

**Population Ecology of Polar Bears in Davis Strait, Canada and Greenland**

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## 1 **Summary**

- 2 1. Until recently, the sea ice habitat of polar bears was understood to be variable, but  
3 environmental variability was considered to be cyclic or random, rather than progressive.  
4 Harvested populations were believed to be at levels where density effects were considered  
5 unimportant relative to harvest pressure. Because it is now apparent that polar bear  
6 demography can also be influenced by progressive change in the environment, and some  
7 populations have recovered to higher densities from historically lower numbers, a broader  
8 suite of factors should be considered in demographic studies and management.
- 9 2. We analyzed 35 years of capture and harvest data from the polar bear population in Davis  
10 Strait, including data from a new study (2005–2007), to quantify its current demography. We  
11 estimated the population size in 2007 to be  $2,158 \pm 180$  (SE), a likely increase from the  
12 1970s.
- 13 3. We detected variation in survival, recruitment and age-structure of polar bears from  
14 geographic sub-regions of Davis Strait. Survival and reproduction of bears in southern Davis  
15 Strait was greater than in the north, probably because of a concurrent dramatic increase in  
16 harp seals in Labrador. The most supported survival models contained a geographic variable  
17 and a temporal factor. Survival models, in which summer sea ice concentration or harp seal  
18 numbers was the single ecological co-variate, were not supported, in comparison to the more  
19 general models. Our estimates of declining harvest recovery rate of marked bears, and  
20 increasing total survival, suggest that the rate of harvest has declined over time.
- 21 4. *Synthesis and applications.* Low recruitment rates, average adult survival rates and high  
22 population density, in an environment of high prey density, but deteriorating and variable ice  
23 conditions, currently characterize the Davis Strait population of polar bears. Low

24 reproductive rates may reflect negative effects of higher densities or the worsening ice  
25 conditions. The current level of recorded harvest appears sustainable, but the population is no  
26 longer increasing.

27 **Key-words:** Arctic, harp seal, harvest, density effects, mark-recapture, population demography,  
28 sea ice, *Ursus maritimus*, wildlife management

## 29 Introduction

30 There has been a long history of demographic assessments of polar bear *Ursus maritimus*  
31 (Phipps 1774) populations (e.g. Stirling, Calvert & Andriashek 1980; Taylor *et al.* 2009). A  
32 primary objective of these studies was to estimate sustainable harvest (Taylor *et al.* 1987),  
33 because hunting was considered to be the primary source of mortality of polar bears. Although  
34 regulation of harvest remains a vital tool for management (Amstrup *et al.* 2008), management for  
35 this species should consider all sources of risk. Threats to polar bears also include reduced sea  
36 ice due to climate warming (Stirling & Derocher 1993). The availability of annual sea ice in the  
37 primary feeding areas of polar bears is of critical importance because polar bears largely require  
38 the ice as a platform from which to hunt their primary prey (Stirling & Derocher 1993; Stirling,  
39 Lunn & Iacozza 1999). Other considerations for polar bear population dynamics include density-  
40 dependent effects (Derocher & Taylor 1994) and the abundance of their marine mammal prey  
41 (Stirling 2002).

42 Reductions in vital rates and habitat decline have been correlated in three populations of  
43 polar bears: Western Hudson Bay (Regehr *et al.* 2007) and the Northern (Stirling *et al.* In Press)  
44 and Southern (Regehr *et al.* 2010) Beaufort seas. Studies have found significant relationships  
45 between ice habitat decline and reductions in natality (Stirling, Lunn & Iacozza 1999), body  
46 condition (Stirling, Lunn & Iacozza 1999; Rode *et al.* 2010), survival rates (Regehr *et al.* 2007)

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47 and population size (Regehr *et al.* 2007). Polar bear populations in Hudson Bay, Davis Strait,  
48 Foxe Basin and Baffin Bay (Fig. 1) have a seasonal-ice ecology (Amstrup, Marcot & Douglas  
49 2008), where ice melts completely so that the bears must spend autumn months ashore. Another  
50 prediction in a scenario of climate warming is the increased duration that bears must spend on  
51 land during the increasing open water period (Stirling & Derocher 1993; Stirling & Parkinson  
52 2006). In Western Hudson Bay, the number of bears defined as ‘problems’ on land has increased  
53 (Stirling & Parkinson 2006) and in Foxe Basin, the number of defense kills has increased  
54 (Peacock *et al.* 2010). Concurrently, some populations of polar bears have increased in density,  
55 from earlier over-exploitation in response to harvest restrictions in effect since the 1960s  
56 (Prestrud & Stirling 1994; Derocher 2005; Amstrup, Stirling & Lentfer 1986); more abundant  
57 populations in poor-ice years or whose individuals are in poorer condition, likely exacerbate  
58 human-bear interactions. Thus density, harvest levels, environmental change and their  
59 interactions are important to consider for understanding polar bear population ecology; this  
60 broader perspective is also warranted for harvest management.

61 The abundance, demography and status of polar bears in the Davis Strait population have  
62 not been assessed since the 1970s (Stirling & Kiliaan 1980; Stirling, Calvert & Andriashek  
63 1980). In recent years, local people throughout Davis Strait reported seeing more bears during all  
64 seasons (Kotierk 2009a; A. Simpson, J. Mercurasuk, Torngat Mountains National Park, personal  
65 observations). Their conclusion that the population was increasing was supported by anecdotal  
66 scientific observations (Stirling & Parkinson 2006). A relatively low harvest, and a large increase  
67 in the abundance of harp seals (*Pagophilus groenlandicus*), which are a particularly important  
68 prey species for Davis Strait polar bears (Iverson, Stirling & Lang 2006), were suggested as  
69 factors which have contributed to an increase in polar bear abundance (Stirling & Parkinson

70 2006). In addition, after a period of generally cool temperatures during which the sea ice was  
71 relatively stable (Skinner *et al.* 1998), the overall amount of sea ice declined and the breakup  
72 date became progressively earlier (Stirling & Parkinson 2006; See Appendix, Fig. S1 in  
73 Supporting Information).

74 We conducted a new capture study of polar bears in Davis Strait from 2005–2007. We  
75 pooled polar bear mark-recapture and harvest recovery data from 1974 through 2009 and  
76 estimated current rates of reproduction, survival and population abundance, and population  
77 growth rate. To examine survival rates in an ecological context, we considered the effects of  
78 geography, and time series effects of harp seal abundance and ice conditions on annual survival,  
79 and how the rates have changed over time. We further discuss the impacts of harvest rate and  
80 population density. Finally, we discuss management of abundant populations of polar bears that  
81 may be experiencing increased stress from both density effects and habitat decline.

## 82 **Materials and methods**

### 83 STUDY AREA

84 Polar bears in Davis Strait are distributed between Canada and Greenland, from Cape Dyer on  
85 eastern Baffin Island (66° N) south to northern Newfoundland (Fig. 1; Taylor *et al.* 2001).  
86 During winter and spring, Davis Strait polar bears occur on approximately 420,000 km<sup>2</sup> of sea  
87 ice (Taylor & Lee 1995), in Davis Strait proper, the Labrador Sea, and west to Ungava Bay and  
88 eastern Hudson Strait, in Nunavut and Québec (Taylor *et al.* 2001). Using cluster analysis of  
89 polar bear movements from satellite telemetry, Taylor *et al.* (2001) concluded that the boundary  
90 between the Davis Strait and Baffin Bay populations was distinct, and movements between  
91 Davis Strait and Foxe Basin were sufficiently infrequent to constitute a demographic

92 discontinuity satisfactory for subpopulation management purposes. From August through mid-  
93 November, the area is ice-free and polar bears concentrate on offshore islands and coastal strips  
94 of land along the Canadian coast. This concentration provides research access to the entire  
95 population.

96         New genetic analyses using clustering methods (Obbard *et al.* 2010) suggest mating-  
97 fidelity of polar bears to geographic sub-regions: Southern Davis Strait, south of Hudson Strait  
98 (SD); central Davis Strait, south of Cumberland Sound on Baffin Island (CD); and Northern  
99 Davis Strait (ND) on Baffin Island, north of Cumberland Sound (Fig. 1). Similar to the  
100 conclusions of previous studies (Taylor & Lee 1995; Taylor *et al.* 2001), we do not suggest that  
101 these sub-regions are demographically independent or genetically divergent. Also, marked  
102 individuals, in the current study, moved among these sub-regions (Fig. 2). However, the sub-  
103 regions differ in that: 1) the harp seal increase has occurred largely in SD (DFO 2010), and harp  
104 seals constitute a significantly larger part of polar bear diet in SD compared to the more northerly  
105 sub-regions (Iverson, Stirling & Lang 2006); 2) harvest regimes in SD differ from those in CD  
106 and ND; and 3) any exchange between polar bears in Davis Strait and Baffin Bay is more likely  
107 to occur in ND than in other sub-regions of Davis Strait. Thus, we felt there were sufficient  
108 ecological reasons to also evaluate whether demography varied within these sub-regions.

#### 109 CAPTURE AND RECAPTURE DATA

110 From August to October 2005–2007, we searched for, captured and marked polar bears on the  
111 coastline and offshore islands of Davis Strait. We also conducted inland transects several times a  
112 day, because polar bears can be found further inland (e.g. Taylor *et al.* 2005). We found very few  
113 bears inland throughout Davis Strait, likely because the steep terrain along the coast.

114 We captured polar bears from a Bell 206L helicopter (in compliance with Québec  
115 Certificat de bon soin au animaux, CPA-Faune: 05-00-21, 06-00-08 and 07-00-08). Every bear  
116 observed was captured, providing that it was safe to do so. Bears were immobilized with Pneu-  
117 darts (dependent young) or Palmer cap-chur darts (subadults and adults) with the drug Zoletil ®  
118 at 5 mg/kg (Stirling, Spencer & Andriashek 1989). Each immobilized bear was given a unique  
119 number (ear tags and lip tattoo). Additional data collected for the purposes of this study included  
120 numbers from recaptured bears, a field age, family status, sex, location and date of capture. A  
121 premolar tooth was collected to determine age from cementum layers (Calvert & Ramsay 1998).

