Polar Biol (2015) 38:879–893
DOI 10.1007/s00300-015-1648-5

ORIGINAL PAPER

# Shifts in female polar bear (*Ursus maritimus*) habitat use in East Greenland

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Received: 19 June 2014 / Revised: 9 January 2015 / Accepted: 25 January 2015 / Published online: 6 February 2015

**Abstract** Few studies have investigated the impacts of climate change on polar bears (*Ursus maritimus*) in East Greenland (EG), where some of the largest rates of sea ice loss have occurred. We used remotely sensed sea ice data to quantify changes in timing of sea ice freeze-up and breakup in EG polar bear habitat between 1979 and 2012. We then quantified movement rates, area use, habitat selection, and distribution and phenology of maternity denning using data from adult female polar bears tracked with satellite transmitters between 2007 and 2010 ($n = 7$). We compared results to historical data collected from adult females in the 1990s ($n = 4$). Adult females in the 2000s used areas with significantly lower sea ice concentrations (10–15 % lower) than bears in the 1990s during winter, a pattern influenced by delayed freeze-up in October–December. Adult females in the 2000s were located significantly closer (100–150 km) to open water in all seasons and spent approximately 2 months longer in areas with <60 % sea ice concentration than bears in the 1990s. Multivariate resource selection models contrasting preference between decades showed that there was a statistically significant and stronger winter preference in the 2000s for adult females to select for higher sea ice concentrations. Timing of maternity denning did not significantly differ between decades. Results indicate that multi-decadal loss of sea ice has resulted in shifts in polar bear habitat use in EG.

**Keywords** *Ursus maritimus* · Arctic · Greenland · Polar bear · Resource selection · Sea ice

## Introduction

The loss of Arctic sea ice (Perovich and Richter-Menge 2009; IPCC 2013) has been determined to be a threat to many ice-associated marine mammals (Laidre et al. 2008, 2015; Kovacs et al. 2011). In the case of the polar bear (*Ursus maritimus*), declines in sea ice habitat have been associated with declines in natality, survival, body condition, and abundance in some subpopulations (Regehr et al. 2007, 2010; Rode et al. 2010, 2012; Bromaghin et al. 2015). Sea ice acts as a platform for foraging, traveling, and mating and is critical during spring after females emerge from maternity dens with cubs (Derocher et al. 2004). Most projections indicate a summertime ice-free Arctic in the next several decades (Overland and Wang 2013), and continued habitat loss and degradation for polar bears are expected.

Of the 19 recognized subpopulations of polar bears in the circumpolar Arctic, the East Greenland (EG)

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subpopulation ranges over one of the largest geographic areas, covering the annual and offshore multi-year pack ice along the entire Greenland coast between 60°N and 80°N including Fram Strait, the Greenland Sea, and the Denmark Strait (Fig. 1). The size of the EG subpopulation is unknown (Born et al. 2010; Obbard et al. 2010), and satellite tracking studies indicate limited exchange with other subpopulations nearby (Wiig 1995). However, genetic differences between the EG and Barents Sea subpopulations indicate some degree of exchange between the two regions (Paetkau et al. 1999).

Based on the historical record, the pack ice of EG has receded at an average rate of −9.8 % per decade from 1979 to 2006 (Perovich and Richter-Menge 2009), with the rate varying from −6 % per decade in May and June to −16 % per decade in August and September. The rate of sea ice loss during winter (October–March) has been between −8.3 and −10.6 % per decade, while loss rates during summer (July–September) have ranged between −9.3 and −16.1 % (Ibid.). The current extent of sea ice between Greenland and Svalbard is believed to be the lowest since AD 1200 (Macias Fauria et al. 2009), and there has been a continuous retreat of sea ice edge in the Fram Strait, Greenland Sea, and Denmark Strait since the second half of the nineteenth century (Divine and Dick 2006), with the strongest reduction observed in the Greenland Sea in spring. Some forecasts suggest that polar bear pack ice habitat will be largely absent in EG during summer by the end of the twenty-first century (Durner et al. 2009), and this is expected to have impacts on the subpopulation (Born et al. 1997; Wiig et al. 2003; Durner et al. 2009).

