{array}$ | $\begin{array}{r} -1.15 \pm \\ 0.218 \end{array}$ | $\begin{gathered} -0.33 \pm \\ 0.694 \end{gathered}$ | $\begin{gathered} -2.06 \pm \\ 0.540 \end{gathered}$ | $\begin{aligned} & 0.04 \pm \\ & 0.764 \end{aligned}$ | $\begin{gathered} -1.69 \pm \\ 0.636 \end{gathered}$ |

Table 10. Reported mean harvest for the Davis Strait (DS) polar bear subpopulation by jurisdiction between 1999-2008 and 2009-2019 [Numbers represent mean $\pm$ standard deviation (range); NU = Nunavut, NL = Newfoundland and Labrador, GL = Greenland].

| Harvest Years | Jurisdiction |  |  |  | DS Mean | Proportion Female |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | NU | Quebec | NL | GL |  |  |
| 1999-2008 | $\begin{gathered} 39.4 \pm 4.6 \\ (34-48) \end{gathered}$ | $\begin{gathered} 16.5 \pm 8.4 \\ (7-31) \end{gathered}$ | $\begin{gathered} 5.9 \pm 1.4 \\ (4-8) \end{gathered}$ | $\begin{gathered} 2.3 \pm 2.0 \\ (0-7) \end{gathered}$ | $\begin{gathered} 64.1 \pm 10.1 \\ (53-81) \end{gathered}$ | 0.345 |
| 2009-2019 | $\begin{gathered} 44.2 \pm 10.1 \\ (31-60) \end{gathered}$ | $\begin{gathered} 30.2 \pm 5.9 \\ (12-59) \end{gathered}$ | $\begin{gathered} 10.9 \pm 3.5 \\ (2-14) \end{gathered}$ | $\begin{gathered} 1.5 \pm 1.5 \\ (0-4) \end{gathered}$ | $\begin{gathered} 86.8 \pm 23.6 \\ (62-126) \end{gathered}$ | 0.350 |

## SUPPLEMENTARY MATERIALS

## Supplementary Methods

Table SM1. Parameters, their definitions, and prior distributions used in a multistate model for Davis Strait polar bears.

| Parameter | Definition | Prior Distribution |
| :---: | :---: | :---: |
| $S_{\text {coy }}$ | Survival probability of cubs-of-the-year | Uniform (0, 1) |
| $S_{y r l}$ | Survival probability of yearlings | Uniform (0, 1) |
| $S_{s a}$ | Survival probability of subadults | Beta (14.07, 2.68) $m u=0.84, s d=0.09$ |
| $S_{\text {saf }}$ | Survival probability of subadult females | $\begin{aligned} & \text { Beta }(29.24,4.04) \\ & m u=0.88, s d=0.06 \end{aligned}$ |
| $S_{\text {sam }}$ | Survival probability of subadult males | $\begin{aligned} & \text { Beta }(12.23,2.90) \\ & m u=0.81, s d=0.10 \end{aligned}$ |
| $S_{a d}$ | Survival probability of adults | $\begin{aligned} & \text { Beta }(46.49,4.70) \\ & m u=0.91, s d=0.04 \end{aligned}$ |
| $S_{\text {adf }}$ | Survival probability of adult females | $\begin{aligned} & \text { Beta }(36.45,2.70) \\ & m u=0.93, s d=0.02 \end{aligned}$ |
| $S_{\text {adm }}$ | Survival probability of adult males | $\begin{aligned} & \text { Beta }(47.20,6.01) \\ & m u=0.89, s d=0.04 \end{aligned}$ |
| $\sigma_{s a}$ | Standard deviation for temporal variance of subadult survival | Uniform (0, 4) |
| $\sigma_{\text {ad }}$ | Standard deviation for temporal variance of adult survival | Uniform (0, 4) |
| $\beta$ | Regression coefficient | Normal (0, 10) |
| $\boldsymbol{r}_{\boldsymbol{f}}$ | Recovery probability for females | Uniform (0, 1) |
| $r_{m}$ | Recovery probability for males | Uniform (0, 1) |
| $\boldsymbol{p}_{f d}$ | Recapture probability for females and offspring | Uniform ( 0,1 ) |
| $\boldsymbol{p}_{\text {sa }}$ | Recapture probability for subadults | Uniform (0, 1) |
| $\boldsymbol{p}_{\text {am }}$ | Recapture probability for adult males | Uniform (0, 1) |
| $\boldsymbol{\beta}_{\text {year }}$ | Year fixed effect term for recapture probability | Normal (0, 10) |

Table SM2. Point estimates of total survival (includes natural and harvest mortality) from capture-recapture studies for polar bears. These values were used to generate informative priors for survival in a multi-state capture-recapture-recovery model for polar bears in Davis Strait. Further details on their use in the main text (Methods - Model implementation, fit, selection). Table adapted from supplementary table S3 in Regehr et al. (2018).