122 We combined this new capture information with similar data collected in Davis Strait  
123 since 1974. Between 1974 and 1979, capture work for the purpose of population inventory was  
124 conducted on the spring sea ice over various subsets of the Davis Strait subpopulation area (I.  
125 Stirling, unpublished data; Stirling, Calvert & Andriashek 1980; Stirling & Kiliaan 1980).  
126 Capture data were also collected in both the spring and fall (1991–1994 and 1997–1999) for  
127 satellite-telemetry studies (I. Stirling, unpublished data; Taylor *et al.* 2001). Incidental captures  
128 occurred throughout the study period (Government of Newfoundland and Labrador, unpublished  
129 data).

#### 130 HARVEST AND RECOVERY DATA

131 We compiled polar bear harvest data from Davis Strait from Greenland, Québec, Nunavut (prior  
132 to 1999, the Northwest Territories) and Newfoundland and Labrador, 1974–2009. Officers  
133 recorded identification numbers, sex and location of bears harvested by hunters. We assume all  
134 harvested bears with tags were reported, because the harvest is monitored and reporting has  
135 occurred for several decades (Prestud & Stirling 1994). It is expected that hunters neither

136 preferentially shoot nor avoid tagged animals, because the ear tags are not visible at a distance.  
137 Any violation of this assumption would negatively bias estimates of natural survival. We used all  
138 harvest recovery events of bears marked in Davis Strait, including those marked in Davis Strait  
139 but harvested in neighboring populations. The Burnham (1993) survival estimation model  
140 incorporates reported recoveries from a broader geographic area than the marking study area  
141 (Cooch & White 2007).

#### 142 MARK-RECAPTURE-RECOVERY ANALYSIS

143 We estimated capture ( $p$ ), harvest recovery ( $r$ ), and survival ( $S$ ) probability of marked  
144 individuals using the model of Burnham (1993), which combines live recaptures and dead  
145 recoveries of marked animals. We constructed user-specified submodels for each parameter  
146 using environmental covariates, and sex and age-class groupings in the RMark interface (Laake  
147 & Rexstad 2007) using R (R Development Core Team 2008). Via RMark, we ran models in  
148 MARK (White & Burnham 1999). We built capture histories with all initial captures (1974–  
149 2007), and included recapture events during the period during which capture effort was  
150 systematic and most bears were available for capture (2005–2007), so as to not bias estimates of  
151  $p$  and subsequently  $S$ , with years of unsystematic effort (1974–2004; Taylor *et al.* 2005). Harvest  
152 recoveries of marked individuals were included from April 1974–October 2009 (2 years post the  
153 last marking period).

154 We evaluated models where the fidelity parameter ( $F$ ) was allowed to be estimated with  
155 no constraints, to vary by geography, or was fixed at 1. When  $F$  is fixed at 1, all alive bears are  
156 assumed to be in the surveyed area during each capture occasion. Between occasions bears can  
157 move out of the survey and be harvested, but if they survive it is assumed they move back into

158 the survey prior to the next capture occasion. We fit submodels for  $S$ ,  $r$ , and  $p$  with various  
159 groupings of sex and age-classes. For  $S$ , we modeled five age-classes: cubs-of-the-year (COY);  
160 yearlings (1 year old); subadults (2–4 years old); adults (5–20); and senescent adults ( $\geq 21$ ).  
161 Bears were assigned age-classes (*ageclass*) based on: 1) known age (captured as COY or  
162 yearling); 2) age derived from tooth in the laboratory; or 3) age-class deduced in the field. We  
163 are unaware of any systematic bias in terms of which bears have or do not have laboratory ages.  
164 Preliminary analyses suggested that  $S$  and  $r$  varied between sexes only for independent bears ( $> 2$   
165 years old); this effect is identified by the model term *non-juv:male*. Preliminary models, in which  
166 capture probabilities of unencumbered and encumbered adult females were estimated separately,  
167 were not supported. Therefore, we modeled  $p$  with three sex-age groups: 1) adult females and  
168 dependent young (*femandyoung*); 2) subadult males and females (*subadult*); and 3) adult males.  
169 We also built submodels for  $p$  to allow for time variation between 2005, and 2006 and 2007  
170 combined (*time*); in preliminary modeling we found little difference in  $p$  between 2006 and  
171 2007. Capture probability was fixed at zero for 1974–2004 (see above). We built submodels for  
172  $S$ ,  $p$ , and  $r$  to examine whether variation in model parameters could be explained by the three  
173 geographic sub-regions (*Geo*); bears were assigned to a sub-region by location of their first  
174 capture.

175 We included a factor *timeperiod* (1974–1978, 1979–1983, 1984–1988, 1989–1993,  
176 1994–1998, 1999–2008) when building submodels for  $S$  and  $r$  to examine temporal variation.  
177 This time-binning variable would include variation that could not be explained solely by  
178 ecological temporal covariates (*ice*, *harp*), or by other factors for which there no data (e.g.  
179 changes in population density). We used the mean weekly estimate of total ice concentration in  
180 Davis Strait from 14 May to 15 October (Archives of the Canadian Ice Service,

181 glaces.ec.gc.ca/) as the covariate *ice* (see Fig S1); this metric encompasses variation in the length  
182 of the ice-free season. The North Atlantic population of harp seals has increased over the last 30  
183 years from 2.7 to 6.8 million (DFO 2010). We used this time series of seal abundance as the  
184 covariate, *harp*, in our submodels for *S*. The harp seal abundance time series is from whelping  
185 patches in the southern sub-region (SD) of Davis Strait. Seal numbers are not available in the  
186 other sub-regions of Davis Strait, although local knowledge suggests that the migratory harp  
187 seals have also been increasing in CD and ND (E. Peacock, minutes from meetings with Hunting  
188 and Trapping Organizations of Pangnirtung, Kimmirut and Iqaluit, Nunavut, January 2009). The  
189 variables *ice* and *harp* have explicit relationships with time; *timeperiod* encompasses changes in  
190 *ice* and *harp*. As a result, *time* and *harp* are not used in models together with *timeperiod*. As the  
191 explicit relationship between *harp* and *geo* is not known, these variables were used together in  
192 some models.

193 We used the *median* approach to calculate over-dispersion based on our most general  
194 model:  $S(\text{timeperiod} + \text{ageclass} * \text{Sex})r(\text{timeperiod} + \text{ageclass} + \text{nonjuv:male})p(\text{femandyoung} +$   
195  $\text{suibadult} + \text{time})F(1)$ . We used the logit link function to link the estimated real and beta  
196 parameters for all submodels. We rated models using Akaike's Information Criterion (Burnham  
197 & Anderson 2002) with correction for sample size (AICc), and provide model-averaged  
198 estimates for models with  $\Delta\text{AICc} < 10$ . We assessed model competitiveness (for the survival  
199 sub-models) for those models with  $\Delta\text{AICc} < 2$ , by also examining the associated reduction in  
200 deviance of each model with additional parameters, relative to the top model (Burnham and  
201 Anderson 2002; Arnold 2010). We used Wald's statistic ( $\beta/\text{SE}$ ;  $\alpha = 0.05$ ) as a guide for the  
202 relative importance of the ecological variables of interest (*geo*, *timeperiod*, *harp* and *ice*) in  
203 explaining variation in total survival (Faraway 2006: 122).

204 We calculated natural survival ( $S_N$ ) such that  $\hat{S}_N = \hat{S} + (1 - \hat{S})\hat{r}$ . The variance of  $S_N$  was  
 205 calculated using the delta method (Seber 1982):

$$206 \quad \hat{\text{var}}(\hat{S}_N) = \hat{\text{var}}(\hat{S})(1 - \hat{r})^2 + \hat{\text{var}}(\hat{r})(1 - \hat{S})^2 + 2 \hat{\text{cov}}(\hat{S}, \hat{r})(1 - \hat{r})(1 - \hat{S})$$

207 We developed abundance estimates as per Taylor *et al.* (2002) and McDonald & Amstrup  
 208 (2001), where the number captured in ( $n$ ) is divided by the estimated recapture probability ( $\hat{p}$ ):

$$209 \quad \hat{N} = \frac{n}{\hat{p}} \text{ (this is the general model, but separate estimates partitioned } n \text{ and } p \text{ based on year, age-}$$

210 class and sub-region). We estimated variance following Huggins (1989) and Borchers *et al.*

$$211 \quad (1998): \hat{\text{var}}(\hat{N}_i) = \frac{n_i(1 - \hat{p}_i)}{\hat{p}_i^2} + \frac{\hat{N}_i^2}{\hat{p}_i^2} \hat{\text{var}}(\hat{p}_i). \text{ We provided abundance estimates for the three}$$

212 geographic sub-regions of Davis Strait, as  $p$  varied among these sub-regions. Total estimated  
 213 population size was the sum of estimates for each sub-region and the variance estimator included  
 214 covariances:

$$215 \quad \hat{N}_i = \sum_j \frac{n_{ij}}{\hat{p}_{ij}} \quad \text{and} \quad \hat{\text{var}}(\hat{N}_i) = \sum_j \frac{n_{ij}(1 - \hat{p}_{ij})}{\hat{p}_{ij}^2} + \sum_j \sum_{j'} \frac{n_{ij}n_{ij'}}{\hat{p}_{ij}^2 \hat{p}_{ij'}^2} \hat{\text{cov}}(\hat{p}_{ij}, \hat{p}_{ij'})$$

216 The above equation was also used to combine population estimates derived for separate sex-age  
 217 groups which had different  $p$ .

