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Changes in winter and spring resource selection by polar bears *Ursus maritimus* in Baffin Bay over two decades of sea-ice loss

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ABSTRACT: Loss of Arctic sea ice has implications for the distribution and population structure of ice-dependent species such as polar bears *Ursus maritimus*. We used remotely sensed sea-ice concentration data for Baffin Bay, Canada, and satellite telemetry for adult female polar bears in the 1990s (n = 43) and 2000s (n = 38) to assess whether sea-ice habitat changes have influenced movements and habitat selection. Both the timing and availability of sea-ice habitat changed significantly between the 1990s and 2000s. Mean sea-ice concentration in June–October declined from 22 to 12%. Spring sea-ice retreat occurred 2 wk earlier and fall sea-ice advance 2 wk later in the 2000s. These changes translated directly to changes in habitat use by polar bears. In the 2000s, bears used significantly lower sea-ice concentrations in winter and spring. Also, bears were significantly closer to land in all months, except at the end of spring breakup when they remained on offshore sea ice as long as possible, likely to maximize foraging time prior to coming on land where they are largely food deprived. The presence of summer offshore sea ice facilitated broad movement of bears in the 1990s; however, this ice disappeared in the 2000s and resulted in significant declines in monthly movement rates. In the 2000s, adult females selected for lower sea-ice concentrations if they facilitated access to the continental shelf (<300 m). Our findings indicate that significant changes in available sea-ice habitat and habitat use in Baffin Bay have occurred since the mid-1990s and this subpopulation will likely experience negative population-level impacts related to a changing climate in the coming decades. In some other parts of the Arctic, such changes have preceded negative nutritional and demographic impacts.

KEY WORDS: Arctic · Canada · Greenland · Habitat models · Polar bear · *Ursus maritimus* · Sea ice

INTRODUCTION

Polar bears are distributed throughout the circumpolar Arctic in 19 subpopulations (PBSG 2010). Their life history is dependent on sea ice (Amstrup 2003), which is used as a platform to hunt ringed seals *Pusa hispida* and bearded seals *Erignathus barbatus*. Sea ice also facilitates seasonal movements, mating activities and, in some areas, maternal denning (Mauritzen et al. 2001, Fischbach et al. 2007, Derocher et

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al. 2011). Earlier sea-ice breakup and reductions in preferred ice habitat have been linked to reductions in body condition, survival, reproduction, and abundance in some polar bear subpopulations (Stirling et al. 1999, Derocher 2005, Regehr et al. 2007, 2010, Rode et al. 2012, Bromaghin et al. 2015, Lunn et al. 2016, Obbard et al. 2016). Additional studies have documented use of less optimal sea-ice habitat in several polar bear subpopulations but have not found evidence for negative demographic effects (e.g. Durner et al. 2009, Wilson et al. 2014, Laidre et al. 2015a, McCall et al. 2016, Lone et al. 2018). This indicates that a time lag exists between habitat loss and detection of population-level impacts, and suggests that changes in habitat use may be a useful indicator of future demographic change. Based on current and projected declines in sea ice, the polar bear is listed as 'Vulnerable' on the IUCN Red List of Threatened Species (Wiig et al. 2015) and 'threatened' under the US Endangered Species Act (USFWS 2008). Accordingly, resource managers need improved knowledge and tools to effectively manage and conserve polar bears under climate-induced sea-ice loss while concurrently managing subsistence harvest (Regehr et al. 2017a) and mitigating human–polar bear conflicts (Wilder et al. 2017).

The Baffin Bay (BB) polar bear subpopulation occurs in the eastern Canadian Arctic and West Greenland and is harvested by subsistence hunters from 3 communities in Nunavut, Canada, and from 35 communities in Greenland (SWG 2016). BB is considered part of the seasonal ice ecoregion (Amstrup et al. 2008), where melting sea ice forces bears onto land for several months, where they have negligible access to seals (Ferguson et al. 1997, Taylor et al. 2005, Stirling & Parkinson 2006, Rode et al. 2012). Bears hunt seals throughout the ice-covered season and during spring have a hyperphagic period when ringed seal pups are abundant. A portion of the energy obtained during this period is converted to fat stores that are subsequently used during the ice-free season while bears are fasting or have restricted access to food (Stirling et al. 1977, Wiig et al. 2008, Stirling & Derocher 2012, Whiteman et al. 2017). Thus, the timing and availability of sea ice has significant impact on body condition and reproduction (Rode et al. 2012, 2014), and ultimately survival of polar bears (Regehr et al. 2007, 2010, Lunn et al. 2016).

General assessments of sea-ice habitat suggest that the BB region has experienced a long-term reduction in sea-ice cover and a trend towards earlier spring break-up and later fall freeze-up (Stirling & Parkinson 2006, Stern & Laidre 2016), consistent with declining sea-ice trends across the Arctic (Comiso 2002, 2012, Stroeve et al. 2012, Parkinson 2014). Experienced polar bear hunters living on the coasts of BB have reported changing sea-ice conditions during the last few decades and noted that these changes affected the distribution and body condition of polar bears (Dowsley & Wenzel 2008, Born et al. 2011). Scientific understanding in BB has been aided by live-capture sampling and movement data collected by satellite radio-telemetry (e.g. Taylor et al. 2001), but until now were restricted to data from the 1990s and did not provide information about changes in movements or habitat use during the current era of sea-ice loss. In this study, we use resource selection functions (RSFs) based on 2 decades of satellite telemetry movement data from BB adult female polar bears to quantify changes in movement rates and sea-ice habitat use during 2 periods of intensive population studies (1991–1997 and 2009–2015). The results of this work provide important insight as to how environmental change broadly impacts polar bears in seasonal ice ecoregions and how these changes may affect management and conservation.

MATERIALS AND METHODS

Study area

BB is bounded by Greenland to the east, Baffin Island to the west, the North Water polynya in the north, and Davis Strait to the south (Fig. 1). During late spring and summer break-up, sea ice recedes from Greenland across Baffin Bay; the last remnants of ice typically occur off the coast of Baffin Island. Approximately 28% of BB has a mean depth <300 m, with a continental shelf located along the east coast of Baffin Island and a wider shelf along the west coast of Greenland. The management boundaries of the BB polar bear subpopulation encompass an area of ~1 million km^2, covering portions of Baffin Island and all of Bylot Island (66.2° N to 73.8° N) in Nunavut, Canada, as well as parts of West and Northwest Greenland (66.0° N to 77.0° N; Taylor et al. 2005).