We report on the movements and habitat selection of adult female polar bears tagged with satellite transmitters in EG in 2007 and 2008 and tracked until 2010. We built

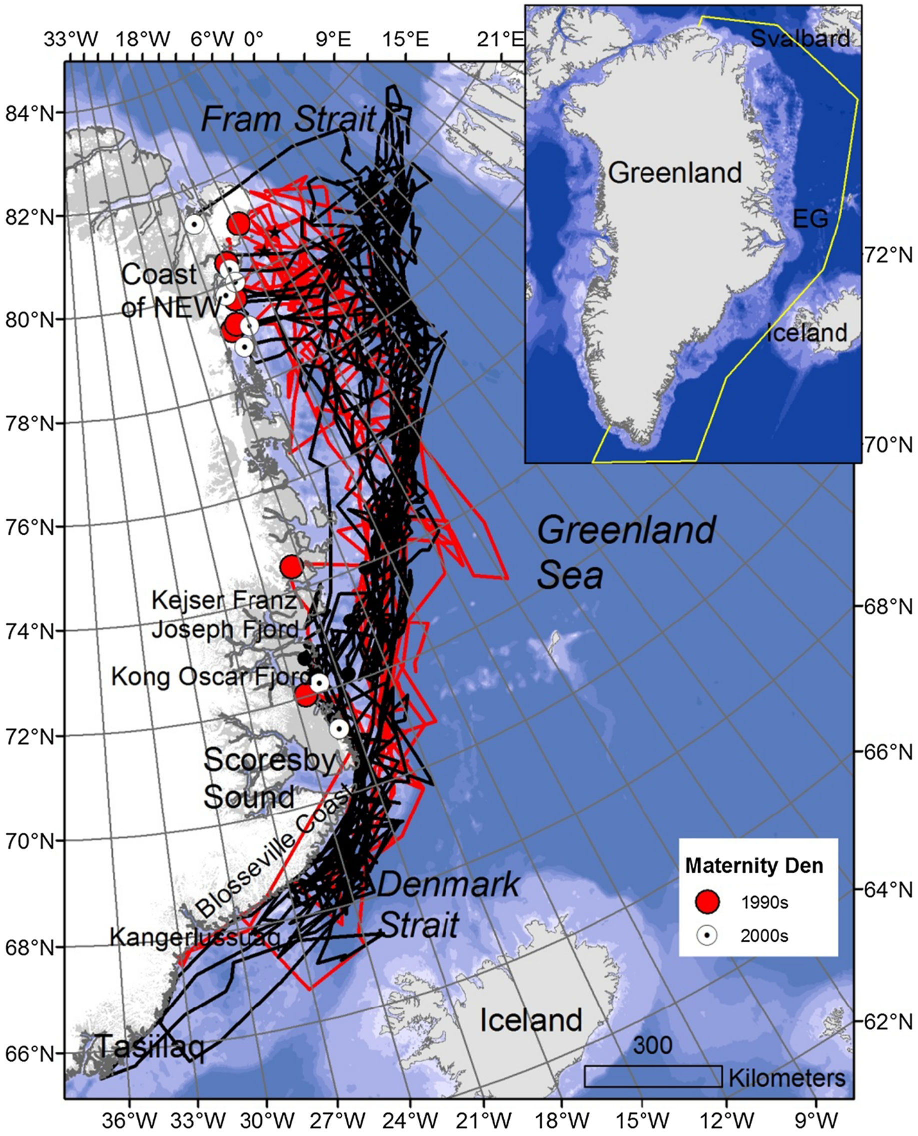


**Fig. 1** Map of movements of adult female polar bears in EG. Movements of polar bears tracked on the pack ice between 1993 and 1998 shown in *red* (n = 4), and polar bears tracked on the pack ice between 2007 and 2010 shown in *black* (n = 7). Maternity den locations shown as *symbols*, see legend. Capture locations are shown with *black stars* for the 1990s and *black circles* for the 2000s. The IUCN boundary for the EG subpopulation is shown in *yellow* on the *inset*

resource selection models using multiple sea ice habitat covariates to quantify habitat selection and contrast it with historical data collected from adult females tracked in the 1990s (Born et al. 1997; Wiig et al. 2003) to understand how decadal habitat changes may have affected EG polar bears. We also examined changes in the distribution and phenology of maternal dens over two decades. The results of this study may inform future work on EG polar bears and may improve predictions about the impacts of sea ice loss in EG or for other subpopulations with access to offshore multi-year pack ice during summer.

