The Utility of Harvest Recoveries of Marked Individuals to Assess Polar Bear (*Ursus maritimus*) Survival

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ABSTRACT. Management of polar bear (*Ursus maritimus*) populations requires the periodic assessment of life history metrics such as survival rate. This information is frequently obtained during short-term capture and marking efforts (e.g., over the course of three years) that result in hundreds of marked bears remaining in the population after active marking is finished. Using 10 additional years of harvest recovery subsequent to a period of active marking, we provide updated estimates of annual survival for polar bears in the Baffin Bay population of Greenland and Canada. Our analysis suggests a decline in survival of polar bears since the period of active marking that ended in 1997; some of the decline in survival can likely be attributed to a decline in springtime ice concentration over the continental shelf of Baffin Island. The variance around the survival estimates is comparatively high because of the declining number of marks available; therefore, results must be interpreted with caution. The variance of the estimates of survival increased most substantially in the sixth year post-marking. When survival estimates calculated with recovery-only and recapture-recovery data sets from the period of active marking were compared, survival rates were indistinguishable. However, for the period when fewer marks were available, survival estimates were lower using the recovery-only data set, which indicates that part of the decline we detected for 2003–09 may be due to using only harvest recovery data. Nevertheless, the decline in the estimates of survival is consistent with population projections derived from harvest numbers and earlier vital rates, as well as with an observed decline in the extent of sea ice habitat.

Key words: Baffin Bay, polar bear, *Ursus maritimus*, climate warming, community-based monitoring, harvest, mark-recapture, survival rates

Контроль популяции белого медведя (*Ursus maritimus*) подразумевает периодическую оценку параметров жизненного цикла, например, коэффициента выживания. Такую информацию регулярно получают в ходе экспедиций по отлову медведей на короткий период и мечению (напр., в течение трех лет), в результате которых в популяции остаются сотни помеченных особей. Мы представляем обновленную оценку годового коэффициента выживания в субпопуляции белого медведя в Баффиновом заливе на территории Гренландии и Канады по результатам 10 лет анализа животных, убитых охотниками, после окончания периода мечения. Согласно нашим результатам, коэффициент выживания белых медведей снизился с момента мечения, которое было закончено в 1997 году; в некоторой степени уменьшение коэффициента выживания может быть связано с уменьшением концентрации полярных льдов в весенний период в континентальном шельфе Баффиновой земли. Стандартное отклонение оценок сравнительно велико, так как количество меток сокращается, и соответственно, следует интерпретировать результаты с осторожностью. Наиболее существенное увеличение стандартного отклонения оценок коэффициента выживания наблюдалось на шестой год после мечения. При проведении анализа меток, найденных на медведях, убитых охотниками, и меток, найденных и на отловленных, и на убитых животных, данные по этим двум группам животных не отличались друг от друга. Тем не менее, коэффициент выживания оказался ниже при анализе только меток, найденных на убитых животных, притом что сохранилось меньшее количество меток, что указывает на то, что снижение оценки коэффициента выживания, выявленное в 2003–2009 годах, может быть связано с тем, что анализировались только данные по убитым животным. Несмотря на это, снижение оценки коэффициента выживания согласуется с прогнозами численности популяции, основанными на данных о количестве отловленных животных и других показателях, а также с наблюдаемым сокращением площади полярных льдов.

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RÉSUMÉ. La gestion des populations d'ours polaires (*Ursus maritimus*) nécessite l'évaluation périodique des mesures du cycle biologique, tel que le taux de survie. Cette information est souvent obtenue dans le cadre des efforts de capture et de marquage à court terme (par exemple, sur une période de trois ans) qui se traduisent par le marquage d'une centaine d'ours au sein de la population une fois les travaux terminés. En nous appuyant sur dix années supplémentaires de données de récoltes de reprises suivant une période de marquage actif, nous aboutissons à des estimations actualisées de la survie annuelle des ours polaires faisant partie de la population de la baie de Baffin du Groenland et du Canada. Notre analyse suggère qu'il y a eu un déclin sur le plan de la survie des ours polaires depuis la période de marquage actif qui a pris fin en 1997. Une partie de ce déclin en matière de survie peut être attribuable à la diminution de la concentration de glace printanière sur le plateau continental de l'île de Baffin. La variance entourant les estimations de survie est comparativement élevée en raison du nombre à la baisse de marquages disponibles. Il y a donc lieu de faire preuve de prudence dans l'interprétation des résultats. La variance des estimations de survie augmentait considérablement au cours de la sixième année suivant le marquage. Lorsque nous avons comparé les estimations de survie avec les ensembles de données de reprise seulement et celles de recapture et de reprise pour la période de marquage actif, les taux de survie étaient indistinguables. Cependant, pour la période pendant laquelle un moins grand nombre de marquages était disponible, les estimations de survie étaient moins élevées lorsque nous nous sommes appuyés sur l'ensemble des données de reprise seulement, ce qui indique qu'une partie du déclin que nous avons constaté pour les années 2003 à 2009 pourrait être attribuable au fait que nous n'avons utilisé que les données des récoltes de reprises. Néanmoins, le déclin en matière d'estimations de survie est conforme aux projections de population dérivées des résultats des récoltes et des indices vitaux antérieurs, ainsi qu'à la diminution qui a été observée sur le plan de l'étendue de l'habitat de la glace de mer.