Sea-ice habitat analysis

Following Stern & Laidre (2016), we used the 'Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data' (Cavalieri et al. 1996, updated yearly) dataset (National Snow and Ice Data Center) in our analyses. This product is

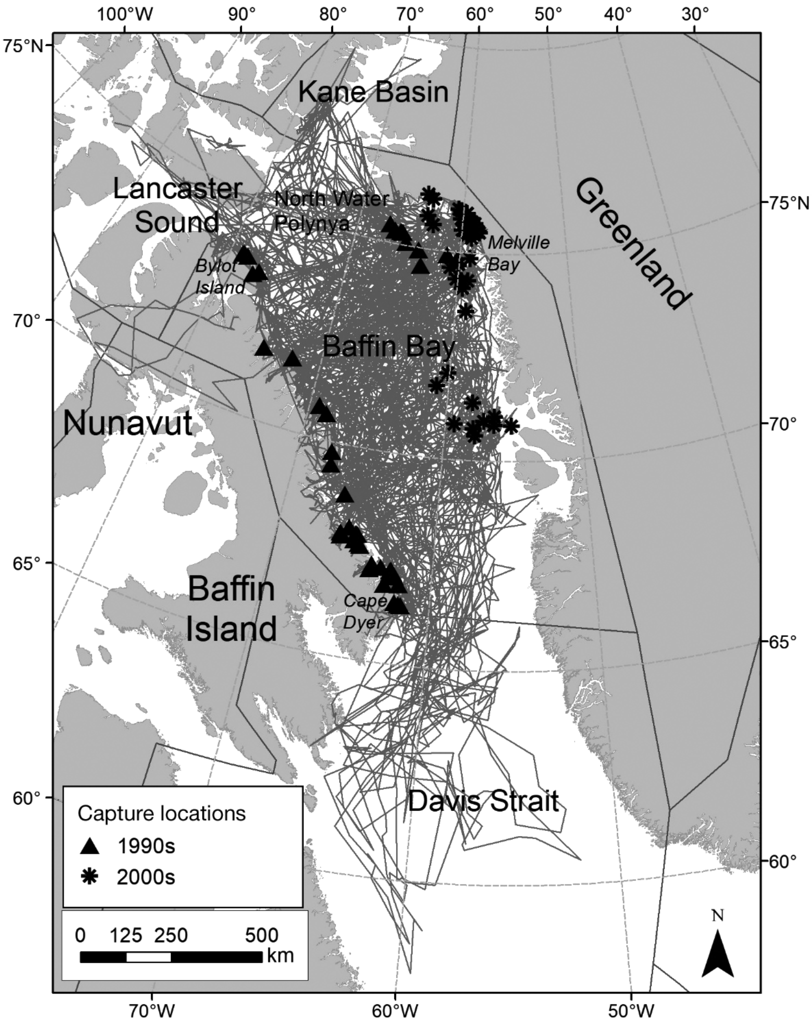

Fig. 1. Distribution of capture locations (symbols) and movements of collared adult female polar bears in Baffin Bay (gray tracks). Note in the 1990s, bears in Baffin Bay were captured mainly on Baffin Island in fall whereas in the 2000s bears were captured on the sea ice in West Greenland, before moving to Baffin Island

designed to provide a consistent time series of sea-ice concentrations (the fraction, or percentage, of ocean area covered by sea ice) spanning the coverage of several passive microwave instruments. Sea-ice concentrations are produced using the NASA Team algorithm, and provided in a polar stereographic projection (true at 70° N) with a nominal grid cell size of 25 × 25 km (cell size varies slightly with latitude). Temporal coverage is every other day from 26 October 1978 to 9 July 1987, then daily to 31 December 2016.

We assessed sea-ice habitat change in BB in 3 regions: (1) the entire marine area in the BB management unit, (2) the area over shallow depths (<300 m) along the coast of Baffin Island, and (3) the area over shallow depths (<300 m) along the coast of West Greenland. In each region, we calculated the mean March sea-ice area and the mean September sea-ice area over the period 1979–2014, and defined a threshold (*T*) to be halfway between the 2 means. We then identified the date each spring when the sea-ice area dropped below *T* on its way to the summer minimum and the date each fall when the sea-ice area rose above *T* on its way to the winter maximum (Fig. 2). These are referred to as the date of sea-ice retreat and the date of sea-ice advance, respectively. For each of the 3 regions and 2 BB scientific study periods (1991–1997 and 2009–2015), we calculated the mean date of sea-ice retreat, the mean date of sea-ice advance, and the mean sea-ice concentration from June to October.

For every 25 × 25 km grid cell, we calculated the number of days per year that sea-ice concentration exceeded 15% and called this the number of ice-covered days (e.g. Cherry et al. 2013). We then used these data to examine trends in the number of ice-covered days at every grid cell over the period 1979–2016 (Fig. 3).

Sea-ice habitat use and resource selection models

Between mid-March and mid-April 2009–2013, we used an Ecureuil AS350 helicopter to search for polar bears on the fast ice and pack ice of BB in Northwest Greenland. Searches occurred out to a maximum distance of 150 km from the coast or along areas with consolidated glacier ice at the foot of marine-terminating glaciers. Polar bears were chemically immobilized using a projectile syringe fired from the helicopter, and handled using standard techniques (Stirling et al. 1989). Field estimates of age and reproductive status were recorded. Age was confirmed by counting cementum growth layers in a pre-molar tooth extracted during handling (Calvert & Ramsay 1998). Adult females were defined as ≥5 yr old and classified as independent, with an adult male (AM), or with dependent cubs (cub of year [COY], yearling [YRL], or 2-yr-old [2YR]) (Table 1).

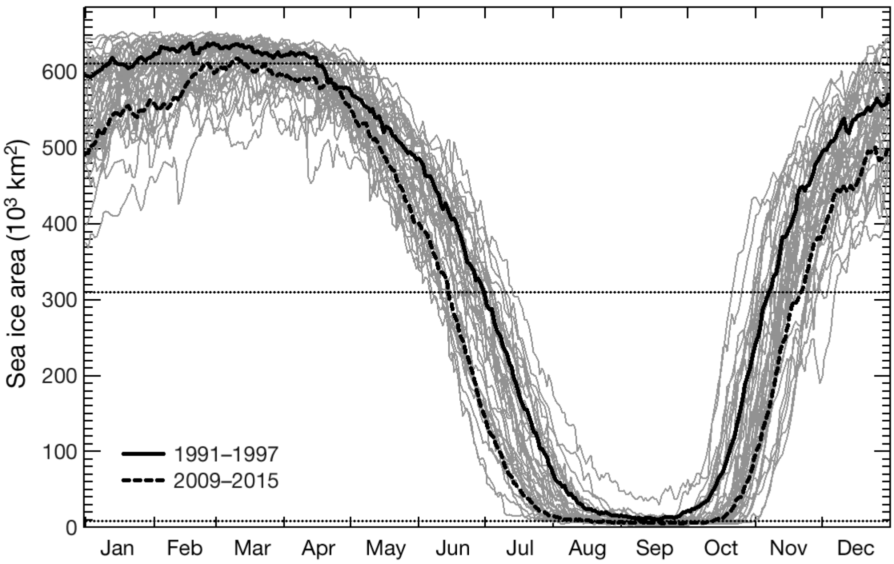

Fig. 2. Seasonal cycle of sea-ice area in Baffin Bay for 1979–2016 (light gray curves). The heavy lines through the annual curves represent 7 yr averages for the 2 sampling periods when polar bears were collared and tracked (1991–1997 and 2009–2015). The threshold for defining the dates of sea-ice retreat and advance (middle horizontal dotted line) is halfway between the average March sea-ice area (upper dotted line) and the average September sea-ice area (lower dotted line)