| Subpopulation | Subadult Females | Adult Females | Subadult Males | Adult Males |
| :---: | :---: | :---: | :---: | :---: |
| Baffin Bay ${ }^{1}$ | NA | 0.95 | NA | 0.87 |
| Davis Strait - Central ${ }^{2}$ | 0.92 | 0.95 | 0.89 | 0.94 |
| Davis Strait - North ${ }^{2}$ | 0.9 | 0.94 | 0.87 | 0.92 |
| Davis Strait - South ${ }^{2}$ | 0.92 | 0.95 | 0.89 | 0.94 |
| Gulf of Boothia ${ }^{3}$ | 0.9 | 0.92 | 0.88 | 0.92 |
| Kane Basin ${ }^{1}$ | 0.73 | 0.95 | 0.52 | 0.87 |
| Lancaster Sound ${ }^{4}$ | 0.88 | 0.94 | 0.79 | 0.89 |
| McClintock Channel ${ }^{5}$ | 0.90 | 0.90 | 0.90 | 0.88 |
| Northern Beaufort Sea ${ }^{6}$ | 0.91 | 0.91 | 0.83 | 0.83 |
| Norwegian Bay ${ }^{4}$ | 0.88 | 0.94 | 0.79 | 0.89 |
| Southern Beaufort Sea ${ }^{7}$ | 0.92 | 0.95 | 0.87 | 0.93 |
| Southern Hudson Bay ${ }^{8}$ | 0.92 | 0.91 | 0.86 | 0.86 |
| Viscount Melville ${ }^{9}$ | 0.91 | 0.91 | 0.77 | 0.77 |
| Western Hudson Bay ${ }^{10}$ | 0.82 | 0.94 | 0.75 | 0.90 |
| Chukchi Sea ${ }^{11}$ | 0.79 | 0.90 | 0.71 | 0.89 |

1. SWG (Scientific Working Group to the Canada-Greenland Joint Commission on Polar Bear). Re-Assessment of the Baffin Bay and Kane Basin Polar Bear Subpopulations: Final Report to the Canada-Greenland Joint Commission on Polar Bear. 31 July 2016: x + 636 pp (2016).
2. Peacock, E., Taylor, M. K., Laake, J. \& Stirling, I. Population ecology of polar bears in Davis Strait, Canada and Greenland. J Wild Manage 77, 463-476 (2013).
3. Taylor, M. K., Laake, J., McLoughlin, P. D., Cluff, H. D. \& Messier, F. Demography and population viability of polar bears in the Gulf of Boothia, Nunavut. Mar Mamm Sci 25, 778-796 (2009).
4. Taylor, M. K., Laake, J., McLoughlin, P. D., Cluff, H. D. \& Messier, F. Markrecapture and stochastic population models for polar bears of the high Arctic. Arctic 61, 143-152 (2008).
5. Taylor, M. K., Laake, J., Mcloughlin, P. D., Cluff, H. D. \& Messier, F. Demographic parameters and harvest-explicit population viability analysis for polar bears in M'clintock Channel, Nunavut, Canada. J Wildl Manage 70, 16671673 (2006).
6. Stirling, I., McDonald, T. L., Richardson, E. S., Regehr, E. V. \& Amstrup, S. C. Polar bear population status in the northern Beaufort Sea, Canada, 1971-2006. Ecol Appl 21, 859-876 (2011).
7. Regehr, E. V., Hunter, C. M., Caswell, H., Amstrup, S. C. \& Stirling, I. Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. J Anim Ecol 79, 117-127 (2010).
8. Obbard, M. E., McDonald, T. L., Howe, E. J., Regehr, E. V. \& Richardson, E. S. Polar Bear Population Status in Southern Hudson Bay, Canada. U.S. Geological Survey Administrative Report, Reston, Virginia, USA., 32 pp (2007).
9. Taylor, M. K., Laake, J., Cluff, H. D., Ramsay, M. \& Messier, F. Managing the risk from hunting for the Viscount Melville Sound polar bear population. Ursus 13, 185-202 (2002).
10.Lunn, N. J. et al. Demography of an apex predator at the edge of its range: impacts of changing sea ice on polar bears in Hudson Bay. Ecol Appl 26, 13021320 (2016).
10. Regehr, E. V. et al. Integrated population modeling provides the first empirical estimates of vital rates and abundance for polar bears in the Chukchi Sea. Scientific Reports 8, 16780 (2018).

## Supplementary Results

## Prior sensitivity analysis

To evaluate the sensitivity of our parameter estimates to the choice of priors, we fit the "top" model (M2) using informative (Beta distributions; Table SM1) and uninformative (Uniform ( 0,1 )) priors and compared the resulting estimates and posterior distributions. Results generated from the model initialized with uninformative priors were not used for making inference. We report the results below with direct comparisons.