#### 218 AGE STRUCTURE

219 We compiled age structures using polar bears captured and aged during the two population  
 220 inventories, 1974–1979 ( $n = 271$ ) and 2005–2007 ( $n = 1,628$ ); cubs of un-aged adult females  
 221 were not included. Because we did not estimate capture probabilities for the 1970s, we cannot

222 present age distributions that are adjusted for capture rate. Additionally, because capture teams  
223 could not search for polar bears in the spring pack ice, the relationship of the age structure of  
224 bears available to capture on the spring time sea ice to the actual population age structure is  
225 ambiguous. Thus, we did not statistically compare the age structures of captured animals between  
226 the 1970s and 2000s. We do provide the graphs for comparisons to age distributions of capture  
227 samples (also not adjusted for capture probability) for other polar bear populations, which are  
228 believed to have increased in size (Amstrup, Stirling & Lentfer 1986; Derocher 2005). We  
229 compared the age structure of polar bears captured 2005–2007, north and south of Hudson Strait,  
230 by dividing the number of male and females captured, by geographic-, age- and sex-specific  
231 estimates of capture probability. These age frequencies were compared with Chi-square tests for  
232 independence ( $\alpha = 0.05$ ). We compared mean ages of independent bears in north and south of  
233 Hudson Strait with Mann-Whitney U tests ( $\alpha = 0.05$ ).

#### 234 REPRODUCTION

235 We calculated reproductive parameters for polar bears in Davis Strait from the live-capture data  
236 collected 2005–2007. We calculated mating interval and age-specific litter production rate (LPR)  
237 according to the formulation provided by Taylor, Carley & Bunnell (1987) using program  
238 VITAL RATES (Taylor, Kuc & Abraham 2000). The formulation of Taylor, Carley & Bunnell  
239 (1987) estimates the litter production rate of females available to mate (i.e. not encumbered with  
240 cubs) in each year, and is appropriate for annual population projection for animals with three-  
241 year reproductive cycles. We also calculated mean age-specific litter-produced rate (LP)  
242 according to the formulation provided by Stirling, Calvert & Andriashek (1980) for all females  
243 (including females unavailable to mate), 4–27 years of age. We provide formulations of LPR and

244 LP to facilitate comparisons to the published literature on polar bears, which uses both  
245 approaches. We determined the probability of first birth at each age from the age-specific LPR  
246 and the standing age distribution; the average age of first reproduction is then the average age  
247 weighted by the probability of first birth at each age (Taylor, Carley & Bunnell 1987). Our  
248 estimate of  $m(x)$ , adult per capita recruitment rate, is the average number of offspring (both  
249 sexes) accompanying adult females aged 7+. This value is an abstraction because polar bears  
250 have a three-year reproduction cycle due to extended parental care;  $m(x)$  is provided to facilitate  
251 comparison with other birth-pulse species in which mature females produce young each year. For  
252 each year, COY litter size (LS) was calculated as the number of COY per number of females  
253 with COY. We compared LS among geographic sub-regions and years with Kruskal-Wallis tests  
254 on ranks, and Dunn's method for pair-wise comparisons. We assessed variation of LS with age  
255 of mother using polynomial regression, using the square root transformation of litter size. Using  
256 the age-specific dataset, we determined that there was no trend in COY litter size with the age of  
257 the mother. Thus to calculate mean LS, we used the entire dataset of females with COY. We did  
258 not compare reproductive parameters between the 1970s and 2000s, because data were collected  
259 during different seasons; Derocher & Stirling (1996) found, in Western Hudson Bay, there to be  
260 significant cub mortality from spring to fall.

#### 261 POPULATION GROWTH RATE

262 We used the individual-based stochastic PVA program RISKMAN (Taylor *et al.* 2003) to  
263 estimate natural and harvested population growth ( $\lambda_n$ ,  $\lambda_h$ ). RISKMAN is a PVA that can  
264 specifically examine population growth (e.g. McLoughlin *et al.* 2003; Howe, Obbard & Shaefer  
265 2007; Taylor *et al.* 2005) for animals with multiple-year reproduction cycles. See Taylor, Carley

266 & Bunnell (1987) and Taylor *et al.* (1987; 2003) for mathematical details. While we estimated  
267 lambda for the entire population, we did not use an estimate of  $S_M$ , as an input, which was  
268 generated from a model where both  $r$  and  $S$  had no geographic component, because this was a  
269 very low performing model ( $\Delta AICc = 28.3$ ). Rather, we used an average  $S_M$ , calculated from  $S_M$ 's  
270 of the three geographic sub-regions (from the model-averaged  $S$  and  $r$  from models  $\Delta AICc < 10$ ),  
271 weighted by estimated abundance in each geographic sub-region and for each age-sex class for  
272 2007. Because LS did not vary with age (see Results), we used the mean LS for females ages 4–  
273 27 (2005–2007), expressed as the proportion of mothers with one or two COY. We used LPR  
274 values calculated from a data set of adult females ages 5–27. The age of first reproduction was  
275 assumed to be 5. Females aged 7+ were assumed to reproduce litters at a mean adult LPR rate.  
276 The proportion of males at birth was estimated as the average over 2005–2007 of the proportion  
277 of males that were COY each autumn. We set whole litter survival to 1, i.e. assuming loss of  
278 litters is fully explained by estimated individual cub survival. We modeled the population growth  
279 from the stable age distribution determined by the vital rates. For simulations to estimate  $\lambda_h$ , we  
280 used the 5-year mean (2004–2009) harvest of polar bears from Davis Strait. We created a  
281 selectivity-vulnerability (to harvest) matrix which is a product of the empirical population  
282 standing age-sex distribution and an age-sex distribution of polar bears harvested from Davis  
283 Strait 1990–2006. We calculated annual  $\lambda_n$  and  $\lambda_h$  for each year of the simulation as the mean of  
284 2,500 geometric means of  $\lambda_n$  and  $\lambda_h$  for each of the 10 years of the simulation. Taylor *et al.*  
285 (2009) comprehensively explains how variance is modeled in RISKMAN; we assumed 80% of  
286 variance was sample variance and 20% environmental variance (White 2000). These simulations  
287 assume that the vital rates, and the variance of those rates, remain constant for the duration of the  
288 10-year simulation.

## 289 Results

### 290 CAPTURE AND RECOVERY DATA

291 We marked 1,518 individual polar bears during 2,128 capture events in 2005–2007 in Davis  
292 Strait (see Table S1). These figures include bears captured west of the management boundary  
293 with Foxe Basin (Fig. 1). The actual demographic location of this western boundary has not been  
294 ascertained with satellite-telemetry or tag return data (Taylor & Lee 1995; Taylor *et al.* 2001).  
295 Our data and other capture data from Foxe Basin (E. Peacock, unpublished data; M. Taylor  
296 unpublished data) suggest a distinct discontinuity in the late summer and early autumn  
297 distribution of polar bears east of Kimmirut, Nunavut (at approximately 69° W), i.e. west of the  
298 boundary suggested by Taylor *et al.* (2001).

299 We analyzed live-capture data consisting of 2,529 captures of 1,860 individuals (866  
300 females, 990 males) in Davis Strait, collected 1974–2007 (Fig. 1). We incorporated 145  
301 harvested bears (49 females, 95 males) that were marked in Davis Strait, as dead encounters (i.e.,  
302 recoveries), 1974–2009 (Fig. 2). Over this 35-year period, eight of the recoveries were harvested  
303 in Foxe Basin and 13 in Baffin Bay (including 1 by Greenlandic hunters). We compiled known  
304 ages or generated laboratory ages for 2,249 of 2,674 (84%) capture and recovery events.

### 305 MARK-RECAPTURE-RECOVERY MODELS

306 We found no over-dispersion ( $\hat{c} = 1$ ) with the general model, and no adjustments were made to  
307 parameter estimates. We present model-averaged estimates of all parameters, estimated over 27  
308 models where model  $\Delta\text{AICc} < 10$  (see Table S2). The four top models ( $\Delta\text{AICc} < 2$ ) of capture  
309 probability had a geographic component, with highest rates of capture in SD and lowest in ND

310 (see Table S3). Top models suggest that capture rates were consistently highest for adult males,  
311 followed by subadults and then adult females and dependent young, a finding consistent with  
312 other fall-time polar bear capture studies (e.g. Taylor *et al.* 2005). Model-averaged estimates of  
313 the probability of capture ranged from 0.14 (0.07–0.25, 95% CI) for adult females and dependent  
314 young in 2005 in ND to 0.51 (0.45–0.58) for adult males in SD in 2006–07.

315 Recovery rates varied by geography, dependent status and time period (see Fig. S2, Table  
316 S4). Recovery rates were highest for non-juvenile males, 1984–1988 in CD (0.48, 0.24–0.73)  
317 and lowest for juveniles and independent females in SD, 1999–2008 (0.08, 0.04–0.15). There  
318 was no consistent trend in recovery rates over the study period. However, disregarding the first  
319 time period 1974–1978, when harvest reporting was incomplete, recovery has generally declined  
320 from 1980 to 2008. A declining recovery rate, combined with increasing total survival (see  
321 below), suggests a declining rate of polar bear harvest from the 1980s to 2000s.

#### 322 SURVIVAL AND ABUNDANCE

323 The two most supported sub-models for total survival ( $\Delta AICc < 2$ ; cumulative weight, 0.78)  
324 included effects of time period (Fig. 3), age-class, sex (for non-juveniles) and geography (Table  
325 1, See Table S2). Both sub-models [(*ageclass + nonjuv:male + timeperiod*) and (*ageclass +*  
326 *nonjuv:male + timeperiod + geo*)] are competitive, because the addition of the single parameter  
327 (*geo*;  $\Delta AICc = 0.82$ ) is also accompanied by a reduction in model deviance (See Table S2).