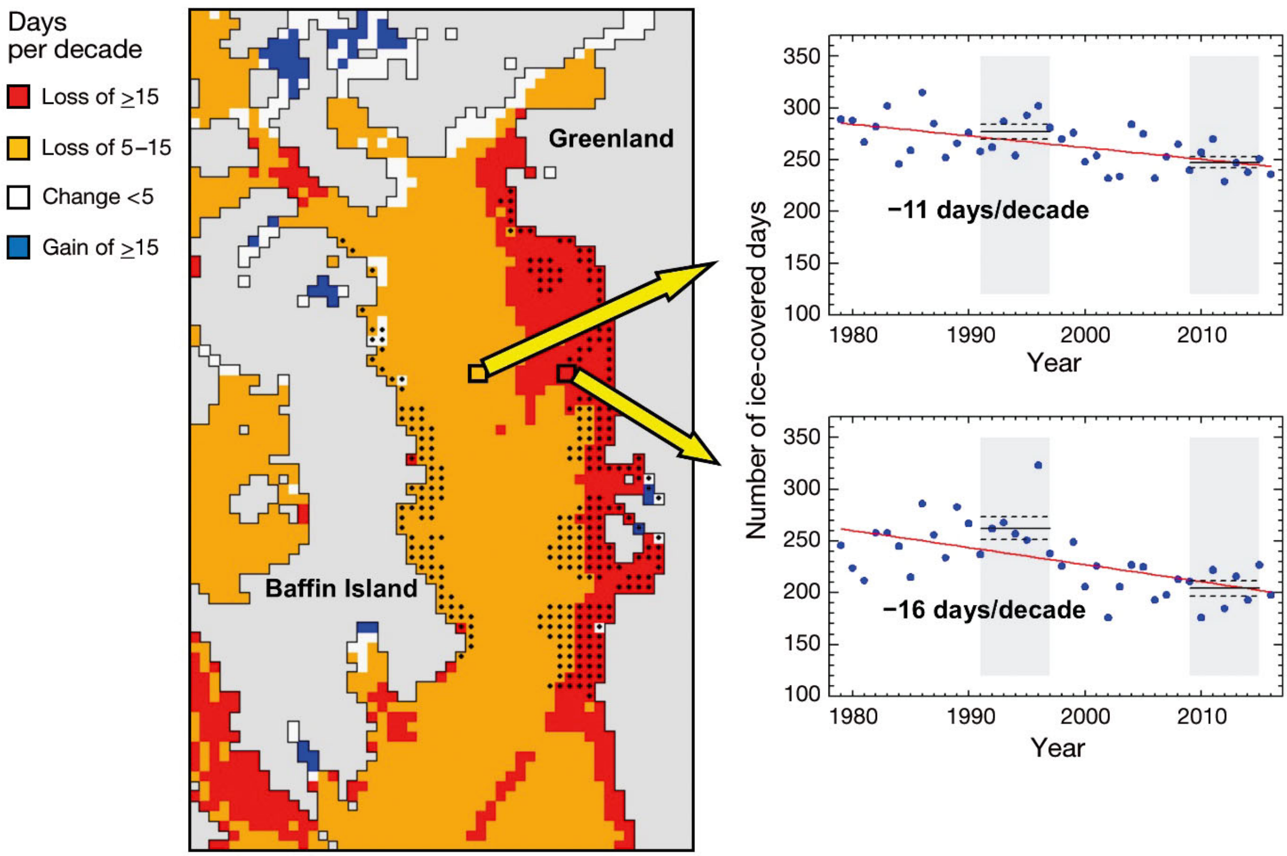

Fig. 3. Change in the number of ice-covered days (sea-ice concentration >15%), 1979–2016. Grid cells (25 × 25 km) containing black dots are those where depth <300 m. Time series of the number of ice-covered days are shown for 2 representative grid cells, one in central Baffin Bay (upper right) and one close to the coast of Greenland (lower right). Least-squares fits (red lines) and numerical trends are indicated. Gray bars indicate the early (1991–1997) and late (2009–2015) study periods. Within each study period, the mean number of ice-covered days is shown (horizontal black segment) along with ±1 SE of the mean (horizontal dashed segments). The decline in the number of ice-covered days from the early period to the late period is statistically significant

Table 1. Number of adult female polar bears from the Baffin Bay subpopulation collared in the 1990s and 2000s in relation to accompanying bears. AM: adult male as mating pair; COY: cub of the year; YRL: 1-yr-old cub; 2YR: 2-yr-old cub. Table includes adult females (n = 7) that were collared in the 2000s but remained at glacier fronts, and which were not included in resource selection function analyses

Decade	Alone	Adult female accompanied by				Sum
		AM	COY	YRL	2YR	
1990s	9	0	19	13	2	43
2000s	10	2	6	12	8	38

Adult female polar bears were fitted with TAW-4610H satellite radio collars (Telonics) that provided information on geographic location, internal transmitter temperature, and activity. Collars were programmed to transmit during one 6 h period each day at 4 d intervals. Each collar came from the manufacturer with a programmable release mechanism that opened on a preset date and time, which allowed the collar to drop off without the need to relocate and immobilize the bear.

We combined the movement data from these bears with historical data from 43 adult female polar bears from BB that had been collared as part of subpopulation studies conducted during 1991–1997 (Ferguson et al. 2000, Taylor et al. 2001, Greenland Institute of Natural Resources and Government of Nunavut unpubl. data), to assess whether changes in movements and habitat use have occurred.