Mots clés : baie de Baffin, ours polaire, *Ursus maritimus*, réchauffement climatique, programme communautaire de surveillance, récolte, marquage et recapture, taux de survie

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INTRODUCTION

The productivity and abundance of harvested wildlife populations must be assessed periodically to determine harvest sustainability. Ideally, the frequency of these assessments would depend on the period over which point estimates of vital rates (survival, reproduction, abundance) remain valid, but realistically, it may be dictated by human and financial capacity. Population assessment of polar bears (*Ursus maritimus*) requires large financial investment and considerable logistic effort and expertise because of the inherent difficulties of studying this wide-ranging species in remote regions of the Arctic. For several populations of polar bears, these constraints limit how often large-scale mark-recapture studies (e.g., Taylor et al., 2005) or aerial surveys (Aars et al., 2009) can be done. Consequently, the quality of information on population status varies widely among the 19 circumpolar populations (Obbard et al., 2010). Although some populations are studied annually to assess population parameters, most have been studied only once, or periodically at intervals of 10 to 25 years. Some populations have never been assessed (Vongraven et al., in press).

Historically, the harvest of polar bears has been considered the most significant source of mortality for populations (Prestrud and Stirling, 1994), and this view has largely fueled the need for periodic population assessments. Climate warming has now emerged as another significant factor: it has been associated with declines in polar bear sea ice habitat, natality, survival, body condition, and population abundance (Stirling and Parkinson, 2006; Wiig et al., 2008; Rode et al., 2012). More frequent assessments of population status may be warranted because changing habitat can influence vital rates, rendering them valid for a shorter duration. Moreover, because of increased conservation risk, it is incumbent upon managers to design efficient monitoring strategies that use all available information to the fullest extent possible. For polar bear populations that are hunted (i.e., in the United States, Canada, and Greenland), community-based monitoring (CBM) of the harvest provides a valuable supplementary element in evaluation of population status (Vongraven and Peacock, 2011). CBM of polar bears includes the reporting of the harvest of marked bears (i.e., recovery). Because polar bears are often marked during intensive but short-term field studies, many marked individuals remain in populations after the last year of marking. These marks are often used in mark-recapture-recovery studies (Taylor et al., 2005), but they also can continue to contribute meaningful information in the absence of a continuous marking effort. In this paper, we evaluate the utility of using information from the harvest recovery of marked polar bears to estimate annual survival in Baffin Bay (Fig. 1), where conservation concern has increased because of habitat decline, reduction in body condition (Rode et al., 2012), and long-term overexploitation of the population (Derocher et al., 1998; Lunn et al., 2002; Taylor et al., 2005; Aars et al., 2006; Obbard et al., 2010).

Status of the Baffin Bay Population

In the mid-1990s, Canada's eastern Northwest Territories (now Nunavut) and Greenland, the jurisdictions sharing management authority for Baffin Bay polar bears, collaborated to assess the status of this population using mark-recapture-recovery techniques (Taylor et al., 2005). Taylor
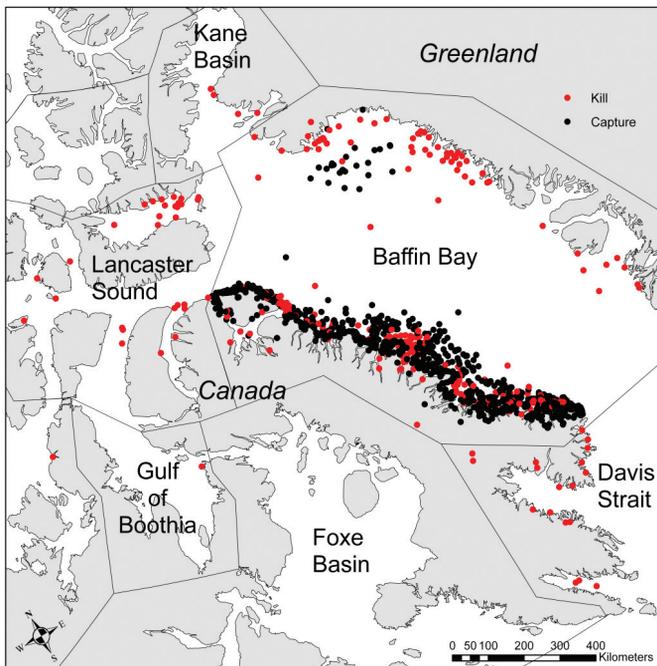
FIG. 1. The Baffin Bay population of polar bears and neighboring populations, as designated by the IUCN/SSC Polar Bear Specialist Group. Black dots represent polar bears caught and marked (n = 1418), while red dots indicate bears killed and reported in the harvest (n = 289).

et al. (2005) incorporated data from polar bears (identifiable by tattoo numbers and ear tags) that had been marked, recaptured, or recovered from sporadic efforts (Schweinsburg et al., 1982) in Baffin Bay between 1974 and 1998. (The last year of marking was 1997.) A preliminary estimate of 2200 bears for Baffin Bay based on these data was presented in 1997 (Derocher et al., 1998). The final estimate of abundance of polar bears was 2074 (SE = 266) for 1994 – 97 (Taylor et al., 2005). Estimated natural survival (i.e., excluding mortality due to harvest) and reproductive rates were high, and consequently, the natural population growth rate was estimated to be relatively high (Taylor et al., 2005).