328 Across all geographic sub-regions,  $S$  was highest for adult females and lowest for senescent  
329 males; all rates were lowest in ND. Estimates of  $S$  increased from 1974 to 2008 (Fig. 3; for  $S_N$   
330 see Fig. S3). In non-competitive models, *harp* supplants *timeperiod* in explaining variation in  $S$ .  
331 The influence of increasing harp seal abundance on survival appears first in a model with  $\Delta AICc$

332 = 5.5 (Table 1, See Table S2), and further, in an interaction with geography ( $\Delta\text{AICc} = 5.8$ ; See  
 333 Table S2). In these models, as seal abundance in Davis Strait increased, survival increased ( $\beta/\text{SE}$   
 334 for *harp*  $\geq 2.0$ ; Table 1). Polar bear survival increased with harp seal abundance at the lowest  
 335 rate in ND (logit coefficient = 0.10 (0.10, SE), = 0.20 (0.09), = 0.22 (0.08)). An  
 336 interaction between *harp* and *subadult* also appears in a non-competitive model ( $\Delta\text{AICc} = 6.3$ ;  
 337 see Table S2); this model would suggest the increase of seal abundance positively influenced  
 338 survival of non-subadults (adults and dependent young) to an extent 1.7 times larger than for  
 339 subadults ( = 0.14 (0.10), = 0.23 (0.09)).

340 A break-point regression ( $R^2 = 0.51$ ,  $P = 0.001$ ; see Fig. S1) indicated that a break in the  
 341 time series occurs between 1984 and 1985, with two significant and opposite trends in summer  
 342 ice concentration from 1974–1984 and 1985–2008 ( $y = 0.01x - 23.06$ ,  $R^2 = 0.52$ ,  $P = 0.01$ ;  $y_2 =$   
 343  $8.47 - 0.004x$ ,  $R^2 = 0.49$ ,  $P = 0.000$ ). The effect of total concentration of summer ice as a second-  
 344 order variable on polar bear survival first appears in a low-performing model with  $\Delta\text{AICc} = 7.91$   
 345 (Table 1, see Table S2); estimated logit coefficients suggest that our *ice* metric as a sole  
 346 ecological predictor variable is unimportant in modeling survival in this dataset (Table 1). Total  
 347 survival estimates (and 95% CIs) for adult female polar bears (for ND and SD) from the top  
 348 model that included both time and geographic effects ( $\Delta\text{AICc} = 0.82$ ) are plotted with *ice* and  
 349 *harp* to graphically show relationships (Fig. 4).

350 Model-averaged estimates of adult female  $S_N$  in 2008 for SD, CD and ND were 0.954  
 351 (0.913–0.977, 95% CI), 0.964 (0.916–0.985) and 0.936 (0.862–0.972), respectively (Table 2).  
 352 We estimated the abundance of polar bears in Davis Strait for 2007 to be 2,158 (1833–2542; see  
 353 Table S5).

## 354 AGE STRUCTURE

355 We built population age structures using information from 271 polar bears captured and aged in  
356 1974–1979, and from 1,628 in 2005–2007. The age structures of captured bears in Davis Strait  
357 appear to differ between the two decades, with older bears more represented in the capture  
358 sample in the 2000s compared to the 1970s (Fig. 5). The average age for polar bears > 2 years of  
359 age in the 2000s was 9.3 (0.1, SE) and in the 1970s, 7.9 (0.4). In 2005–2007, the age structure  
360 (weighted by capture probability) of both males (See Fig. S4;  $\chi^2 = 35.17$ ,  $df = 23$ ,  $p = 0.01$ ) and  
361 females (See Fig. S5;  $\chi^2 = 28.87$ ,  $df = 18$ ,  $p = 0.01$ ) differed between north and south of Hudson  
362 Strait, with a trend towards older bears in the north. The mean age of female bears > 2 years old  
363 between the two regions was not different (Mann-Whitney  $U = 26,772$ ,  $p = 0.50$ ,  $n = 371$ ). Males  
364 > 2 years old north of Hudson Strait were older ( $10.2 \pm 0.2$ ) than bears south of Hudson Strait  
365 ( $9.2 \pm 0.4$ ; Mann-Whitney  $U = 48,427$ ,  $P = 0.001$ ,  $n = 557$ ).

## 366 REPRODUCTION

367 During 2005–2007, two four-year-old females were captured with COY litters, and the oldest  
368 mother captured with COY was 27 years old. Average age of first reproduction was  $5.33 \pm 0.78$   
369 (SE) years. We estimated mating interval as 1.8 (0.21) years. COY LS did not differ among years  
370 (Kruskal-Wallis,  $H = 1.63$ ,  $df = 2$ ,  $P = 0.44$ ). There was neither a linear nor a 2<sup>nd</sup>-order trend of  
371 LS with age of mother (ages 4–27;  $y = 0.001x + 1.53$ ,  $p = 0.93$ ;  $y = 0.001x^2 - 0.010x + 1.47$ ,  $p =$   
372  $0.86$ ;  $n = 90$  aged mothers with COY). Mean LS in Davis Strait in autumn was  $1.49 \pm 0.14$  ( $n =$   
373  $119$  COY litters). LS significantly differed among the three geographic sub-regions within Davis  
374 Strait (Kruskal-Wallis,  $H = 10.72$ ,  $df = 2$ ,  $P = 0.005$ ). However, the comparison (Dunn's method)  
375 of the pair of geographic sub-regions with the largest difference of ranks (SD with COY LS of

376  $1.71 \pm 0.08$  and ND with  $1.33 \pm 0.14$ ) was not statistically significant ( $Q = 1.96, p > 0.05$ ). Mean  
377 adult (ages 7–21) LPR (based on females available to mate) was  $0.44 \pm 0.11$  (SE; Table 3); LP  
378 (includes females unavailable to mate) was  $0.33 \pm 0.04$  (Table 3). The mean proportion of males  
379 in COY litters 2005–2007 was 0.55 (0.04, SE). The mean annual adult per capita recruitment rate  
380  $m(x)$  was 0.361 (SE=0.055) (Taylor *et al.* 1987).

#### 381 POPULATION GROWTH RATE

382 Using demographic parameters calculated from this study (see Table S6) and PVA,  
383 average  $\lambda_N$  over 10 years was 1.037 (0.01, SE). Using an annual harvest reflecting the legal  
384 quotas (Nunavut, 46; Greenland, 2; Newfoundland and Labrador, 6) and 5-year mean reported  
385 Québec harvest ( $13.4 \pm 2.1$  bears/year), current  $\lambda_t$  is 1.008 (0.01). Unreported harvest is not  
386 included in this assessment of population growth.

## 387 Discussion

#### 388 CURRENT POPULATION DEMOGRAPHY

389 We estimated the abundance of the Davis Strait polar bear population to be 2,158, which  
390 results in a relatively high population density of polar bears of approximately 5.1 bears/1,000  
391 km<sup>2</sup> of sea ice habitat (Taylor & Lee 1995). This density is higher than polar bear densities in  
392 other seasonal-ice populations, which are approximately 3.5 bears/1000 km<sup>2</sup> (Taylor & Lee  
393 1995; Taylor *et al.* 2005; Regehr *et al.* 2007; Obbard 2008).

394 Reproductive rates of polar bears vary greatly, even when comparing rates for  
395 populations within the same ecoregion and same season of capture. For example, the litter  
396 production rate for adult females in Davis Strait (2005–2007) is low (0.44) compared to western  
397 Hudson Bay (0.79; Aars *et al.* 2006) and Baffin Bay (1.0; Taylor *et al.* 2005), which have also

398 been measured in the fall. Our point estimate of COY litter size ( $1.49 \pm 0.14$ , SE) is the lowest of  
399 any other population studied in the fall ( $\bar{x} = 1.57 \pm 0.02$ ,  $n = 4$ ; Obbard *et al.* 2010; Peacock *et al.*  
400 2010). Low litter production rate is a function of higher numbers of unencumbered females  
401 and/or fewer females with COY (in the next year; Taylor *et al.* 1987). Estimates of low litter  
402 production rate from fall data may result from high whole-litter loss (poor cub survival) from  
403 spring to fall. This hypothesis is supported further by the short breeding interval estimated for  
404 Davis Strait (1.8 years; Ramsay & Stirling 1988; Taylor *et al.* 2005). Litter size differed  
405 significantly among all sub-regions in Davis Strait; in southern Davis Strait, litter size of COY  
406 (1.71) was greater, but not statistically, than the other sub-regions (1.33 in northern Davis Strait),  
407 possibly due to the greater availability of harp seals in the south.

408 Natural survival rates of adult female polar bears in Davis Strait as estimated for 2008  
409 ( $0.962 \pm 0.019$ , SE, weighted mean of sub-regions) are comparable with two other seasonal-ice  
410 populations: 0.953 (0.020) in Baffin Bay (Taylor *et al.* 2005) and 0.94 (0.01) in Western Hudson  
411 Bay (Regehr *et al.* 2007). In general, seasonal-ice populations appear to show lower natural  
412 survival rates ( $\bar{x} = 0.952 \pm 0.006$ , SE for adult females;  $n = 3$  populations including this study)  
413 than in populations where ice remains throughout the summer ( $\bar{x} = 0.967 \pm 0.007$ , SE;  $n = 6$ ;  
414 Obbard *et al.* 2010). Survival rates are consistently lower in northern Davis Strait than in other  
415 sub-regions (Table 2). Geographically disparate survival rates are likely the result of polar bears  
416 showing fidelity to local areas that have different ecological scenarios. There has been no  
417 concomitant dramatic increase in harp seals in ND, and there is higher harvest pressure on polar  
418 bears in the northern part of Davis Strait (in Nunavut than in Labrador and Québec). In Davis  
419 Strait, there is higher harvest pressure on younger bears; the mean age of bears in the harvest is  
420 6.9 (0.2, SE;  $n = 950$ ), thus lower estimated survival in a group of older bears (bears are older in

421 ND than SD) is not necessarily inconsistent. Throughout Davis Strait, COY natural survival rates  
422 are high (0.90–0.93), largely because the estimation of COY mortality from fall census to fall  
423 census means that COYs are actually yearlings for the winter-fall period of the survival year.  
424 Eighty percent of our captures of COY were from a fall census, so the COY natural survival rates  
425 do not reflect COY mortality from spring to fall. High COY survival may also be a function of  
426 the higher frequency of singleton versus twin litters.