Data filtering and subsampling

Data on location and transmitter status from all polar bears were collected via the Argos Location Service Plus system (Toulouse, France). Location qualities were assigned by ARGOS to each position, with location qualities of 0–3 estimated to have errors of 1.5 km or less, whereas those categorized as 'A,' 'B,' or 'Z' did not have a predicted accuracy (Argos 2016). Unrealistic and poor-quality locations were removed using a speed and angle filter in R version 2.13.2 (R Development Core Team 2013) using the package 'argosfilter' (Freitas et al. 2008). The filtering algorithm removed locations that exceeded a maximum between-location speed of 10 km h^{-1} (based on previous movement studies of polar bears, Laidre et al. 2013) and between-location angle (measured from the track between 3 successive locations; set to the default). The resulting locations for each bear were reduced to a single position per day to reduce autocorrelation bias, standardize temporal sampling, and reduce the effects of variable duty cycling among collars. To obtain a daily position for each collar, the first, best-quality location within the period of peak satellite passage was selected. Daily positions, after filtering and optimal daily position selection, only consisted of ARGOS location qualities 1–3. Distances between successive daily positions were calculated as the great circle route and used to compute minimum daily displacements.

Due to variable objectives in both decades, different duty cycles were used to extend battery life or gather information from specific time periods. The 1990s collars were programmed to transmit on varying and intermittent intervals, ranging from 1 to 6 d, while the 2000s collars were all on a 4 d cycle. We subsampled the 1990s data and created a strict 4-, 5- or 6-d interval time series for each individual to best match the 2000s data. This ensured that the impact of serial autocorrelation was largely consistent.

Data were divided into 3 seasons: spring (March–July, which included the peak of sea-ice coverage and initiation of sea-ice break-up in the 1990s or end of break-up in the 2000s), summer (August–October, which included the end of break-up in the 1990s and the on-land period) and winter (November–February, which included the freeze-up period and time when bears return to the sea ice). Location data associated with maternity and shelter denning periods were identified (Escajeda et al. 2018) and removed from habitat models. Telemetry data were truncated at 1 April 2015 for analysis.

Comparison of 1990s and 2000s BB satellite telemetry data

Polar bears collared in this study ranged over the entire BB region (SWG 2016). All captures occurred within the bounds of the BB subpopulation management unit (PBSG 2010), and bears moved back and forth freely between Canada and Greenland during both periods (Fig. 1). However, seasonal and geographic differences in capture locations occurred in our study between the 2 periods of field work. In the 1990s, it was possible to deploy collars on adult females (AFs) on both the Canadian and Greenlandic sides of BB (Fig. 1). However, in the 2000s it was only possible to deploy collars on the Greenlandic side of BB due to opposition to immobilization and handling of polar bears in Nunavut, Canada (SWG 2016). This reservation was not shared in Greenland by hunters and management authorities.

Prior to conducting interdecadal analyses of polar bear movement data, we evaluated the 1990s and 2000s data to identify potential effects of differences in collar deployment location. First, we compared the fall telemetry locations of bears collared on the Greenlandic side in spring in the 2000s with the fall telemetry locations of bears collared on the Canadian side (on Baffin Island) in the 1990s. Second, we quantified the range of latitudes on land on Baffin Island that were used by polar bears in both decades. Third, we compared an RSF model based on location data for the subsample of bears collared on the Greenlandic side in spring in the 1990s (n = 9) with a model based on location data for bears collared in the same area in spring in the 2000s. We tested for differences across decades in environmental selection effects through the use of covariate-by-decade interaction terms. Fourth, we evaluated seasonal effects by building a RSF based on location data for the 1990s only, with interaction terms between each predictor and an indicator of capture season. This overall sensitivity analysis examined resource selection patterns across decades for bears only collared in spring with this smaller but more homogeneous sample. Of note, this exercise substantially reduced the sample size in the 1990s (two-thirds of the data were removed and power was limited) but addressed any potential differences in resource selection by collaring site or season.

Overall, this evaluation suggested that the 1990s and 2000s data provided a valid basis for comparison of habitat-use patterns in BB across decades. Excluding bears that were permanent residents of Melville Bay, 92% of the AF bears collared in spring in West Greenland in the 2000s moved to Baffin Island by fall and were located inside the same fall collaring area used in the 1990s (defined as a polygon around 1990s collaring sites). Further, AF bears collared in West Greenland in the 2000s were distributed over the same range of on-land latitudes on Baffin Island in fall as those collared in the 1990s (66°30′N to 73°50′N), confirming that bears from West Greenland in the 2000s used the same areas as those captured in the 1990s. Finally, our sensitivity modeling using the subset of 1990s AF bears collared in spring on the sea ice in West Greenland (n = 9) compared with the full sample of 2000s bears showed the same habitat selection in spring (see 'Results' for details). These analyses demonstrate that bears captured in West Greenland in spring used the same geographical areas, had the same seasonal movement patterns, and the same habitat preferences as bears captured on the east coast of Baffin Island in fall.

Movement rates

We calculated daily (4 or 5 d) movement rates for AFs and summarized averages by decade and month. We used the decade-specific mean monthly movement rate (±2 SD) for the radius of potential habitat selection at each time step in the RSFs, following the approach used by Durner et al. (2009) and Laidre et al. (2015a). We used 400 km (or roughly 12 d of travel) as the maximum step length possible in the data.

Habitat covariates for RSF

We used daily sea-ice concentration values in comparative analysis between the 1990s and 2000s. Sea-ice habitat for each polar bear location was defined at 2 spatial scales: (1) the sea-ice concentration pixel value where the bear was located and (2) the mean sea-ice concentration within a region consisting of the 3 × 3 block of pixels centered at the bear location (nominal area 5625 km^2). We also calculated the distance from each polar bear location to the sea-ice edge and the distance from each polar bear location to the Baffin Island coastline. The sea-ice edge covariate estimated the distance (in km) from the bear's location to the center of the nearest pixel using 2 concentration thresholds: 15 and 50%. The 15% sea-ice concentration was used as a delimiter between sea ice and open water, whereas the 50% sea-ice concentration was a delimiter between suitable polar bear habitat and ice break-up conditions (see Stirling & Parkinson 2006, Cherry et al. 2013). Distances were determined by great circle calculations based on latitude and longitude.

We used the International Bathymetric Chart of the Arctic Ocean (IBCAO 3.0, 500 m grid cell size; Jakobsson et al. 2012) to estimate the depth (m) at the bear location and to determine whether the bear was in one of 3 depth categories (shelf: <300 m; intermediate: 300–1000 m; basin: >1000 m). We also calculated the distance of the bear to the shelf break (considered to be the 300 m contour). There were no values in the IBCAO grid that occurred at the southern extent of the BB management area (south of 64°N); therefore, we used the Earth topography five minute grid (ETOPO-5) digital relief dataset (1 km grid cell size) for depth (Edwards 1989). For both winter and spring models, we also included a variable that indicated whether polar bears moved to land from sea ice, to evaluate temporal changes in the relative selection of land versus ice.