Polar bears are managed differently in Canada and Greenland. In Nunavut, harvest quotas have existed since 1968 (Prestrud and Stirling, 1994). During the 1990s, the annual quota within Nunavut for Baffin Bay was 65 polar bears per year. In 2005, on the basis of updated information on population productivity, this quota was increased to 105 bears per year. In Greenland, although various measures to protect polar bear populations and regulate hunting have been in force since 1974 (cf. Born, 1995), quotas were not introduced until 2006 (Lønstrup, 2006). Known harvest of polar bears from both Nunavut and Greenland are reported every four years to the IUCN/SSC Polar Bear Specialist Group and annually to the Federal and Provincial/Territorial Polar Bear Technical Committee of Canada. Population viability analyses based on the preliminary mark-recapture population estimate from 1997 and the harvest reporting suggested that the Baffin Bay population was subject to overexploitation (Derocher et al., 1998). The combined

Greenland-Canada harvest continued to be high during the late 1990s and 2000s. Population projections using these harvest data and vital rates from the mark-recapture study continued to suggest that the combined harvest was unsustainable and that the population would decline (Lunn et al., 2002; Aars et al., 2006; Obbard et al., 2010). Because of these conservation concerns, the Greenland quota for Baffin Bay has gradually been reduced from 92 animals in 2006 (Born et al., 2010: Table 3) to 70 in 2010 (Anon., 2011). In addition, co-management authorities in Nunavut have implemented a phased reduction in harvesting that will reduce the quota from 105 bears per year in 2010 to 65 bears per year by 2014 (Nunavut Wildlife Management Board letter of decision to the Government of Nunavut, available at http://www.nwmb.com).

In marked contrast to conclusions reached on scientific grounds, some local observers from communities on Baffin Island suggested that the abundance of polar bears in Baffin Bay had increased (Dowsley and Wenzel, 2008), and some hunters in Greenland also held this view (Born et al., 2011). In both traditional knowledge studies, however, other hunters suggested that an apparent increase of polar bears near the shore may represent a change in distribution caused by a decrease in sea ice (Dowsley and Wenzel, 2008; Born et al., 2011). The attempt to resolve the varying perspectives offered by science and traditional knowledge was impaired by a lack of ongoing monitoring necessary to provide new information on population abundance or vital rates. Consequently, some opposition to harvest reduction measures in Nunavut converged on whether the scientific data on productivity and population abundance, collected 10 years earlier, were still valid (Peacock et al., 2011).

Objectives

We used additional harvest recovery (1999 – 2009) of marked individuals from Greenland and Canada to (1) provide updated estimates of natural and total survival rates of polar bears in Baffin Bay, (2) examine how the variance of survival estimates changed as a function of time since marking, and (3) examine whether survival estimates differ between data sets comprising only harvest recovery information and data sets including both recapture and recovery data. We also (4) assess whether the sea ice concentration in spring, when polar bears are hyperphagic (Stirling, 2002), has been declining. Finally, we (5) assess the relationship between annual survival of polar bears and ice metrics for Baffin Bay.

METHODS

We assembled all data on polar bear captures in Baffin Bay (1979 – 97) and harvest recovery data for 1979 – 2009 from both Greenland (Schweinsburg et al., 1982; Taylor et al., 2005; Greenland Institute of Natural Resources [GINR], unpubl. data) and Nunavut (Government of Nunavut [GN],

unpubl. data). Taylor et al. (2005) outline harvest reporting (until 1998), the study area, and capture and marking methods. For the current study (1999–2009) in Nunavut, the harvest recovery of marked bears was reported by hunters to Department of Environment conservation officers or hunting and trapping organizations in each village. In Greenland, harvest reporting is also mandatory. The harvest of a marked bear is reported on a separate form to the GINR and the Department of Fishery, Hunting and Agriculture in Nuuk. In each country, information on date, location, sex, and approximate age is recorded, and ear tags and tattoo numbers are also submitted. Hunters in both Nunavut and Greenland receive token payment for this harvest information. The mark-recapture-recovery model (Burnham, 1993) requires the incorporation of all tag returns, including those from outside the marking area; therefore, tag returns outside of Baffin Bay (Fig. 1) were included in the analysis.