427 It is important to note that the decision to model capture probability, and consequently  
428 survival and abundance, by geography, allowed us to account to some extent for violation of the  
429 assumption of temporary emigration, which likely differed by geography. Not including a  
430 geographic covariate would have resulted in lower survival estimates.

#### 431 CHANGES IN POPULATION DEMOGRAPHY

432 Our abundance estimate for Davis Strait polar bears is higher than the 1979 estimate of  
433 approximately 900 animals, which was the sum of separate estimates for southeast Baffin Island  
434 (Stirling, Calvert & Andriashek 1980) and Labrador (Stirling & Kiliian 1980). These earlier  
435 population estimates were derived from spring capture, and may be biased low if some portion of  
436 the population was consistently offshore on pack ice and unavailable for capture. The earlier  
437 studies also did not sample from Hudson Strait and Ungava Bay (Fig. 1). Consequently, we  
438 cannot directly compare the abundance estimates. The apparent increasing age in the population  
439 may reflect recovery from lower numbers due to increased survival, as observed in the Barents  
440 Sea after elimination of harvest (Derocher 2005), and in the southern Beaufort Sea after  
441 reduction of harvest (Taylor 1982; Amstrup, Stirling & Lentfer 1986; Stirling 2002).  
442 Alternatively, increasing age may also occur because of a decline in recruitment resulting in

443 relatively fewer young individuals. This latter hypothesis is supported by both older bears and  
444 lower litter sizes in northern Davis Strait. Using the recorded harvest in Davis Strait and  
445 assuming the 1979 abundance was under estimated, a linear increase from 1,200 to 2,158 bears  
446 from 1979–2007 would have required an annual growth rate of approximately 2.1%, resulting in  
447 a mean annual harvest rate of 3.2% and natural population growth rate of 5.4%. This natural  
448 growth rate is consistent with that of the neighboring Baffin Bay population (Taylor *et al.* 2005).  
449 Thus, biologically, it is possible that the population could have doubled over the past 30 years,  
450 but our data are not sufficient to confirm or reject this hypothesis.

451         Our estimates of polar bear survival in the 1970s and 1980s may be biased low. A  
452 negative bias could be due to a positive skew between the sample of the population that was  
453 captured and the segment that was harvested. In Baffin Bay, Taylor *et al.* (2005) found that polar  
454 bears captured in the spring are more likely to be harvested than those captured in the fall. This  
455 phenomenon may also occur in Davis Strait, although the differences in capture season are  
456 confounded by time period, and whether survival was estimated by recapture, or recapture and  
457 recovery. Early recovery rates are also likely underestimated, because the harvest reporting  
458 systems were still being implemented in the 1970s and early 1980s; reporting became mandatory  
459 in 1993 in the Northwest Territories. Thus, we suggest our estimates of  $S_N$  in the earlier years are  
460 likely biased low, and the pattern in the increasing estimates of  $S_N$  may be, to some degree,  
461 artificial. Based on a meta-analysis of standing age distributions, Taylor *et al.* (1987) suggested  
462 that populations of polar bears cannot increase with adult female  $S_N \leq 0.93$ . However, even in the  
463 1990s with good harvest reporting,  $S_N$  estimates for adult females were approximately 0.93 and  
464 lower (see Fig. S3), indicating the majority of an increase in population size would have been  
465 more likely to have occurred in the 2000s and/or there is additional un-modeled recovery

466 heterogeneity. A population increase in the 2000s is consistent with local observations of the  
467 increase of bears seen in Labrador having occurred in the past decade (A. Simpson, J.  
468 Merkurasuk, Torngat Mountains National Park, personal observations).

469         There are a few lines of evidence to suggest that the population of polar bears in Davis  
470 Strait is currently experiencing density-dependent effects (Fowler 1981). First, the population  
471 density is relatively high (Taylor & Lee 1995). Second, our simulations suggest the population is  
472 probably stationary (at reported harvest rates), following a likely period of increase as suggested  
473 by local, Inuit and scientific observations. Third, Davis Strait is now experiencing very low  
474 reproduction in comparison to other populations of polar bears (e.g., Ramsay & Stirling 1988;  
475 Taylor *et al.* 2002, 2005, 2009; Regher *et al.* 2010). Concurrently, the prey base increased during  
476 this interval (DFO 2010), and this may be related to increased survival rates, especially in the  
477 southern portion of the population. Thus we propose that a density-dependent reduction in  
478 population growth for Davis Strait polar bears from 1974 to 2007 has been a complex interaction  
479 that appears to have been partly mitigated by increased prey abundance. We concur with Taylor  
480 (1994) that only manipulative experiments can unambiguously confirm density-dependence.  
481 However, we suggest that the combination of our parallel lines of evidence and the expectation  
482 of patterns for large mammals (Taylor 1994; Fowler 1981), the Davis Strait population is likely  
483 experiencing the effects of density dependence. Derocher (2005) found a decreasing trend in  
484 litter production over nine years for polar bears in the Barents Sea, and attributed the decline to  
485 either climate change and/or the effects of density dependence. The abundance of the Barents  
486 Sea population likely increased since the 1973 ban on harvest in Norway, but is now  
487 experiencing habitat decline – a similar ecological scenario to that we suggest has occurred in  
488 Davis Strait.

489 In our top models, polar bear survival in Davis Strait varied with time and geography,  
490 factors that include changes in sea-ice habitat, prey density, but also other, unknown variables.  
491 Survival models with environmental covariates as independent factors were not supported in  
492 comparison to models with broader variables (time and geography); positive and significant  
493 effects of harp seal abundance on total survival were demonstrated. We note that our ability to  
494 relate changes in survival with the more recent ice habitat decline is limited; 63% of the  
495 recoveries of marked bears between 1985 and 2008 (the period of ice decline) are from 2006–  
496 2008, and 100% of the recaptures are from 2006–2007. Indeed, a wealth of information on the  
497 ecological covariates with polar bear survival lays in the future patterns of recovery and  
498 recapture of recently marked bears (1,518 individuals marked, 2005–2007).

499 In contrast to populations in Western Hudson Bay (Regher *et al.* 2006) and the Southern  
500 Beaufort Sea (Regher *et al.* 2010), point estimates of survival rates increased over a period of  
501 declining ice concentration; increasing total survival rates are consistent with our conclusion that  
502 the abundance of polar bears in Davis Strait has increased. The increases in estimated survival  
503 rates also occurred over a period of increasing abundance of harp seals (Fig. 4) and a likely  
504 decline in relative rate of harvest. Our observation of a currently reduced population growth in  
505 Davis Strait has perhaps been exacerbated by the progressive sea ice decline since the mid-  
506 1990s, and is most likely due to low reproductive rates (and cub survival from birth to time of  
507 fall census). This result corroborates predictions for the effect of sea ice decline on litter size in  
508 seasonal-ice populations (Molnár *et al.* 2011). We could not analyze reproductive parameters  
509 from the 1970s to 2000s, and thus cannot disentangle the effects of sea-ice habitat change and  
510 population density. Population density and sea-ice habitat decline may have interacted to  
511 influence the vulnerable age-classes (young). Rode *et al.* (unpublished data) concluded that the

**Comment [ESP2]:** Will be submitted for review soon. When it is, I can forward to the editors:

Rode KD, Peacock E, Taylor MK, Stirling I, Born EW, Laidre KL, Wiig O (In Prep) A tale of two polar bear populations (*Ursus maritimus*): ice habitat, harvest, and body condition.

512 body condition of polar bears in Davis Strait varies with annual changes in ice habitat, and that  
513 body condition has declined from the 1970s to 2000s. Declines in body condition and  
514 reproduction/recruitment are likely to precede declines in survival in a long-lived species,  
515 including polar bears (Stirling *et al.* 1999, Regher *et al.* 2007), whether the trigger is an increased  
516 density, a decline in habitat or an interaction of both. Our conclusion of reduced reproductive  
517 rates, in concert with declines in body condition (K.D. Rode *et al.* unpublished data), but  
518 currently high rates of survival, is consistent with this theory.

#### 519 FUTURE POLAR BEAR POPULATION MANAGEMENT

520 Precautionary strategies for polar bear conservation, including harvest management, are  
521 required for polar bear populations experiencing changes in density, population productivity,  
522 reductions in habitat, and increased human contact. The low reproductive rates of polar bears in  
523 Davis Strait, and declines in body condition suggest habitat and/or density impacts on the  
524 population. Our conclusions that survival varies across geography and over time, variation which  
525 incorporates ecological changes of prey abundance, ice, and harvest rates, underpin the need to  
526 for managers to develop a broader ecological perspective in harvest management. Further, a  
527 social carrying capacity for polar bear abundance in Davis Strait has been underscored by local  
528 users (Kotierk 2009b). If sea ice habitat continues to decline, a management strategy to maintain  
529 current levels of abundance may only exacerbate density-dependent effects, and would  
530 ultimately not be possible. Similarly, management to reduce population density and thereby  
531 increase population productivity may not result in anticipated reduction of density effects if  
532 habitat declines simultaneously to population reductions, or if the current low recruitment rates  
533 are entirely due to habitat deterioration.