Circular buffers created around each polar bear location represented the available habitat bears could select, where the size of the buffer depended on collar duty cycle (i.e. a 4, 5, or 6 d interval) and the mean monthly decade-specific movement rates (±2 SD). Fifty random locations in each buffer were sampled for each time step to represent candidate locations not selected by the bear (i.e. pseudo-absence locations). This control dataset was considered to represent local habitat availability (see also Laidre et al. 2015a). All pseudo-absence locations were linked to the same habitat variables listed above using ArcGIS (ArcGIS 10.1, ESRI). A maximum time gap of 12 d or 400 km distance was used.

RSF sea-ice models

Univariate habitat utilization was quantified and contrasted for each habitat covariate (e.g. only pixels where the bear was present) in the 1990s and 2000s. Multivariate conditional logistic RSF models were then built for each season and decade. We selected variables for multivariate analyses *a priori* based on biological hypotheses; thus we did not include variables in the same model that were biologically redundant (e.g. continuous depth vs. distance to 300 m shelf) or highly correlated (e.g. distance to 15 and 50% sea-ice concentration). Models were fit to data from each decade separately, and a combined model was fit to data from both decades to evaluate temporal changes using covariate-by-decade interaction terms. We used conditional logistic regression with matched location/pseudo-absence sets (CLOGIT function from SURVIVAL package) (R Development Core Team 2013, Therneau 2015) to model the strength of preference for habitat parameters in the 1990s and 2000s.

RESULTS

Sea-ice changes in BB

Over the interval between research programs (1991–1997 to 2009–2015), sea-ice retreat (break-up) occurred 2 wk earlier in spring and sea-ice advance (freeze-up) occurred 2 wk later in fall across the whole region (Table 2). Similar changes in sea-ice retreat occurred over the Baffin Island and West Greenland continental shelves (<300 m depth). Sea-ice advance over the Baffin Island shelf in fall occurred, on average, 9 d later in the 2000s than in the 1990s; however, on the West Greenland shelf, sea-ice advance occurred 30 d later. Mean sea-ice concentration during June–October declined significantly across the whole region (22 to 12%), over the Baffin Island shelf (29 to 21%), and over the West Greenland shelf (13 to 5%) (Table 2). The number of ice-covered days in BB declined at every 25 × 25 km grid cell (Fig. 3), with the steepest declines occurring on the shelf along the coast of West Greenland.

Movements of BB polar bears

Thirty-eight adult females in all reproductive states (alone, as mating pairs, or together with COY, YRL or 2YR cubs) were collared in the 2000s and 43 were collared in the 1990s (Fig. 1). Over the course of these studies, individuals were tracked from ~6 mo to 4 yr. Bears captured in 2009 had a mean tracking duration of 1188 d (range 304–1607), in 2010 a mean of 691 d (range 35–1161), in 2011 a mean of 524 d (range 24–1173), in 2012 a mean of 235 d (38–823), and in 2013 a mean of 674 d (310–754). The shorter tracking duration of 2012 collars was believed to be the result of mechanical failure of release mechanisms. General patterns of movement showed that adult females broadly covered and used most of the available sea

Table 2. Mean date of spring sea-ice retreat, mean date of fall sea-ice advance, and mean June–October sea-ice concentration, during the early period (1991–1997) and the late period (2009–2015). All differences between periods are statistically significant (*t*-test, plain font: $p < 0.05$; **bold font**: $p < 0.01$). Means are shown together with ± standard error of the mean. Shelves are <300 m depth

Baffin Bay subregion	Area (10^3 km^2)	Mean date of sea-ice retreat: Spring 1991–1997	Spring 2009–2015	Fall 1991–1997	Fall 2009–2015	Mean June–October sea-ice concentration (%) 1991–1997	2009–2015
Whole region	656	**1 Jul ± 2.8**	**15 Jun ± 2.6**	**8 Nov ± 2.8**	**22 Nov ± 3.6**	**21.7 ± 2.1**	**11.6 ± 1.1**
Baffin Island shelf	48	19 Jul ± 2.4	6 Jul ± 5.0	**5 Nov ± 1.6**	**14 Nov ± 1.6**	29.2 ± 1.2	21.5 ± 2.5
West Greenland shelf	130	**6 Jun ± 3.9**	**19 May ± 2.6**	8 Dec ± 5.5	7 Jan ± 9.9	**13.1 ± 1.7**	**5.5 ± 0.6**

ice in BB in each year and decade. Both the landfast and pack ice were used during winter and spring; during summer as the sea ice receded, bears moved towards Baffin Island. Exceptions to this were a subset of n = 7 polar bears that remained at glacier fronts in Melville Bay, West Greenland (SWG 2016) using fast ice in spring and remnants of fast ice, freshwater glacier ice, or land through the summer and fall. These bears were excluded from the RSF models reported here because they may represent a different ecotype (coastal residents) not tracked in the 1990s. There was some movement by n = 5 bears between BB and Kane Basin during the on-ice season.

Mean monthly movement rates ranged from 5.5 km d^{-1} (October) to 15.8 km d^{-1} (December) in the 1990s and from 1.9 km d^{-1} (September) to 13.8 km d^{-1} (December) in the 2000s (Fig. 4). In general, movement rates were lowest during September and October, and highest in December in both time periods. Adult females had significantly higher movement rates in the 1990s during the ice-free season. In the 2000s, in August, September, and October, movement rates were one-half to one-third of the rates in the 1990s ($p < 0.001$) (Fig. 4). Overall, there was also greater variability in movement rates in the 2000s than the 1990s, perhaps representing a broader range of strategies with changing habitats. The greatest variability in movement rates occurred in the early winter months, November and December, especially in the 2000s, which may be related to variation in timing of freeze-up when bears access the sea ice.