Following Taylor et al. (2005), we used the Burnham (1993) recovery-recapture model to estimate total survival (S), recapture (p), and recovery (r) probabilities and their variances. For harvest recovery probability, we incorporated factors allowing recovery to vary with sex and age groupings: juvenile, ages 0 and 1; male non-juveniles; and female non-juveniles. We also examined how recovery and survival varied over time. We grouped years into time periods (*timeperiod* variable) for modeling of recovery and survival probabilities, because low sample size resulted in parameters hitting boundaries (0 and 1) if allowed to vary annually. Because the calculation of natural survival (S_N; survival not including harvest mortality) is dependent on both total survival and recovery $(\hat{S}_N = \hat{S} + (1 - \hat{S})\hat{r})$, we used the same groupings of *timeperiod* for both S and r. To define the time periods, we examined the total recorded harvest in Baffin Bay for temporal patterns (Fig. 2a) and grouped years into time periods that corresponded approximately to changes in levels of recorded harvest. For example, recorded harvest increased in 2003, so the last time period was 2003–09. Other time periods spanned approximately 8 years. Season of capture was an important variable describing the survival of polar bears in the earlier study (Taylor et al., 2005), and therefore both S and r were modeled by season of capture (fall vs. spring). For modeling total survival, we also assessed various age groupings: subadult (age 2–4 years) vs. adult (5 years or more); juvenile vs. non-juvenile; four age classes (cub-of-the-year or COY, yearling, subadult, adult); and the age classes used in Taylor et al. (2005). We examined models for survival separately for male and female adults. Preliminary modeling results suggested the submodel (*females and young + subadult*) best explained variation in recapture probability, and we therefore report only on models that include this specific submodel for recapture probability. Females (with or without dependent young) and dependent young (COY and yearling) were modeled together, yet were allowed to differ in their recapture probability from both subadults (of either sex) and adult males. We fixed the fidelity parameter
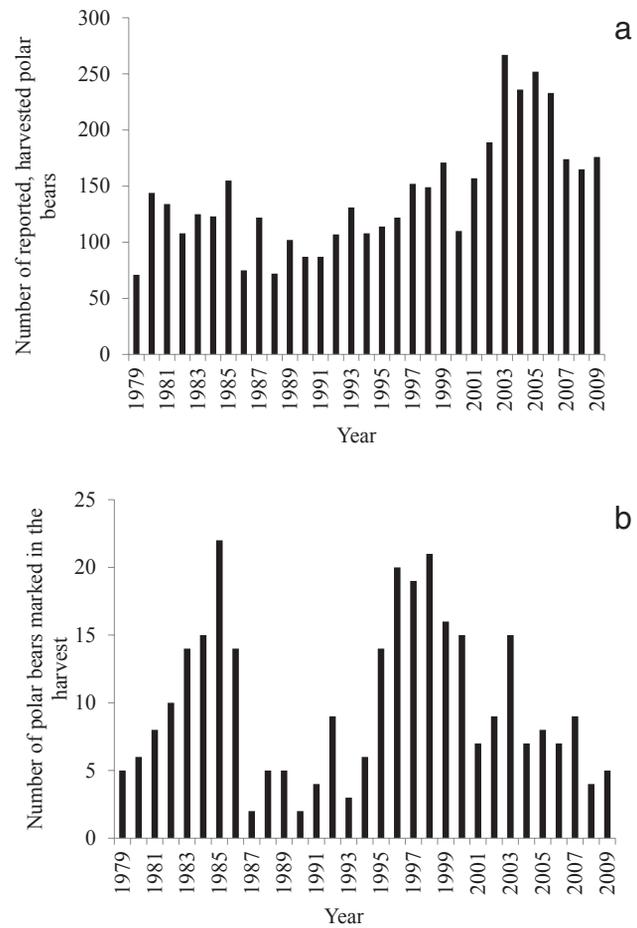

FIG. 2. a) Reported polar bear harvest by Nunavut and Greenland in Baffin Bay (1979–2009). b) Number of polar bears marked in capture efforts in Baffin Bay that were harvested in Nunavut and Greenland (1979–2009). Systematic marking took place in 1974–79, 1980–85, 1989–93, and 1994–97 (with little effort in 1996; cf. Taylor et al., 2005).

at 1; we assumed all bears who emigrated did so temporarily. We implemented models in MARK (White and Burnham, 1999), using the RMark interface (Laake and Rexstad, 2007). We ran models with various combinations of the submodels for S, r, and the p submodel. We provide model-averaged estimates of S and r from models with ΔAICc < 2.0 and sufficient change in deviance to constitute an important model (Arnold, 2010). Natural survival was calculated (see above) from model-averaged estimates of S and r; the variance of S_N was calculated using the delta method (Seber, 1982):

$$\mathrm{v\hat{a}r}(\hat{S}_N) = \mathrm{v\hat{a}r}(\hat{S})(1-\hat{r})^2 + \mathrm{v\hat{a}r}(\hat{r})(1-\hat{S})^2 + 2\,\mathrm{c\hat{o}v}(\hat{S},\hat{r})(1-\hat{r})(1-\hat{S})$$

We present data for adult females as representative for all sex and age classes, as their survival does not markedly differ from that of males; in addition, population growth, in general, is most sensitive to adult female survival.

To assess trend in optimal habitat during spring, we extracted daily sea ice concentration values from satellite passive microwave data available from the National Snow and Ice Data Center (Cavalieri et al., 2008). We then

calculated sea ice concentration specifically for areas over the continental shelves (< 300 m in depth) of Baffin Island (42 282 km^2; *biapriljune*) and West Greenland (127 324 km^2; *wglapriljune*), since this habitat type has previously been defined as optimal habitat for polar bears (Durner et al., 2009). We calculated ice concentrations over these two areas for April, May, and June, the season in which polar bears intensively hunt pups of ringed seal (*Pusa hispida*). We used a break-point linear regression model to assess the trend(s) in the area-weighted average of these concentrations in both areas combined (West Greenland + Baffin Island; *wglbiapriljune*). We evaluated regressions for all possible years as break-points and chose the model with the lowest residual standard error.

We compared a null survival submodel without the broad effect of *timeperiod*, i.e., (*season + juv + subadult*), to models in which ice covariates were added iteratively (Arnold, 2010). We examined the influence of the ice variables described above (*biapriljune, wglapriljune, wglbiapriljune*) and the following other metrics: the average daily ice concentration at peak ice concentration in March (*icemarch*); the average daily ice concentration between May and October from satellite passive microwave data (*summerice*; Rode et al., 2012; Peacock et al., in press); and the day of the year when ice concentration in Baffin Bay declines to a value below 50% (*breakup*; Stirling and Parkinson, 2006). Because survival is not a very sensitive population parameter for long-lived species, we reasoned that it would most likely vary with a cumulative change in environmental conditions. Therefore, we assessed variation in survival with respect to an average of each ice metric in the three years prior to survival estimation (this step required restricting the data set to begin in 1982, as ice data were available only starting in 1979). The importance of these models was assessed by evaluating ΔAICc with respect to the null model (Arnold, 2010) and with chi-square tests (α = 0.05) on the differences in model deviances.