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548

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708 **Figure Captions**

709 **Fig. 1.** Polar bear capture locations from 1974–2007 ( $n = 2,529$ ) in the three sub-regions of  
710 Davis Strait

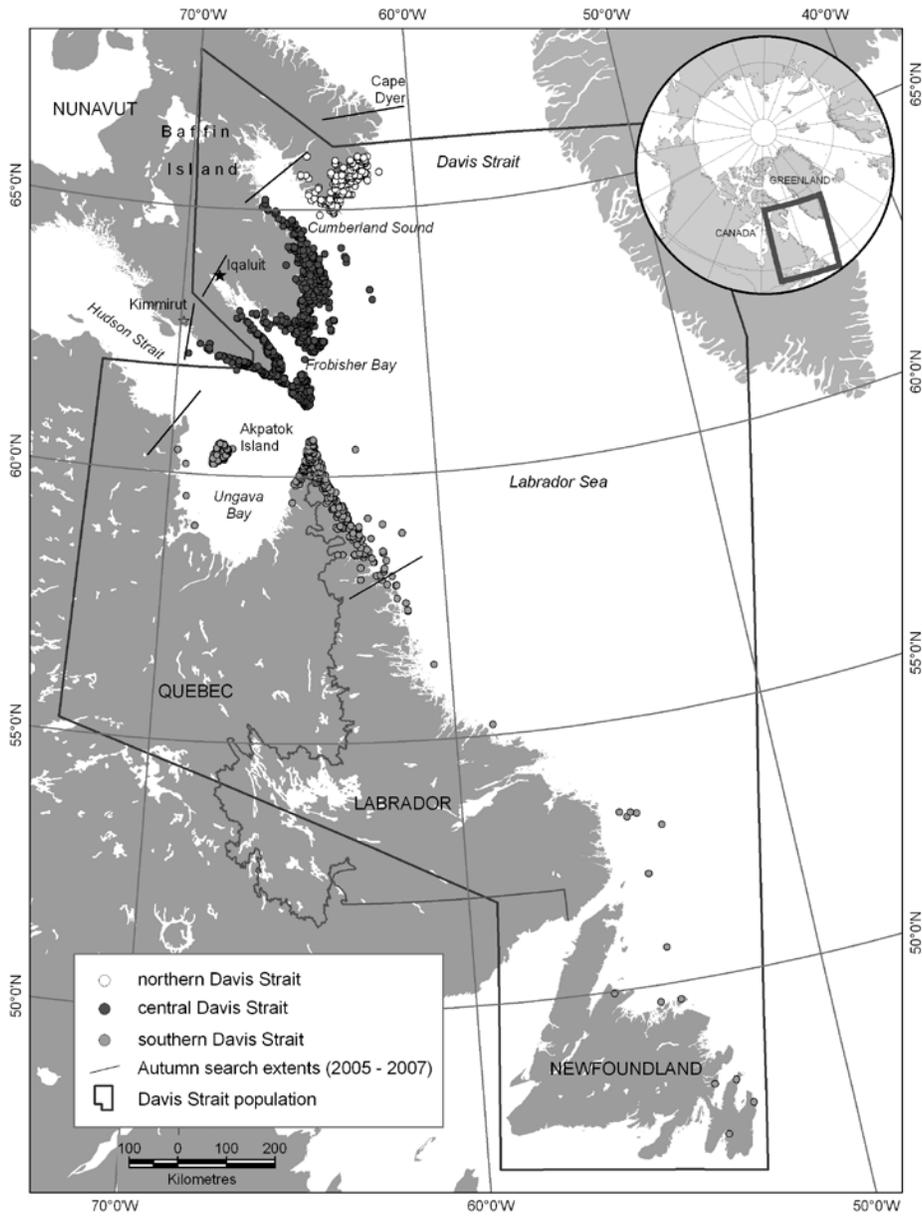
711 **Fig. 2.** Initial capture and recovery locations of polar bears, which have complete location data ( $n$   
712 = 140) in Davis Strait from 1974–2008

713 **Fig. 3.** Total apparent survival estimates ( $S$ ) of marked polar bears in Davis Strait, 1974– 2008

714 **Fig. 4.** Total apparent survival estimates (95% CI) for adult female polar bears, 1975–2008, in  
715 northern and southern Davis Strait and (a) summer ice concentration and (b) harp seal

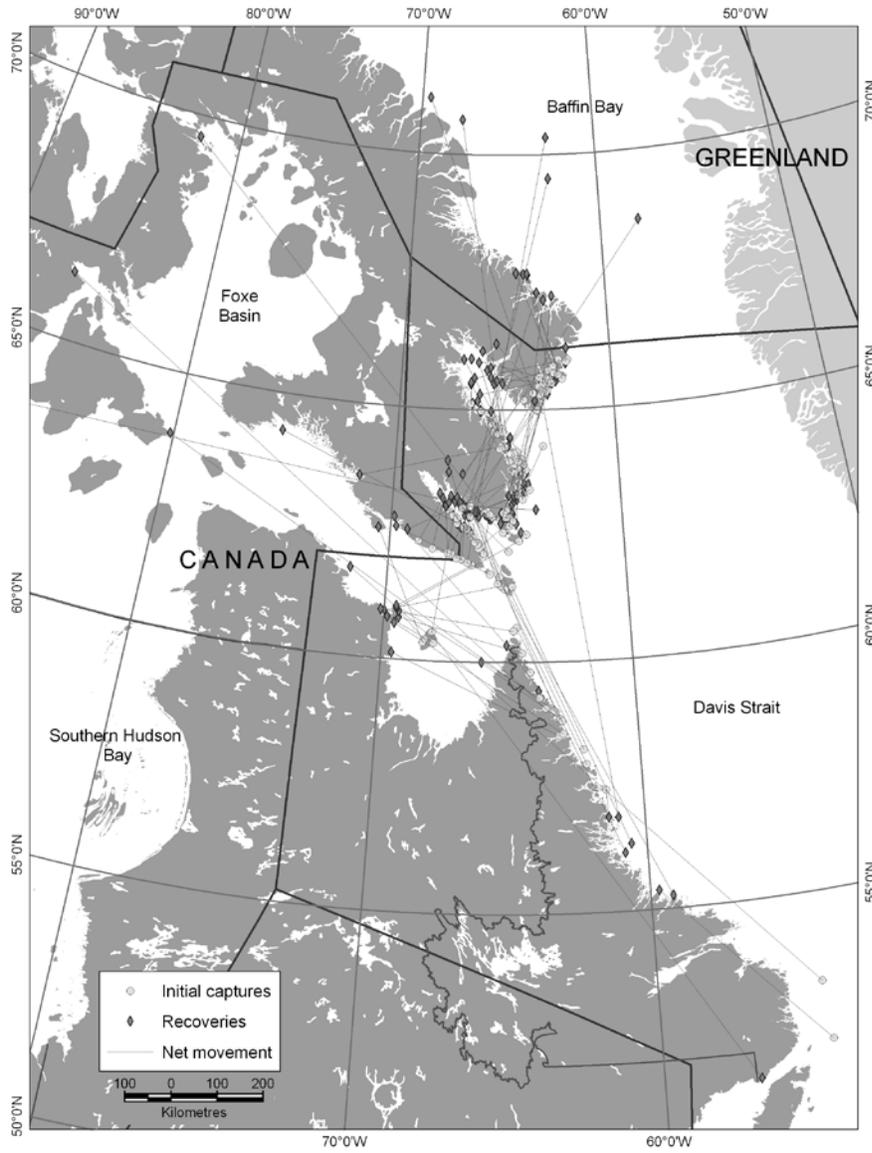
716 abundance. Estimates are from survival model,  $ageclass + timeperiod + nonjuv:male + Geo$   
717 (total model,  $\Delta AICc = 0.82$ )

718 **Fig. 5.** Age structures of captured polar bears in the Davis Strait, 1974–1979 and 2005–2007