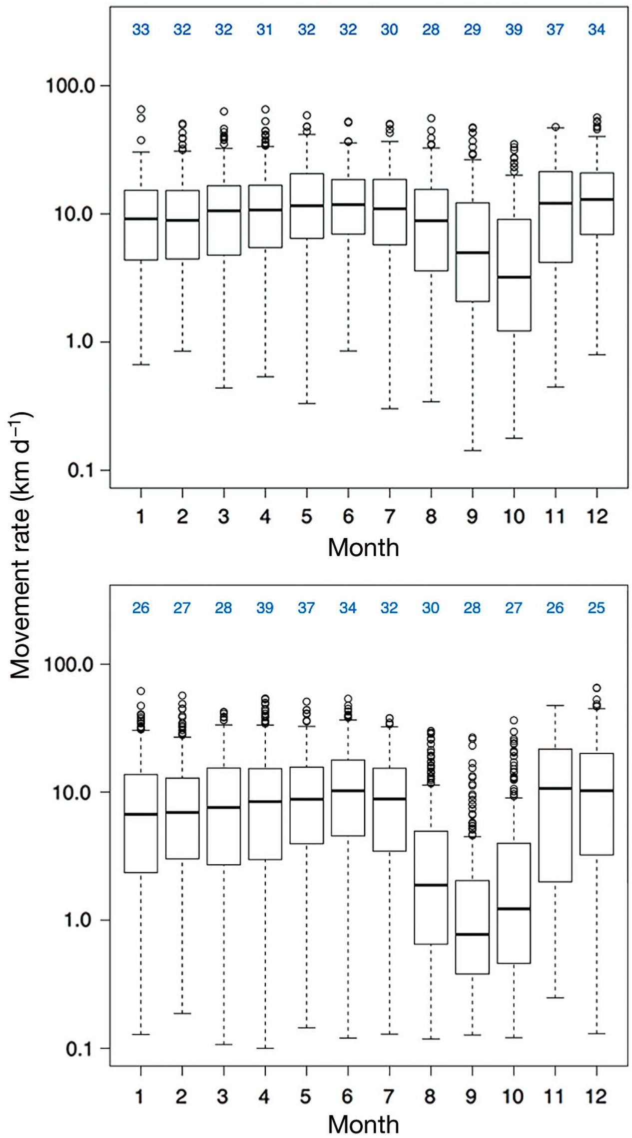

Fig. 4. Movement rate (km d^{-1}) of adult female polar bears from the Baffin Bay subpopulation in the 1990s (top panel) and 2000s (bottom panel). Median is shown with black line and first and third quartiles bounded by the box. Circles represent outliers; *y* axis is on a log scale. The number of individual bears tracked in each month is shown at the top

Sea-ice habitat selection

We first examined univariate relationships for each covariate as a continuous function over the entire sea-ice annual cycle (Fig. 5). Adult female polar bears used significantly lower sea-ice concentrations in the 2000s than the 1990s in all seasons except during April and May ($p < 0.001$) (Fig. 5A). Bears were closer to the sea-ice edges (both 15 and 50 % concentration) in the 2000s during the early winter months (November to February) due to a delay in sea-ice formation (Fig. 5B,C). Bears in the 2000s were significantly closer to land in all months during the on-ice period (November to June); however, in July and early August, bears remained farther from the coast (on offshore sea ice) for longer periods than in the 1990s (Fig. 5D). This was also demonstrated by the distance to 300 m depth contours and by the relationship with depth during summer (Fig. 5E,F). Overall there was a strongly significant lower fraction of bear observations on the sea ice in the 2000s than the 1990s in all months of the year (Fig. 5G).

The full multivariate RSF model for winter demonstrated a positive association between adult female polar bears and sea-ice concentration in the 1990s (e.g. bears preferred areas with higher sea-ice concentrations). The association in the 1990s with depth was negative, demonstrating preference for shallower waters over the shelf (Table 3). In the 2000s,

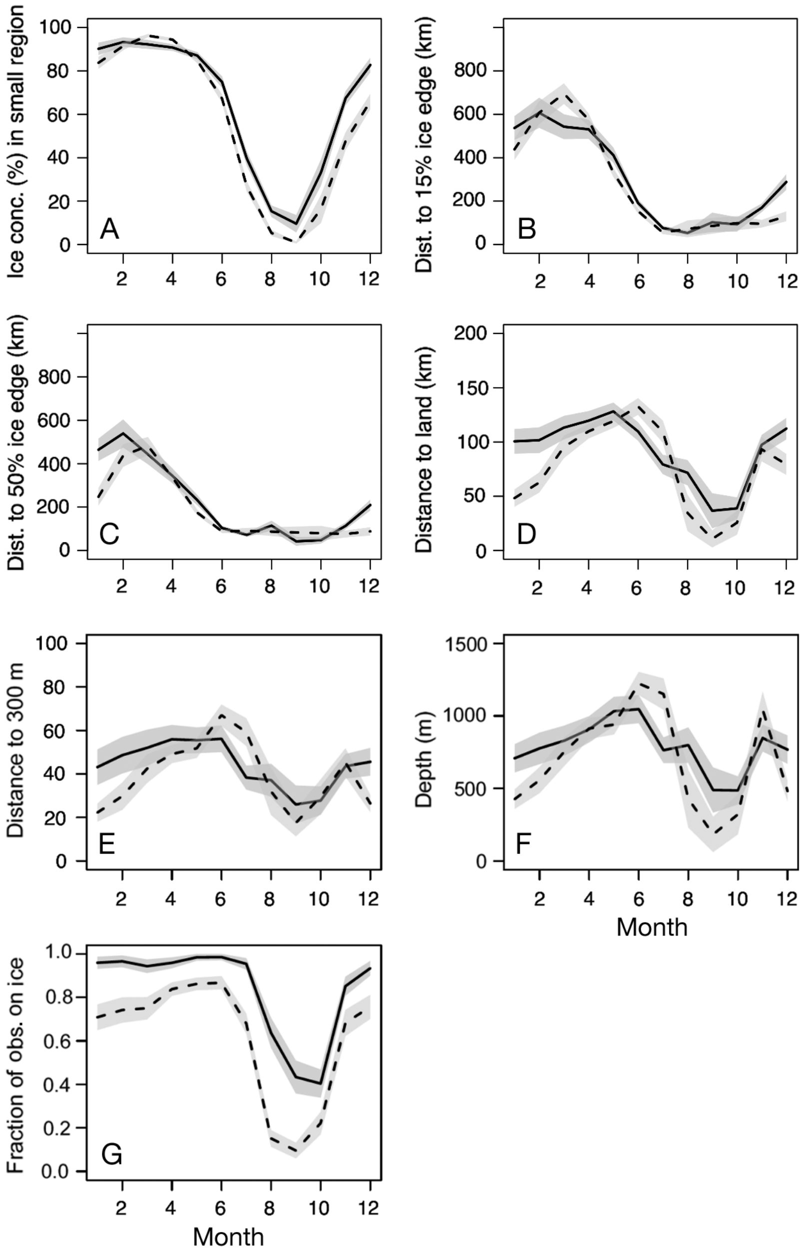

Fig. 5. Habitat use by adult female polar bears in Baffin Bay in the 1990s (solid lines) and 2000s (dashed lines) in relation to 7 sea-ice habitat variables: (A) sea-ice concentration in small buffer region, (B) distance to 15% sea-ice concentration, (C) distance to 50% sea-ice concentration, (D) distance to the nearest land, (E) distance to 300 m depth contour, (F) depth, and (G) percentage of observations on the sea ice. Shaded regions represent ±2 SE of the mean. Months 8–10 largely represent land use by bears

winter preference for higher sea-ice concentrations was not as important as the preference for shallower shelf waters. The distance to the 50% sea-ice concentration threshold was strongly negative, and adult females showed a strong and significant preference for regions <300 m in depth. In both decades, there was a strong negative association with movement onto land in winter. Interactions between decades showed that adult female polar bears in the 2000s used lower sea-ice concentrations in winter than in the 1990s. In the 2000s, there was also an increase in preference for being close to the 300 m depth contour (on shelf waters). Sensitivity analyses examined whether 1990s bears captured in spring versus fall have different selection patterns. An overall test of all 5 interactions comparing RSF effects for fall 1990s captures and n = 9 spring 1990s captures resulted in a p = 0.091 in winter, indicating no differences in selection for fall and spring captures. Using the subset of the 1990s data (n = 9 bears tagged in West Greenland) compared with the full sample from the 2000s for winter, we obtained all of the same directional covariate changes between decades. However, these variables were no longer significant when restricted to using n = 9 bears in the 1990s, likely because the standard errors were 3 times larger, which greatly reduced the ability to detect potential differences.