## Materials and methods

The study area included the coastal and offshore regions of EG (Fig. 1). This region consists of a convergent sea ice zone with sea ice formation along the EG coast driven by transport of multi-year pack ice from the Arctic Ocean (Foldvik et al. 1988). Due to the presence of multi-year ice advected from the Arctic Basin, some sea ice habitat is generally available to polar bears over the entire year (Martin and Wadhams 1999).

### Sea ice trend analysis

We calculated the date of sea ice transition during the growth and recession phases (dates of spring ice retreat and fall ice advance) in the entire EG study area (defined in Obbard et al. 2010, Fig. 1) using sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data (Cavalieri et al. 1996) available from the National Snow and Ice Data Center (NSIDC) in Boulder, Colorado, USA. Sea ice concentrations were provided in a polar stereographic projection with a nominal grid cell size of 25 × 25 km. Temporal coverage was every other day from October 26, 1978, through July 9, 1987, and daily through December 31, 2012. Cells with concentrations <15 % were treated as ice-free.

We calculated the daily total sea ice area in the EG polar bear subpopulation region (<300 m depths, Fig. 1) by summing the products of sea ice concentrations and grid cell areas. We calculated the mean March (maximum) and September (minimum) sea ice area over the decade 1979–1988 and considered the transition threshold to be halfway between these means (50 %). The "spring transition" (or retreat) was defined as the date when the sea ice area fell below 50 % on its way to the summer minimum, and "fall transition" (or advance) was defined as the date when the sea ice area rose above 50 % on its way to the winter maximum. For each year (1979–2012), we then calculated the dates of spring and fall transition. We calculated the trends of these transition dates (days per decade) using standard least-squares regressions and the significance of the trends using a 2-sided *F* test. The transition dates provide an index for the biologically important transitions between winter and summer sea ice conditions (see also Laidre et al. 2015).

### Satellite transmitter data analysis

We used satellite location data from EG polar bears from two decades: 1993–1998 and 2007–2010. In 1993 and 1994, satellite collars were deployed on nine adult female polar bears between ca. 72°30′N and ca. 80°30′N (Born et al. 1997; Wiig et al. 2003). Of these, five bears were tagged on the landfast ice and remained on the landfast ice, while four ($n = 2$, Born et al. 1997; $n = 2$ Wiig et al. 2003) were tagged in the pack ice and almost exclusively used the pack ice during the tracking period (1993–1998). In 2007 and 2008, satellite collars were deployed on seven female polar bears in the pack ice between 72°N and 81°N in the Greenland Sea, with field crew-based onboard R/V Nordsyssel (Institute of Marine Research, Tromsø, Norway) or R/V Lance (Norwegian Polar Institute, Tromsø, Norway) in the second half of March (March 17–29, 2007, March 22–26, 2008) (Table 1, Fig. 1). Because our interest was in the pelagic realm, we used the four bears that were tagged in and utilized pack ice habitat in the 1990s in resource selection comparisons to polar bears tagged in the pack ice in 2007 and 2008 (Table 1).

Polar bears during both periods were darted and immobilized from a helicopter and handled according to procedures described in Stirling et al. (1989). Standard body measurements (standard length of bear and axillary girth) were taken, and total body mass was estimated using the approach in Derocher and Wiig (2002). Field estimates of age and reproductive status were recorded. Individual age was determined by reading annual growth layer groups in the cementum of a lower premolar (Calvert and Ramsay 1998). All female polar bears included in this study were >4 years old and assumed to be sexually mature adults.