In a separate analysis, we used data from 1979–97 and estimated total survival (a) with recovery data only and (b) with both recapture and recovery data to compare the results of using harvest recovery data only (i.e., a situation comparable to 1998–2009) and using recovery and recapture data combined. Differences in point estimates of survival derived from these two data sets can help interpret differences in survival estimates for the later time period in the new main analysis (2003–09), which is based on recovery data only. For this supplementary exercise, we used the competitive model from the main analysis (ΔAICc = 1.62) that used season in each of the submodels for *S* and *r*: *S*(*season + juvenile + subadult + timeperiod*)*r*(*season + juvenile + nonjuv:male + timeperiod*)*p*(*femandyoung + subadult*)*F*(1). The categories for *timeperiod* were slightly different, as we did not include data from 1998 to 2009.

Finally, in a fourth analysis, we examined the variance of total survival probability with respect to time since the last year of marking (1997). We added a time-varying element to the survival and recovery submodels so that the

parameters are estimated with time bins before 1997, as in the primary analysis, but yearly from 1998 on. While this partial time-varying model—*S*(*season + juv + subadult + timeperiod_time varying after 1997*)*r*(*season + juv + nonjuv:male + timeperiod_time varying after 1997*)*p*(*femandyoung + subadult*)*F*(1)—is not a well-supported model in comparison to models that restrict survival and recovery to time bins, we use it heuristically to observe the pattern of variance with respect to time since marking.

RESULTS

We recorded the harvest of 99 polar bears originally marked in Baffin Bay in the 12 years (1998–2009) since the last marking year (note that recoveries in 1998 were included in Taylor et al., 2005). Of 306 marked bears recovered in the harvest during 1979–2009 (Fig. 2b), 18.3% (n = 56) were recovered from other populations outside of Baffin Bay and incorporated in the modeling (31 in Lancaster Sound, 18 in Davis Strait, 4 in Kane Basin, and 1 each in East Greenland, Foxe Basin, and M'Clintock Channel; Fig. 1).

The most competitive models (Table 1) for the estimation of survival, recovery, and recapture using all capture and recovery data from 1979–2009 included factors similar to those found by Taylor et al. (2005); season of capture, time, and sex and age class explained important variation in the modeling of survival, recovery, and recapture (Table 2). Male and female adult bears differed only slightly in survival; sex appeared in the first model with ΔAICc = 1.8. We model-averaged natural and total survival parameter estimates from the top three competitive models (here we present only estimates for polar bears captured in the fall; Table 3). Time was an important variable describing variation in total survival (Table 2, Fig. 3); total and natural survival are lower for the latest time period (β$_{(2003-09)}$ = -2.07 (SE, 0.45); β/SE = -4.48) than for earlier time periods, although variance of these estimates is considerably higher. β/SE is presented (Table 2) as a ratio of signal to noise to indicate the strength of the influence of the variable on survival. Polar bears captured in the spring have lower total survival than those captured in fall (Table 2). Current estimates (2003–09) of natural and total survival of adult female polar bears captured in the fall were 0.871 and 0.859, respectively (Table 3).

We fit a significant break-point regression to the trends of ice concentration over the continental shelves of Baffin Bay from 1979 to 2009 (April–June; $F_{3,27}$ = 23.14; R^2 = 0.72, p < 0.000). We found a significant declining trend in this metric (*wglbiapriljune*) since 1994 (t = 4.147, p = 0.003; Fig. 4). In our null-model approach, the survival submodel (*season + juv + biapriljune*) outperformed the null model (*season + juv + subadult*) (ΔAICc of null model = 1.82; Table 4), demonstrating a positive effect of spring ice concentration over the continental shelf of Baffin Island on polar bear survival (β$_{biapriljune}$ = 0.06 ± 0.03, SE). The variables *wglbiapriljune*,

TABLE 1. Model selection results for models with ΔAICc ≤ 2, fitted to mark-recapture-recovery data for polar bears in the Baffin Bay population (1979–2009). In model names, *timeperiod* denotes estimation of *S* and *r* for these time bins: 1979–86; 1987–94; 1995–2002; 2003–09. The term *nonjuv:male* denotes the estimation of parameters that vary between sex for independent polar bears, whereas *juv* represents COY and yearlings (of both sexes). *Season* is the season (fall or spring) of capture. *Sex* is male vs. female. For all models, the submodel *p* was the same: (*femandyoung + subadult*); *femandyoung* differentiates recapture rates of adult females and dependent young (whether adult females have young or not) from other bears; *subadult* denotes separate estimation of recapture rate (and survival rate) for subadult bears. For all submodels for fidelity, F (~1), indicates that fidelity is fixed at 1. Parameter estimates for total survival (*S*), recovery (*r*), and recapture (*p*) probabilities presented in this paper are model-averaged from estimates from models in this table.