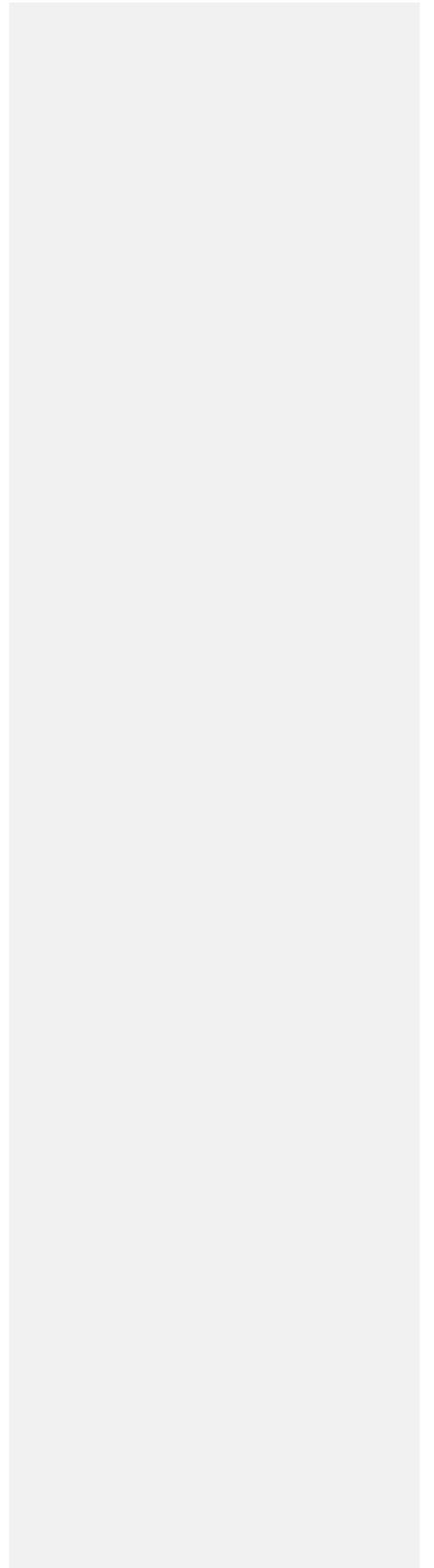


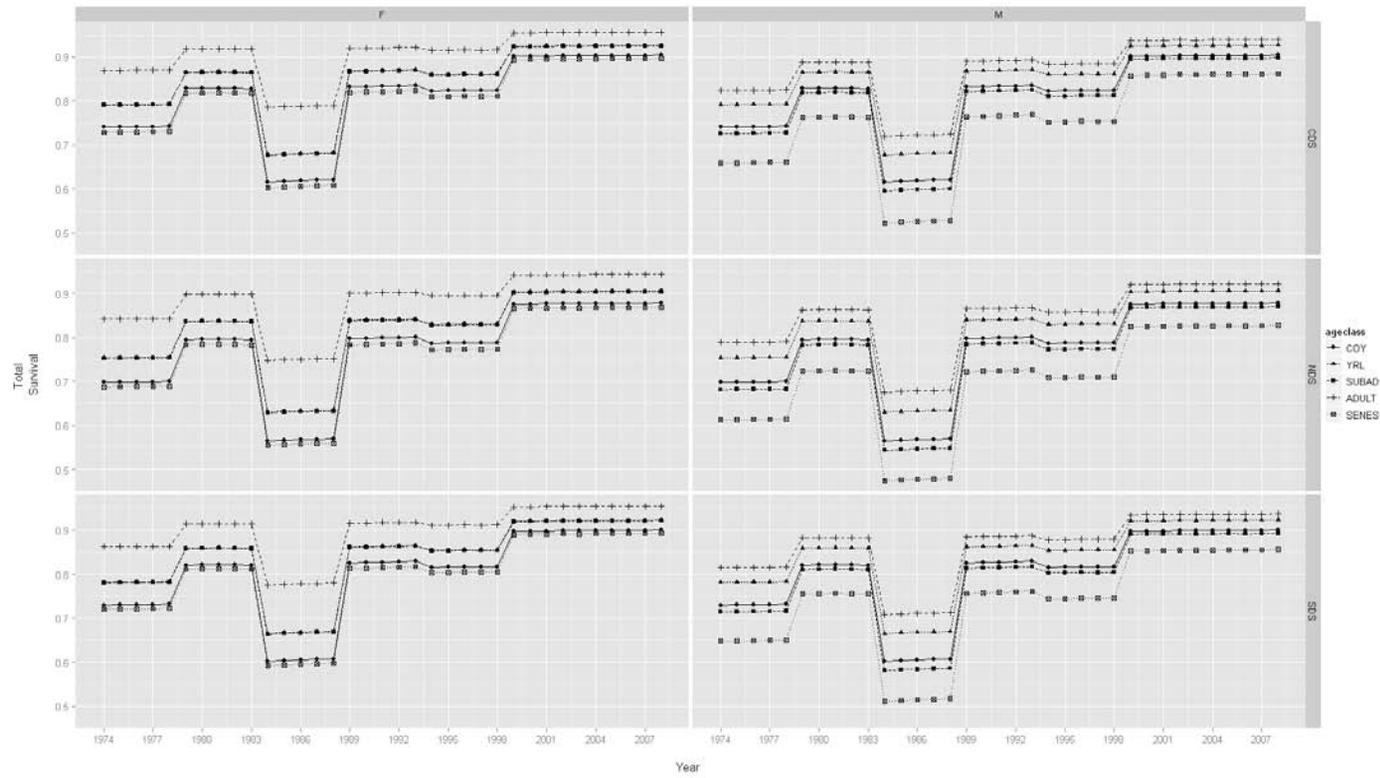
719

720 **Fig. 1.**



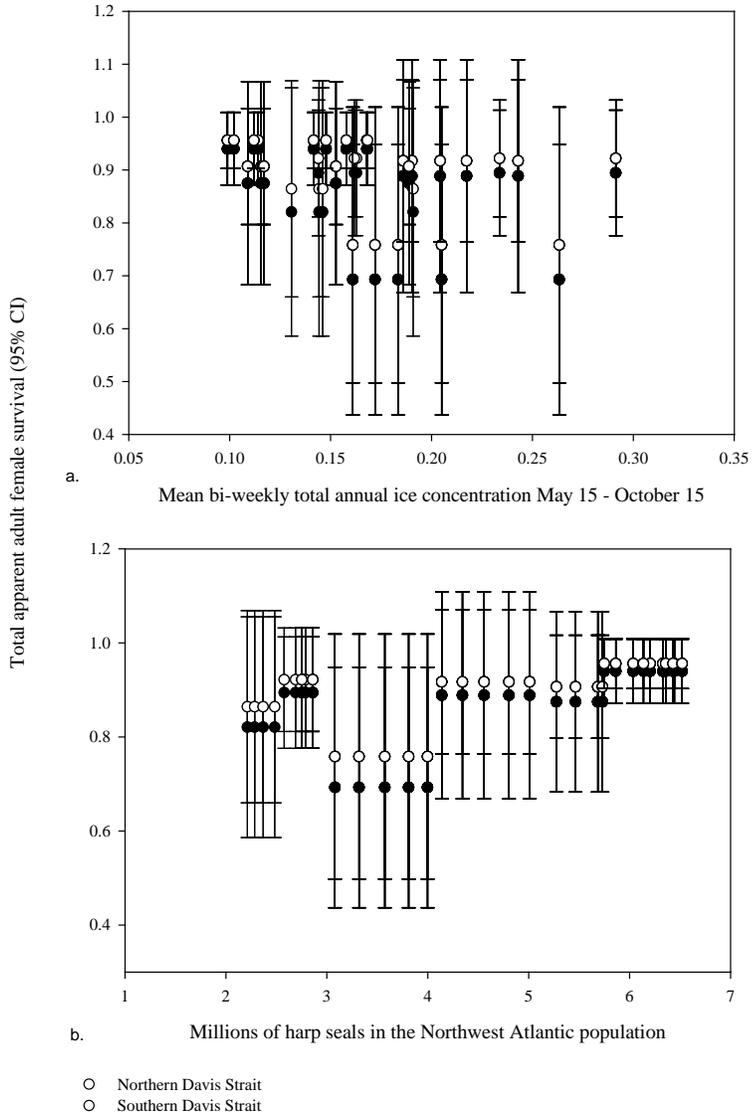
721  
722 **Fig. 2.**





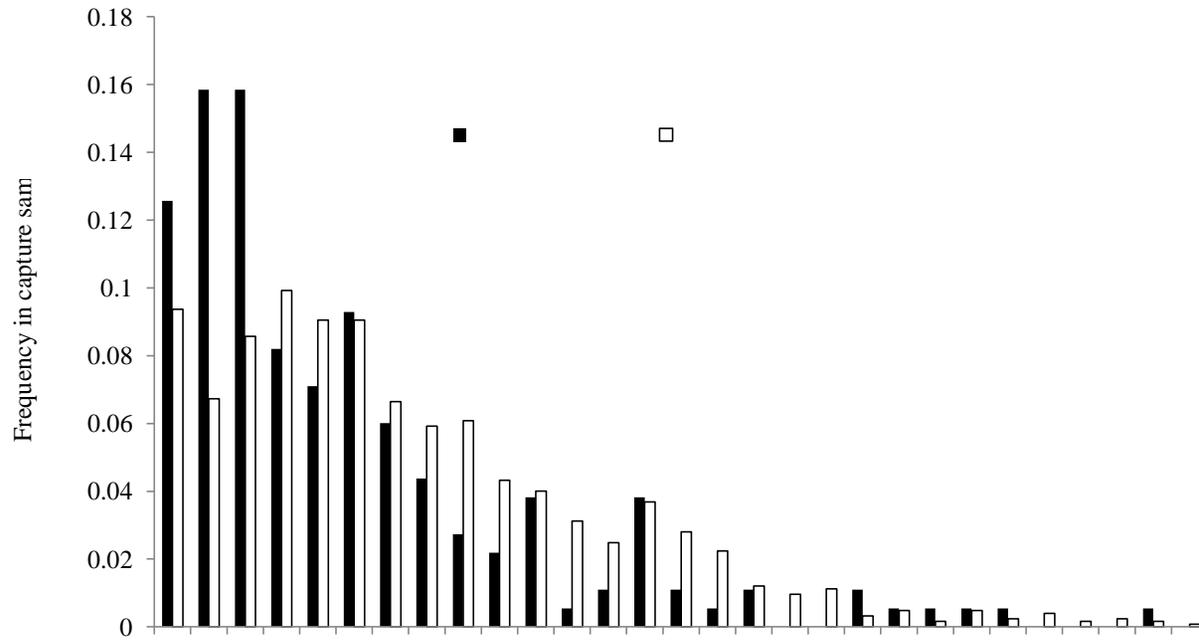
723

724 Fig. 3



725

726 **Fig. 4.**



727

728 Fig. 5.

729 **Table 1.** Logit coefficients ( $\beta$ ) and standard errors (SE) of total survival for ecological variables in survival sub-models of polar bears  
 730 in Davis Strait. Each survival sub-model includes *ageclass + nonjuv:male*, and are from the model with lowest  $\Delta AIC_c$  that contains  
 731 the variable of interest. Each effect is additive to the intercept. Bold values indicate  $\beta/SE \geq 2$  or  $\leq -2$ , suggesting more important  
 732 effects with higher precision

	Survival sub-model						
	<i>time period</i>	<i>time period + geo</i>	<i>harp + geo</i>	<i>ice + ice<sup>2</sup> + harp</i>	<i>geo</i>	<i>harp</i>	<i>ice + ice<sup>2</sup></i>
Minimum $\Delta AIC_c$ of entire model with specified sub-model	0	0.82	5.49	7.91	26.22	13.53	25.52
	Logit coefficients, $\beta$ (SE)						
Intercept*	1.00 (0.59)	1.16 (0.60)	0.55 (0.66)	-0.79 (1.31)	<b>1.88 (0.51)</b>	0.59 (0.60)	<b>2.35 (0.98)</b>
Time*							
<i>time period</i> , 1979–1983	0.60 (0.41)	0.62 (0.41)					
<i>time period</i> , 1984–1988	-0.72 (0.43)	-0.71 (0.43)					
<i>time period</i> , 1989–1993	0.52 (0.57)	0.56 (0.59)					
<i>time period</i> , 1994–1998	0.38 (0.45)	0.42 (0.51)					
<i>time period</i> , 1999–2008	<b>1.23 (0.38)</b>	<b>1.23 (0.38)</b>					
Geographic sub-region**							
<i>geo</i> , ND		-0.46 (0.25)	<b>-0.76 (0.19)</b>		-0.52 (0.27)		
<i>geo</i> , SD		-0.13 (0.27)	0.08 (0.14)		0.06 (0.21)		
Harp seal abundance**							
<i>harp</i>			<b>0.21 (0.10)</b>	<b>0.23 (0.09)</b>		<b>0.24 (0.06)</b>	
Summer ice concentration**							
<i>ice</i>				14.08 (11.75)			-3.58 (10.22)
<i>ice<sup>2</sup></i>				-39.65 (31.35)			-2.96 (27.90)

733 \* Intercept estimate includes estimates of the levels: time period 1974-1978; geographic sub-region CD, no harp and/or no ice variable, depending on survival  
734 sub-model.