The full multivariate RSF model for spring showed that adult females had a strong significant preference for higher sea-ice concentrations in the 1990s (Table 3), even more so than in winter. There was also a negative association with increasing distance from 50% sea-ice concentration. This was similar for bears in the 2000s, where sea-ice concentration and distance to 50% sea-ice concentration were important model variables in spring. When interactions between decades were compared, the preference for high ice concentrations was significantly stronger in the 2000s than the 1990s, as was preference for distance to 50% sea-ice edge and preference for shallower depths. There was no change in the association with land; in both decades, bears strongly avoided going to land in spring during the ice-covered season. In sensitivity analyses, an overall test of all 5 interactions comparing RSF effects for fall 1990s captures and n = 9 spring 1990s captures resulted in

Table 3. Sea-ice resource selection function model coefficients for the winter and spring seasons in Baffin Bay using CLOGIT. The p-value delta is for the interaction between the 1990s and the 2000s for each covariate within the multivariate model. Coefficients are scaled for ease of interpretation. Mean ice: mean sea-ice concentration around the bear in a circular radius scaled by 10%. Dist to 50%: distance to the 50% sea-ice concentration scaled by 100 km. Dist to 300 m: distance to the 300 m depth contour scaled by units of 100 km. Depth: absolute value of bathymetry scaled by 100 m. Land: variable that describes the tendency of a bear to move from sea ice onto land and is unitless

Season	1990s			2000s			p-value
	Coeff	SE	p-value	Coeff	SE	p-value	delta
Winter							
Mean ice	0.072	0.024	0.003	−0.028	0.023	0.218	0.003
Dist to 50%	−0.073	0.043	0.088	−0.107	0.051	0.036	0.604
Dist to 300 m	0.026	0.144	0.859	−0.704	0.202	0.001	0.003
Depth	−0.035	0.009	<0.001	−0.016	0.012	0.183	0.193
Land	−1.633	0.290	<0.001	−2.212	0.265	<0.001	0.141
Spring							
Mean ice	0.162	0.022	<0.001	0.265	0.026	<0.001	0.002
Dist to 50%	−0.114	0.040	0.004	−0.363	0.040	<0.001	<0.001
Dist to 300 m	−0.198	0.110	0.071	−0.116	0.109	0.289	0.597
Depth	−0.012	0.007	0.100	0.013	0.007	0.063	0.013
Land	−1.729	0.290	<0.001	−0.964	0.306	0.002	0.070

a p = 0.051 for spring, which implied strong but non-significant evidence for a difference in preferences. Modeling the subset of the 1990s data (n = 9 bears) compared with the full sample from the 2000s, we obtained the same directional covariate changes between decades. Despite large standard errors in spring, we obtained interdecadal significant differences for the same covariates as in the model with the full 1990s dataset (see Table 3).

DISCUSSION

Sea-ice trends

Over a 36 yr record of satellite observations in the Arctic, sea-ice habitat for polar bears has declined significantly (Stern & Laidre 2016). Across all 19 polar bear subpopulations (PBSG 2010), sea-ice retreat in spring is trending earlier by 3 to 9 d decade^{-1} and sea-ice advance in fall is trending later by 3 to 9 d decade^{-1}, with the largest trends occurring in the Barents Sea and central Arctic Basin. Thus, the length of the sea-ice season has declined by 3 to 9 wk over the last 3.5 decades across most of the Arctic, including BB. Barnhart et al. (2016) used the output of a 30-member General Circulation Model ensemble to map the annual duration of open water in the Arctic to 2100. They found that by 2050, BB is predicted to experience an additional 1 to 2 mo of open water per year, relative to present conditions, which is consistent with extrapolation of the linear trends found here and in Stern & Laidre (2016). Of note, the fall sea-ice advance on the Baffin Island shelf arrived on average 9 d later in the 2000s than in the 1990s. However, in West Greenland, it arrived 30 d later. This is likely due to the influence of the southerly inflow of the relatively warm Irminger Current along the west coast of Greenland (Born et al. 2011 and references therein). The vast, shallow West Greenland shelf is important winter and springtime habitat for a large fraction of BB polar bears. They move directly from west BB into this biologically productive region. This area is also key for the springtime subsistence harvest in West Greenland, as it is the period of time bears are present in the area. Thus, timing of fall ice formation appears to be key for BB bears moving to West Greenland and utilizing this productive habitat.

Changes in habitat use by BB polar bears

A growing body of literature demonstrates the negative impacts of ongoing loss of sea-ice habitat across the Arctic on movements, nutritional condition, and demography of polar bears (e.g. Stirling et al. 1999, Regehr et al. 2007, Durner et al. 2004, 2009, Regehr et al. 2010, Rode et al. 2010, 2012, Wilson et al. 2014, Bromaghin et al. 2015, Laidre et al. 2015a, McCall et al. 2016, Hamilton et al. 2017, Lone et al. 2018), as well as the influence of density dependence, ecological productivity, and other factors on the relationships between sea ice and polar bears. Our study is the first to document how changes in sea ice have impacted habitat use of the BB subpopulation, identified as a subpopulation of concern due to high sea-ice loss rates and reported high subsistence harvest (PBSG 2010). Our results show that BB polar bears exhibit broadly similar habitat preferences to other polar bear subpopulations where resource selection has been modeled (Durner et al. 2009, Wilson et al. 2014, Laidre et al. 2015a, Lone et al. 2018). We further used historical data to document large changes in sea-ice habitat use, including declines in movement rates during summer, use of lower sea-ice concentrations, and overall reduced use of sea ice across the range.