Model	Number of parameters	AICc	ΔAICc	Model weight	Deviance
S(*season + juv + subadult + timeperiod*)r(*timeperiod + juv + nonjuv:male*)	16	7916.42	0.00	0.54	5519.81
S(*season + juv + subadult + timeperiod*)r(*timeperiod + juv + nonjuv:male + season*)	17	7918.04	1.62	0.24	5519.39
S(*season + sex + juv + subadult + timeperiod*)r(*timeperiod + juv + nonjuv:male*)	17	7918.21	1.80	0.22	5519.56

TABLE 2. Estimates and standard errors of logit coefficients for each parameter (*S*, survival; *p*, recapture and *r*, recovery probability) for the top Burnham model (ΔAICc = 0) for mark-recapture-recovery data of polar bears in Baffin Bay (1979–2009). Each effect is additive to the intercept.

| Parameter	β estimate	SE	β/SE
S (Intercept): Adult, fall capture, 1979–86	3.83	0.30	12.96
S: Spring capture	-1.03	0.24	-4.37
S: Juvenile	-1.08	0.40	-2.72
S: Subadult	-0.92	0.16	-5.77
S: 1987–94	-1.21	0.23	-5.16
S: 1995–2002	-0.68	0.39	-1.72
S: 2003–09	-2.07	0.46	-4.48
p (Intercept): Adult male	-1.87	0.14	-13.25
p: Adult females and young	-0.38	0.20	-1.87
p: Subadult	-0.44	0.27	-1.66
r (Intercept): 1979–86, non-juvenile, male	2.35	1.14	2.06
r: 1987–94	-4.72	1.20	-3.92
r: 1995–2002	-3.07	1.17	-2.62
r: 2003–09	-4.65	1.21	-3.85
r: Juvenile	-2.91	1.06	-2.75
r: Non-juvenile, female	0.87	0.20	4.36
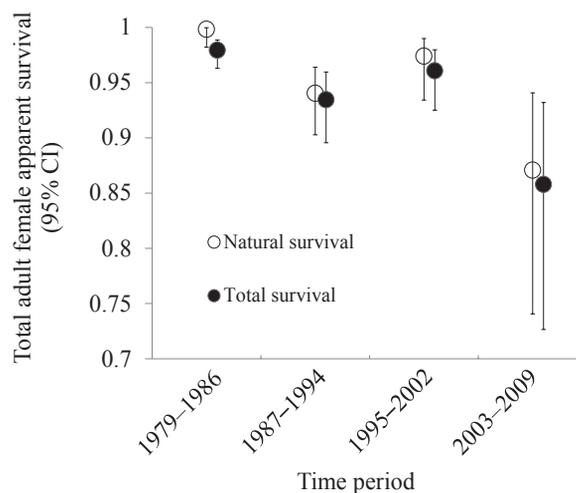
FIG. 3. Model-averaged total apparent (filled circles) and natural (open circles) adult female survival estimates for polar bears captured in the fall and 95% confidence intervals from models (ΔAICc < 2) fitted to mark-recapture-recovery data for polar bears in the Baffin Bay population (1979–2009).

TABLE 3. Model-averaged total apparent and natural survival estimates for polar bears captured in Baffin Bay in the fall in 2003–09. LCL and UCL are the lower and upper limits of the 95% confidence interval.

Age	Sex	Total Survival			Natural Survival		
		Estimate	95% LCL	95% UCL	Estimate	95% LCL	95% UCL
Adult	Male	0.856	0.724	0.930	0.883	0.755	0.949
	Female	0.859	0.726	0.932	0.871	0.741	0.941
Subadult	Male	0.702	0.497	0.849	0.759	0.555	0.888
	Female	0.706	0.501	0.852	0.732	0.527	0.871
Juvenile	Male	0.665	0.392	0.859	0.666	0.393	0.860
	Female	0.669	0.396	0.861	0.670	0.397	0.862

wglapriljune, *icemarch*, *breakup*, and *summerice* appear in models with ΔAICc < 2.0, but the differences in deviances from the null survival submodel (*season + juv + subadult*) are minimal (Table 4).

Using the subset of data for the years when recapture efforts took place (1979–97), we found no consistent pattern in the survival estimates derived from using recapture and recovery data versus recovery-only data (Fig. 5). For the intensive marking period (1992–97), we could not distinguish the point estimates of total survival for adult females from the two data sets (point estimates differ by 1.1%). However, in periods when the marking effort was less intense,

the recovery-only data set gave lower point estimates (1.5% lower for 1979–86 and 4.7% lower for 1987–91).

Using the partial time-varying model, in which we allowed survival and recovery to vary annually only after the 1997 marking effort, variance of the estimates increased, as expected in theory (Fig. 6).

DISCUSSION

Our analysis suggests a decline in both total and natural survival of polar bears in Baffin Bay since the intensive

TABLE 4. Model selection and chi-square results for survival submodels with ice covariates, in comparison to a null survival submodel (without effect of *timeperiod*), fitted to mark-recapture-recovery polar bear data from Baffin Bay (1982–2009). Submodels for *r*, *p* and *F* were kept constant: ($p_{femandyoung + subadult}$, $r_{juv + nonjuv:male + timeperiod}$, F_1). Listed models are those with ΔAICc < 2.0.[1]

Survival submodel	Number of parameters	AICc	ΔAICc	Deviance	ΔAICc from null model	Difference in deviance (compared to null)	df	p-value (compared to null)
(*season + juv + subadult + timeperiod*)	16	7556.73	0.00	5398.11	–	–	–	–
(*season + juv + subadult + biapriljune*)	14	7564.69	7.96	5410.17	-1.22	3.26	1.00	0.07
(*season + juv + subadult*) (null model)	13	7565.91	9.18	5413.43	–	–	–	–
(*season + juv + subadult + ice*)	14	7566.09	9.36	5411.57	0.18	1.86	1.00	0.17
(*season + juv + subadult + icemayoct*)	14	7567.31	10.58	5412.79	1.40	0.65	1.00	0.42
(*season + juv + subadult + wglapriljune*)	14	7567.44	10.71	5412.92	1.53	0.51	1.00	0.48
(*season + juv + subadult + icemarch*)	14	7567.46	10.73	5412.94	1.55	0.49	1.00	0.48
(*season + juv + subadult + breakup*)	14	7567.66	10.93	5413.14	1.76	0.29	1.00	0.59