735 **Table 2.** Model-averaged estimates of total apparent ( $S$ ) and natural survival ( $S_N$ ) of polar bears  
 736 in Davis Strait in 2008. LCL and UCL are lower and upper confidence levels, respectively

Region	Age-class	Sex	Total survival			Natural survival		
			Estimate	95% LCL	95% UCL	Estimate	95% LCL	95% UCL
Northern Davis Strait	Adult	F	0.943	0.853	0.979	0.952	0.861	0.984
		M	0.922	0.826	0.967	0.943	0.847	0.980
	Senescent adult	F	0.869	0.590	0.969	0.889	0.622	0.975
		M	0.828	0.526	0.954	0.873	0.599	0.970
	Subadult	F	0.904	0.764	0.965	0.918	0.778	0.973
		M	0.870	0.727	0.944	0.905	0.763	0.966
	Yearling		0.906	0.784	0.963	0.920	0.796	0.971
COY		0.879	0.639	0.967	0.896	0.661	0.975	
Central Davis Strait	Adult	F	0.956	0.916	0.978	0.967	0.926	0.986
		M	0.939	0.898	0.965	0.964	0.922	0.984
	Senescent adult	F	0.896	0.708	0.969	0.922	0.758	0.978
		M	0.861	0.643	0.955	0.917	0.751	0.976
	Subadult	F	0.925	0.856	0.962	0.944	0.874	0.976
		M	0.897	0.829	0.940	0.940	0.872	0.973
	Yearling		0.926	0.863	0.962	0.945	0.880	0.976
COY		0.904	0.742	0.969	0.928	0.778	0.979	
Southern Davis Strait	Adult	F	0.954	0.918	0.975	0.958	0.922	0.978
		M	0.937	0.897	0.962	0.946	0.907	0.969
	Senescent adult	F	0.893	0.711	0.966	0.901	0.727	0.969

	M	0.857	0.641	0.952	0.878	0.682	0.960
Subadult	F	0.922	0.857	0.959	0.928	0.863	0.963
	M	0.893	0.825	0.936	0.909	0.843	0.949
Yearling		0.923	0.861	0.959	0.929	0.867	0.963
COY		0.900	0.743	0.966	0.908	0.756	0.969

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**Table 3.** Reproductive parameters of captured and aged adult female polar bears in Davis Strait, 2005–2007

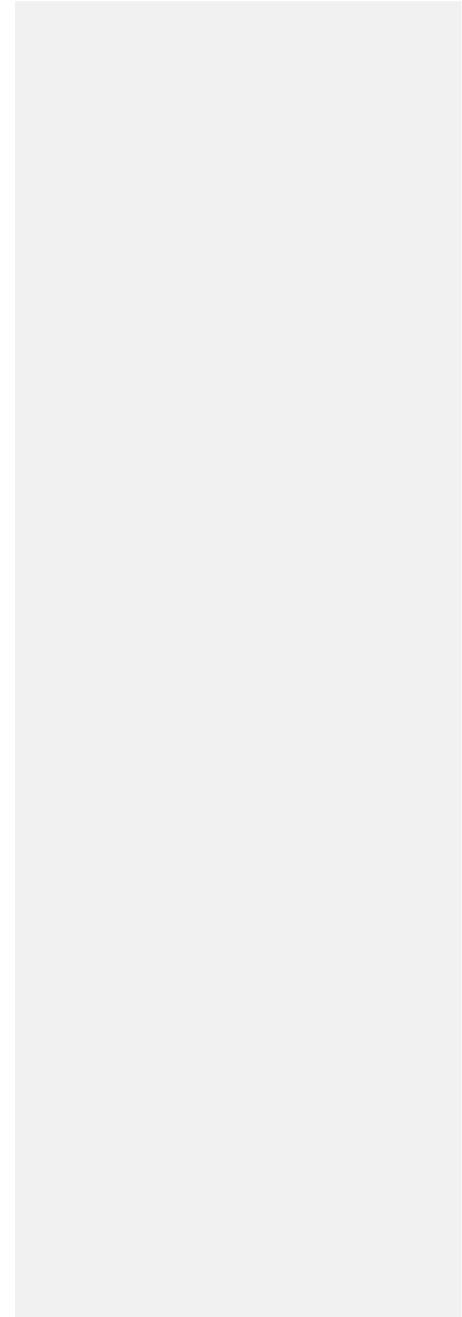
Age of adult female	Aged adult females	No. unencumbered	Number of litters			LP <sup>1</sup>	Age-binned LPR for PVA <sup>2</sup>	No. litters of 1 COY	No. litters of 2 COY	COY LS	Binned COY LS
			2-yr <sup>3</sup>								
			Yearling	COY							
4	29	27	0	0	2	0.16	-	0	2	2.00	
5	58	40	0	11	8	0.16	0.54	4	4	1.50	
6	56	38	0	10	8	0.17	0.34	5	3	1.38	1.55
7	54	37	1	9	8	0.34	0.44	5	3	1.38	
8	50	25	0	9	17	0.14	0.44	6	11	1.65	
9	33	17	1	11	4	0.26	0.44	3	1	1.25	1.44
10	24	12	0	4	8	0.29	0.44	6	2	1.25	
11	19	12	0	3	5	0.19	0.44	2	3	1.60	
12	15	8	0	5	3	0.24	0.44	2	1	1.33	1.39
13	16	7	0	3	6	0.41	0.44	4	2	1.33	
14	9	5	0	0	4	0.22	0.44	1	3	1.75	
15	8	5	0	3	1	0.30	0.44	0	1	2.00	1.61
16	19	9	0	5	5	0.06	0.44	2	3	1.60	
17	8	5	0	3	0	0.38	0.44	0	0	0.00	
18	8	4	0	1	3	0.17	0.44	3	0	1.00	1.10
19	5	2	0	2	1	0.50	0.44	0	1	2.00	
20	1	0	0	0	1	0.33	0.44	0	1	2.00	
21	7	2	0	3	2	0.75	0.44	1	1	1.50	1.73
22	2	0	0	1	1	-	0.44	0	1	2.00	
23	2	0	0	2	0	-	0.44	0	0	0.00	
24	0	0	0	0	0	0.33	0.44	0	0	-	-
25	2	1	0	0	1	0.50	0.44	1	0	1.00	
26	1	0	0	0	1	0.50	0.44	1	0	1.00	
27	1	0	0	0	1	-	0.44	0	1	2.00	1.25
28	1	1	0	0	0	-	-	0	0	0.00	
29	0	0	0	0	0	-	-	0	0	-	
30	1	1	0	0	0	-	-	0	0	0.00	-
Totals and summaries	429	258	2	85	90	0.23 <sup>4</sup>	-	46	44	1.487 <sup>5</sup>	-

<sup>1</sup>LP as estimated using equations per Stirling, Calvert & Andriashek 1980. Denominator of LP is total number of adult females. <sup>2</sup>LPR as estimated using equations per Taylor, Carley & Bunnell 1987. Denominator of LPR is number of adult females available to mate in each year.

<sup>3</sup>not incorporated in LPR or LP calculations

<sup>4</sup>weighted-average LPR for ages 4-21; weighted-average LPR for ages 7-27 is 0.33 (mean adult rate).

<sup>5</sup>Summary figure as estimated in VITAL RATES from standing-age distribution.



- 1 Additional Supporting Information may be found in the online version of this article:
- 2 **Appendix S1.** Supplementary tables and figures.
- 3 **Table S1.** Polar bears of different reproductive status caught (frequency by total caught) in Davis  
4 Strait, 2005–2007
- 5 **Table S2.** Model selection results for models with  $\Delta\text{AICc} \leq 10$  fitted to mark-recapture-recovery  
6 data for polar bears in Davis Strait (1974–2009)
- 7 **Table S3.** Model-averaged capture probability ( $p$ ) of marked polar bears in Davis Strait, 2005–  
8 2007
- 9 **Table S4.** Model-averaged recovery rates ( $r$ ) of marked polar bears in Davis Strait, 1974–2009.
- 10 **Table S5.** Abundance estimates of polar bears in Davis Strait, 2005–2007
- 11 **Table S6.** Demographic parameters used for estimation of population growth rate for Davis  
12 Strait from an initial population size of 2,158 (180, SE) in 2007
- 13 **Fig. S1.** Break-point regression of mean weekly total ice concentration (May–October) in Davis  
14 Strait, 1974–2008
- 15 **Fig. S2.** Recovery rates ( $r$ ) of marked juvenile and non-juvenile (ages 2+) polar bears in sub-  
16 regions of Davis Strait, 1974–2008
- 17 **Fig. S3.** Natural survival ( $S_N$ ) of marked polar bears in three sub-regions of Davis Strait, 1974–  
18 2008
- 19 **Fig. S4.** Age structure of male polar bears captured north and south of Hudson Strait in Davis  
20 Strait, 2005–2007
- 21 **Fig. S5.** Age structure of female polar bears captured north and south of Hudson Strait in Davis  
22 Strait, 2005–2007
- 23