Adult female bears were found to be significantly closer to land in all months in the 2000s, compared with the 1990s, except at the end of break-up (June–July), when they stayed farther offshore in the 2000s on remnant offshore sea ice probably to maximize feeding. This is similar to findings from habitat studies in other seasonal ice ecoregions (e.g. Western Hudson Bay), where bears maximize hunting time by staying on the ice as long as possible during break-up (McCall et al. 2016). Time on ice must be balanced against the costs of remaining offshore for too long, which results in having to swim greater distances to shore or travel in low sea-ice concentrations that can be energetically costly (Durner et al. 2011, Pagano et al. 2012). After break-up, bears in the 2000s were concentrated onshore on Baffin Island, whereas in the 1990s they were dispersed on remnant summertime sea ice, which facilitated wider movements (SWG 2016). This change is also critical information in assessment of subpopulation abundance (SWG 2016), given that prior mark-recapture sampling methods have focused on sampling bears in fall on Baffin Island. Our finding from telemetry that bears were closer to land and concentrated onshore in the 2000s was in general agreement with local observations made by Inuit in BB, where subsistence hunters have observed that bears range closer to coastal human communities more often (Dowsley 2005). As sea ice is reduced and breaks up earlier, bears are likely forced onshore into areas where they would not otherwise occur, similar to what has been found in Svalbard (Hamilton et al. 2017). Of note, we did not include bears in the models that displayed a contrasting summer strategy of remaining at glacier fronts in Melville Bay. These bears appear to use coastal habitats year-round and do not venture into the pack ice or move to Nunavut in summer (SWG 2016). A similar phenomenon of bears that occur within the same subpopulation but have distinctly different habitat-use strategies has been observed in other regions such as the Barents Sea (Aars et al. 2017) and East Greenland (K. L. Laidre unpubl. data).

Broadly, adult female polar bears in BB in the 2000s used areas with significantly lower sea-ice concentrations than in the 1990s. In addition, bears were found in areas closer to the 300 m depth contour (over continental shelf waters) in the 2000s than in the 1990s. However, caution is warranted in concluding that these changes represent shifts in preferences because these have occurred concurrently with ongoing changes in habitat. For example, a 2 wk delay in sea-ice formation in the fall in the 2000s limits how far offshore polar bears could potentially be in winter.

We found that polar bears in BB preferred sea-ice habitat that occurred over shallower waters to areas where it occurred over deeper, unproductive waters. The importance of the shallow, more biologically productive waters over the continental shelf to polar bears and other Arctic marine mammals has been well documented (e.g. Stirling 1997, Ferguson et al. 2000, Derocher et al. 2004, Durner et al. 2004, Bluhm & Gradinger 2008, Laidre et al. 2008, Wilson et al. 2014, Laidre et al. 2015b). The requirement for this type of habitat is also important to predictions about a future ice-free Arctic, when sea ice is expected to only be found over the deep Arctic Basin. Our models indicated that sea-ice concentration alone does not determine preferred habitat; adult females will select areas where sea-ice concentrations are lower if these allow for access to waters over the continental shelf (<300 m).

Our analyses addressed differences in sampling between decades to ensure that the 1990s and 2000s data, which were collected within the boundaries of BB but in different areas and seasons, were comparable. Bears collared in West Greenland in the 2000s used nearly the entire Baffin Island coastline in fall and were distributed over the same capture region and same range of latitudes where females in the 1990s were collared, with the exception of the southern point around Cape Dyer. Further, subsample analyses of a small number of bears collared in spring in a restricted area of West Greenland in the 1990s ($n = 9$) provided the same directional effects and same significant interdecadal covariates as the full model. The spring season is the time period when the largest changes in sea ice have been observed (Stern & Laidre 2016, SWG 2016), so we expected that, despite a low sample size and limited power, we would be able to detect these effects. In winter, we obtained the same directional effects on covariates as with the full model; however, the low sample size resulted in large standard errors around the estimates (3 times larger than with the full 1990s dataset), eliminating power to detect differences. In addition, while winter sea-ice area has declined (620 000 km^2 in the 1990s to 580 000 km^2 in the 2000s), it still affords sufficient habitat for bears to hunt. Overall, in our study, sample sizes for each decade were roughly equivalent, sampling durations were similar (6–7 yr tracking periods in each decade), and collars in both decades transmitted up to 3 yr (see also Laidre et al. 2018). Finally, in both decades, collar deployments were distributed over multiple years and over broad geographic areas within the BB management boundaries (Fig. 1). Of note, some studies have shown that adult females with COYs select for coastal areas with more stable sea-ice concentrations in spring (Freitas et al. 2012). Our study had fewer females with COYs in the 2000s; however, it was not possible to isolate and compare females with COYs because of the differences in capture region and capture season (fall COYs in the 1990s, spring COYs in the 2000s).

As polar bears are specialist predators on ice-obligate seals (Stirling & Archibald 1977, Thiemann et al. 2008), their habitat preferences in BB likely reflect areas where seals are found at higher densities due to higher primary and secondary production. The central portion of BB is an abyss that reaches >2000 m in depth, and is therefore less optimal habitat than the areas along the coasts of West Greenland and Baffin Island. While such relationships between sea ice, productivity, predators, and prey have furthered our understanding of Arctic marine ecosystems, climate-induced change in sea-ice conditions suggests that these relationships may be more complex than first thought (e.g. Thiemann et al. 2008, Rode et al. 2014, Hamilton et al. 2017)

Previous work has shown that the longer periods of time polar bears spend in non-productive waters off continental shelves can lead to population-level declines in survival and reproduction (Regehr et al. 2010, Rode et al. 2010). Rode et al. (2012) examined morphometric data (girth, length, and skull width) of BB polar bears between 1977 and 2010 and detected a decline in body condition concurrent with declining sea-ice cover. Future increase in the ice-free season in BB is expected to be large (Barnhart et al. 2016, Stern & Laidre 2016, this study). Furthermore, evidence for connections between sea ice and body condition, as well as recruitment, have been observed in BB (SWG 2016). It is therefore reasonable to hypothesize that changes in habitat use and selection, as documented in the current study, are or will eventually be associated with negative demographic effects.

Conclusions

Our study documented loss of sea ice in BB between the 1990s and the 2000s, and the associated impacts on habitat use of the BB polar bear subpopulation. These findings, together with evidence for effects of sea-ice loss on nutritional condition and recruitment (Rode et al. 2012, SWG 2016), suggest that environmental carrying capacity may be declining for the BB subpopulation. This information is relevant to the structure and assumptions of demographic models used for population viability analyses, conservation assessments (Regehr et al. 2016), and science-based advice to facilitate harvest recommendations (Regehr et al. 2017a,b). Habitat studies can also provide important context for interpreting estimates of vital rates and population abundance, which often have considerable bias and uncertainty. In this case, these results feed directly into better understanding of the assessment of the BB subpopulation based on mark-recapture studies spanning almost 3 decades (SWG 2016).

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