Adult female polar bears were fitted with A-3610 satellite radio collars (Telonics, Mesa, Arizona, USA) (Table 1). The radio collar provided information on geographic location, internal transmitter temperature (a proxy of ambient temperature), and activity from an internal activity counter. Collars were programmed to transmit during one six-hour period starting at 9 GMT each day on 4-day interval with a repetition rate of 60 s.

Data on locations and transmitter status were collected via the Argos Location and Data collection system (Toulouse, France). All locations were filtered by the Douglas Filter V7.02 (Douglas et al. 2012), and 7 % of locations were removed. Filter settings included a maximum movement speed of 10 km/h. All locations of the highest

**Table 1** Adult female polar bears radio tagged during 1993 and 1994 (Born et al. 1997; Wiig et al. 2003) and during 2007 and 2008

| Year | ID-PTT | Status | Start date | Stop date | # days | Age* | Mass (kg) |
|---|---|---|---|---|---|---|---|
| 1993 | D7351-9679 | Alone | 6/17/93 | 11/16/93 | 152 | 10* | 168 |
| | D7127-9684 | Alone | 6/9/93 | 5/24/95 | 714 | 10* | 205 |
| 1994 | D7356-2170 | Alone | 9/4/94 | 7/8/98 | 1,403 | 4* | 198 |
| | D7357-2174 | Alone | 9/9/94 | 4/20/96 | 589 | 6* | 263 |
| 2007 | D7360-74762 | 1 YRL | 3/17/07 | 8/29/09 | 896 | 7 | 192 |
| | D7364-74764 | 2 2YR | 3/22/07 | 12/20/08 | 639 | 9 | 168 |
| | D7250-74765 | Alone | 3/28/07 | 3/29/10 | 1,097 | 14 | 223 |
| | D7251-74766 | 1 YRL | 3/29/07 | 3/29/10 | 1,096 | 14 | 226 |
| 2008 | D7268-74771 | 2xCOY | 3/26/08 | 5/18/08 | 53 | 10 | 151 |
| | D7260-74769 | Mating pair | 3/22/08 | 3/29/10 | 737 | 13 | 198 |
| | D7264-74770 | 2xCOY | 3/25/08 | 3/29/10 | 734 | 13 | 250 |

The table shows year of tagging, ID and PTT (platform terminal transmitter), start and stop of tag transmissions, duration, age of bear (in years) either obtained from field estimate (*) or from growth layers in tooth cementum, and estimated total body mass. Status indicates if female was alone or with cubs (n = 1 or n = 2) where COY = cub of the year, YRL = yearling, and 2YR = 2-year-old cub

accuracy (class 1–3) with an estimated location error <1,500 m were retained (Douglas et al. 2012).

We estimated utilization distributions (UDs) using kernel methods (Kie et al. 2010) for both decades using a smoothed cross validation (SCV) bandwidth selector (Geospatial Modeling Environment, GME version 0.7.2.0, spatialecology.com; Duong 2007). UDs were created for three seasons: "spring" (April–June, also the mating season), "summer" (July–September, the reduced ice season), and "winter" (October–March). These seasons were based on considerations about environmental conditions in EG (i.e., sea ice, weather, and light), life history of seal prey, and polar bear behavior in previous studies (Born et al. 1997; Wiig et al. 2003). Seasonal focal areas were defined by the 75 % kernel activity range (km$^2$). Relocations were treated as independent across all study animals within each season and pooled to create a seasonal home range. Home range sizes were compared with ANOVA.

## Sea ice habitat analysis

In the comparative analysis between polar bears tracked in the 1990s and 2000s, daily sea ice concentration values were used from satellite passive microwave data (SSM/I). Sea ice habitat was defined around each polar bear location at three spatial scales: the sea ice concentration pixel value where the bear was located and the mean sea ice concentration within regions of two sizes centered on the pixel occupied by the bear. The smaller region consisted of the 3 × 3 block of pixels centered at the bear location (nominal area 5,625 km$^2$), and the larger region consisted of 7 × 7 pixels (nominal area 23,125 km$^2$) with the corners removed in order to approximate a circle. The radius of the large area corresponded to the 75 % percentile of 4-day displacements for adult females. All locations where polar bears were stationary in maternity dens or temporary dens (based on locations and activity data) were removed from the resource selection analysis.