[1] Top model is the same model structure as in Table 2, except using data for 1982–2009.
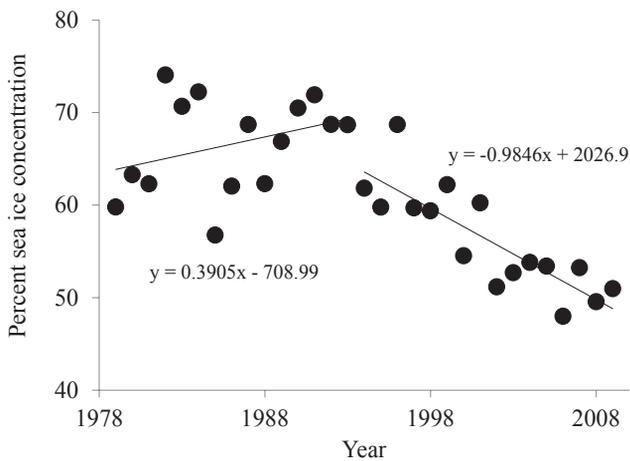

FIG. 4. Break point regression ($R^2 = 0.69$, $p < 0.000$) of area-weighted average of sea ice concentration over the West Greenland and Baffin Island continental shelves (0–300 m; *wglbiapriljune*) for April–June, 1979–2009. Sea ice concentration values were obtained from satellite passive microwave data available from the National Snow and Ice Data Center (Cavalieri et al., 2008).
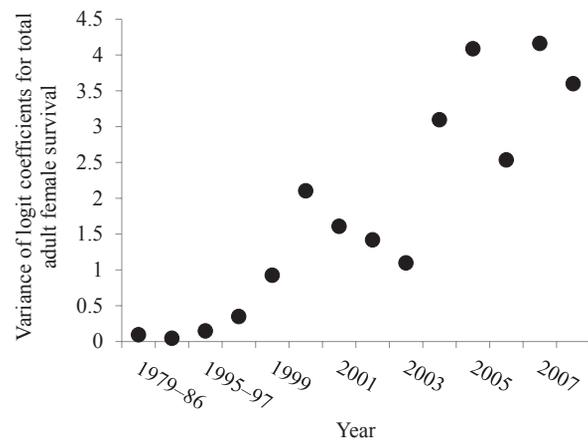

FIG. 6. Variance estimates of logit coefficients of total apparent survival for adult female polar bears (captured in the fall) in Baffin Bay. The principal and last capture effort took place in 1992–97. Estimates are from the model: *S(season + juv + subadult + timeperiod_time varying after 1997)r(season + juv + nonjuv:male + timeperiod_time varying after 1997)p(femandyoung + subadult)F(1)*.
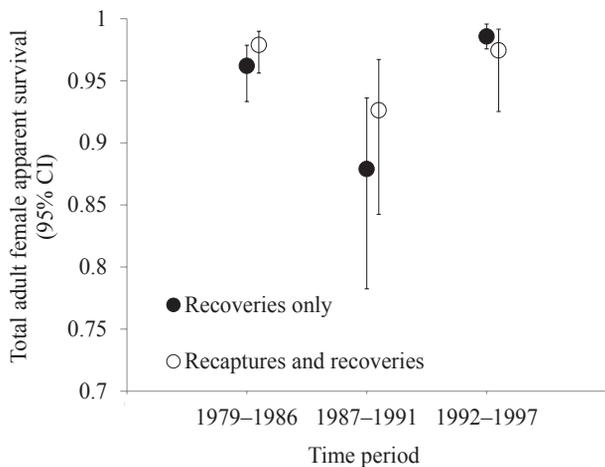

FIG. 5. Total apparent survival rates for adult female polar bears in Baffin Bay (captured in the fall), estimated with recovery data only (filled circles), and recovery and recapture data (open circles) for 1979–97. The principal and last marking effort was 1992–97. Estimates using both data sets are from the model: *S(season + juvenile + subadult + timeperiod)r(season + juvenile + nonjuv:male + timeperiod)p(femandyoung + subadult)F(1)*.

study in the 1990s (Taylor et al., 2005). Because of attrition of marked bears, the variance around the new survival estimates is higher than that of estimates for the period of active marking (coefficient of variation is 6.0% vs. 2.5% for adult male total survival). These new estimates must therefore be interpreted cautiously. However, we suggest any information in the pattern of the recovery of 99 marked individuals over a decade after marking can at least provide contextual information. First, a decline in total survival is consistent with projections of population decline made from data on recorded harvest and from the natural survival and reproductive rates assessed in 1997 (Derocher et al., 1998; Lunn et al., 2002; Taylor et al., 2005; Aars et al., 2006; Obbard et al., 2010). Second, a decline is consistent with previous studies documenting the relationship between decline in sea ice and survival in polar bears. Declines in survival in relation to declining ice habitat, likely due to reduced foraging opportunities or increased energy expenditures, have been found in some populations of polar bears where data are available (Regehr et al., 2007, 2010), but not in all such populations (Obbard et al., 2007; Stirling et al., 2011; Peacock