## Additional analysis - time constant and fixed effect models

To explore more parsimonious models, we compared our top model ( M 2 ) to one with the same age-sex structure assuming survival is constant over time. Such models are more commonly applied in the polar bear literature often due to data limitations. In most cases, sample size, the number of consecutive sampling years, and/or the duration between sampling periods precludes more in-depth exploration of temporal variation (e.g. year random effects) in polar bear survival. Our DS dataset was robust and allowed us to explore temporal variation in survival, which is more biologically accurate. However, we wanted to fully evaluate our top model's performance against models more commonly used in polar bear survival. This model included the same general structure as model M2 but did not include year random effects on subadult or adult survival (model M2X). We do not use this comparison for inference but report the results below with direct comparisons of the posterior estimates and distributions with our random effects top model (M2). All models were initialized using the same prior distributions and MCMC sampling specifications in JAGS (see Methods: Model implementation, fit, and evaluation).

## Prior sensitivity analysis

Table SR1. Results of a prior sensitivity analysis comparing parameter estimates from Model M2 initialized with informative priors for adult and subadult survival compared with estimates from Model M2U initialized with uninformative (uniform) priors for adult and subadult survival. Model M2 includes the best fit model structure for survival, recovery, and recapture probabilities without environmental covariates. Demographic parameters are reported as the posterior mean, standard deviation, and 95\% Bayesian credible intervals (CRI) on the probability scale for averages over time. Temporal variance estimates are reported on the logit scale.

|  | Model M2: informative priors for adult <br> and subadult survival |  | Model M2U: uninformative priors for <br> adult and subadults |  |  |  |
| :--- | :---: | :---: | :---: | :--- | :---: | :---: | :---: |
| Parameter | Mean | SD | $95 \%$ CRI | Mean | SD | $95 \%$ CRI |
| Offspring survival | 0.794 | 0.0353 | $(0.723,0.861)$ | 0.793 | 0.036 | $(0.721,0.862)$ |
| Subadult survival | 0.873 | 0.0230 | $(0.826,0.914)$ | 0.873 | 0.022 | $(0.827,0.913)$ |
| Adult survival | 0.871 | 0.009 | $(0.853,0.892)$ | 0.869 | 0.010 | $(0.849,0.888)$ |
| Male recovery | 0.248 | 0.017 | $(0.215,0.282)$ | 0.247 | 0.016 | $(0.216,0.281)$ |
| Female recovery | 0.072 | 0.010 | $(0.053,0.093)$ | 0.072 | 0.010 | $(0.053,0.093)$ |
| Temporal variance: subadult survival | 0.236 | 0.336 | $(0.0019,1.093)$ | 0.217 | 0.239 | $(0.0003,0.894)$ |
| Temporal variance: adult survival | 0.048 | 0.059 | $(0.000007,0.215)$ | 0.047 | 0.064 | $(0.0001,0.219)$ |

Figure SR1. Density plots of uniform (uninformative; gray line) and Beta (informative; blue line) prior distributions for subadult and adult polar bear survival developed using the mean and standard deviation of the mean across previous polar bear survival studies following the approach of Regehr et al. 2018 (see also Table SM1 and Table SM2).


Figure SR2. Posterior distributions of subadult and adult survival from multistate model (M2) initialized with either uninformative (Uniform ( 0,1 ); gray line) or informative (Table SM1; blue line) priors for Davis Strait polar bear capture-recapture-recovery data.



## Additional analysis - time constant and fixed effect models

Table SR2. Parameter estimates from the top model for Davis Strait polar bears with data from 2005-2018. Demographic parameters are reported as the posterior mean, standard deviation, and 95\% Bayesian credible intervals (CRI) on the probability scale for averages over time. Temporal variances are reported on the logit scale.

|  | Model M2: includes year random <br> effects for adult and subadult <br> survival |  |  | Model M2X: time-constant survival <br> for adult and subadults |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Parameter | Mean | SD | $95 \%$ CRI | Mean | SD | $95 \%$ CRI |
| Offspring survival | 0.794 | 0.0353 | $(0.723,0.861)$ | 0.788 | 0.035 | $(0.717,0.857)$ |
| Subadult survival | 0.873 | 0.0230 | $(0.826,0.914)$ | 0.873 | 0.014 | $(0.845,0.898)$ |
| Adult survival | 0.871 | 0.009 | $(0.853,0.892)$ | 0.870 | 0.007 | $(0.856,0.884)$ |
| Male recovery | 0.248 | 0.017 | $(0.215,0.282)$ | 0.251 | 0.017 | $(0.219,0.286)$ |
| Female recovery | 0.072 | 0.010 | $(0.053,0.093)$ | 0.072 | 0.010 | $(0.054,0.094)$ |
| Temporal variance: subadult survival | 0.236 | 0.336 | $(0.0019,1.093)$ |  |  |  |
| Temporal variance: adult survival | 0.048 | 0.059 | $(0.000007,0.215)$ |  |  |  |


[^0]:    ${ }^{1}$ The MOUs were replaced in 2019 by the Nunavut Polar Bear Co-Management Plan

[^1]:    ${ }^{2}$ (we used Bell 206 Long Ranger, Bell 407 or AS350 B2 AStar helicopters throughout this study)