et al., in press). The concentration of optimal spring habitat for polar bears in Baffin Bay has significantly declined, most notably since the mid-1990s (Fig. 4), and this decline constitutes a plausible hypothesis for a decline in population productivity. The apparent decline in natural survival also suggests that a decline in survival was not attributable to harvest only. Further, our null model approach suggests that the ice metrics explain some of the variation in polar bear survival encapsulated in the broader time variable. The cumulative effect of ice concentration over the Baffin Island continental shelf during spring showed the clearest positive influence on survival. This spring ice variable and other ice metrics did not explain variation in survival in the top models, which suggests that the broad time variable encompasses additional unmeasured and unknown influences on polar bear survival. It must also be stressed that the variance of the estimates of survival rates increased each year after the last marking period, with a substantial increase after the sixth year. Therefore, given this uncertainty, our study does not allow for conclusive results about the relationship between survival and loss of ice habitat in Baffin Bay. Rode et al. (2012) have demonstrated that declines in body condition of bears captured in Baffin Bay from the 1970s to the 2000s were significantly correlated with declines in summertime sea ice concentration; therefore, declines in natural survival may correspond to increased nutritional stress. Studies of traditional ecological knowledge have also reported observations from local Inuit hunters and elders of increasing instances of polar bears in Baffin Bay in poor body condition (Dowsley and Wenzel, 2008; Born et al., 2011). Obbard et al. (2007) suggested that declines in body condition in southern Hudson Bay may precede declines in demographic parameters.

Our modeling exercise comparing analyses using recovery-only and recapture-and-recovery data suggests that a decline in the survival estimates is not due solely to the change in how marks were collected. In years with relatively greater numbers of marks in the population (1992–97), survival rates from recovery-only and recapture-and-recovery data sets were indistinguishable. However, in years when fewer marks were available (as in 1999–2009 in the present study), the point estimates of survival made using recovery-only data were lower (Fig. 5).

Our analysis showed that 56 of 309 harvested polar bears (18%) marked in Baffin Bay between 1979 and 2009 were harvested outside of Baffin Bay. In our study, we fixed the fidelity parameter at 1, and our estimates of survival could be biased low since survival includes both actual mortality and permanent emigration. Therefore, we also re-ran our top models allowing for the estimation of fidelity (best model with estimated F, $\Delta AICc = 1.86$), and obtained an estimate of F of 0.990 (95% CI, 0.494–0.999). In addition, we did not obtain discernibly different estimates of total survival when we allowed F to be estimated. Further, our understanding of polar bear movement leads us to believe that F is approximately 1, for these reasons: 1) the majority of bears harvested outside of Baffin Bay were harvested

in neighboring populations (95%; in Davis Strait, Lancaster Sound, and Kane Basin); 2) of these bears, 77% were harvested during spring, and population distribution of polar bears during spring is different from that in the fall, when the majority (67%) of Baffin Bay polar bears were marked; 3) therefore, these harvest recoveries outside of Baffin Bay may represent seasonal migration, and not permanent emigration. We also found no pattern in the harvest of marked animals outside Baffin Bay over time. Thus, we also do not believe that the potential for change in population boundaries due to climate-induced change in sea ice habitat is an alternative explanation of our estimated declines in survival. However, we do note that polar bear population boundaries are porous, and it is important to include recoveries outside of the study area to provide the most accurate estimates of survival.

Incorporation of recovery of marked polar bears during mark-recapture studies (e.g., Taylor et al., 2005) allows for the differential estimation of natural and total survival. In this paper, we have shown that harvest recovery information collected after active marking ceases can continue to provide information on both natural and total survival. We suggest that our analysis provides empirical insight to inform the discussion on the appropriate frequency of mark and recapture efforts of polar bears and the utility of harvest recovery data acquired through community-based monitoring during periods of no marking effort. In this particular case for polar bears, in which approximately 43% of the population was marked during the last mark-recapture study (Taylor et al., 2005), we suggest that additional information gained from these recovery data becomes less useful after five years because of increased variation in the parameter estimates. Thus, it would be necessary after this point to deploy additional marks in the population to provide robust information on survival. This period of time would undoubtedly differ among populations of polar bears depending on the degree of demographic isolation, as well as the absolute and relative sample size, of the marked population and harvest sample.

Collectively, Greenland and Canada have 14 populations of polar bears requiring monitoring, and thus a population inventory cycle is needed. We recommend that a study rotation cycle be based on intensive marking studies (physical or genetic marking, or both) of shorter duration (e.g., two years), which may permit shorter intervals between such studies (e.g., < 10 years) and systematic use of recovery data during and after periods of active marking for the annual estimation of survival. If intervals between intensive marking periods are extensive (e.g., 10–15 years), survival estimates retain less validity because of rapidly changing environmental conditions, and scientists cannot take advantage of existing marks in the population. A multi-year genetic mark-recovery study in Baffin Bay commenced in 2011 to update population parameters (GN, unpubl. data; and GINR, unpubl. data). Submission of tissue samples from harvested bears in Nunavut and Greenland will enable recovery of genetic marks from the harvest. An adaptive

approach to deciding how often marking studies are needed (Vongraven et al., in press) could include a program of annual ice monitoring in which dramatic changes in sea ice habitat would trigger a more rapid return to intensive marking of polar bears.

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