We also calculated the distance from each polar bear location to the sea ice edge (defined with two concentration thresholds) and the distance from each polar bear location to the coastline. The sea ice edge covariate estimated the distance (in km) from the bear's location to the center of the nearest pixel with either 15 or 50 % sea ice concentration. We used the 15 % sea ice concentration as a delimiter between sea ice and open water. We used the 50 % sea ice concentration as a delimiter between suitable polar bear habitat and breakup conditions (see Stirling and Parkinson 2006). Distances were determined by great circle calculations based on latitude and longitude and therefore were not subject to pixel size.

## Resource selection function (RSF) models

Buffers were created around each polar bear location that were representative of available habitat bears could select on a 4-day (or occasionally 6-day) interval depending on satellite collar duty cycle (cycling of transmissions for battery longevity). The radius of the buffer was based on mean monthly movement rates for bears grouped into decades (1990s and 2000s). In the 1990s, there was no statistical difference among months for bears' movement rates and a 22.5-km-radius buffer was used (approximating the 90th percentile of daily movement rate). In the 2000s, there was stronger and significant variation in movement rate by month and a variable month-specific buffer was used (Table 2), also approximating the 90th percentile. This approach did not assume normality.

Fifty random locations in each buffer were sampled for each time step and represented candidate locations not selected by the bear at each given movement step (i.e., pseudo-absence locations). This control data set was considered to represent local habitat availability. All pseudo-absence locations were linked to the same habitat variables listed above using ArcGIS (ArcGIS 10.1, ERSI, Redlands, CA, USA). A maximum time gap of 12 days was selected between locations to minimize the size of the buffer.

Univariate resource selection models were built to examine habitat selection (pixels where the bear was present) and habitat availability (pixels corresponding to pseudo-absence locations) for bears tagged in 2007 and 2008. We also conducted a univariate interdecadal comparison of habitat use by constructing seasonal regression analyses to test whether the environmental parameter at the location used by adult females in each of three seasons (spring, summer, and winter) in the 1990s was different than that used in the 2000s. We used presence data for each bear and clustered locations with generalized estimating equations (GEE) to account for temporal/spatial correlation (Heagerty and Lumley 2000). For each sea ice metric, we tested for differences in habitat use among adult female polar bears in the 1990s and 2000s across seasons (winter, spring, and summer).

Multivariate conditional logistic RSF models were also built (separate models by season for 1990s and 2000s) for adult female bears to identify for the suite of environmental parameters that best described habitat selection. We used conditional logistic regression with matched location/pseudo-absence sets (CLOGIT function from SURVIVAL package) (R Development Core Team 2011; Therneau 2013) to model the strength of preference for habitat parameters in the 1990s and 2000s. We compared single ice concentration metric models (ice concentration at bear, mean concentration in small and large buffers) using stepwise Akaike information criterion (AIC) to determine which combination of sea ice concentration metrics best explained resource selection. The three sea ice metrics were not combined as potential explanatory variables in the same multivariate model due to colinearity, as the pairwise correlation between sea ice concentration metrics was >97 %.

## Maternity denning

The locations of maternity dens in both decades were identified from the satellite location data. Potential dens were identified by examining re-locations from individual adult female polar bears that remained in a restricted area for an extended period of time. If the starting date for the reception of multiple daily locations occurred in autumn (September–November), with the end date in the following spring (March–April), it was assumed that the 6- to 8-month-long denning period was a maternity den. Denning based on reception dates of stationary geographic locations was compared to temperature and activity data obtained from satellite collars (Born et al. 1997; Ferguson et al. 2000). If dates were associated with a relative increase in temperature (e.g., a bear inside the den) and a decrease in activity level, it was assumed to be a den. Similarly, a decrease in temperature and increase in relative activity, coincident with more variable geographic locations over a wide area, indicated that the bear had emerged from the den. The den location was based on high-quality geographic locations only (location class 1–3). In cases where several re-locations of the same quality had been received during the denning period, then an average

**Table 2** Daily movement rates (km/day) for adult female polar bears on the EG pack ice in 1990s (n = 4) and 2000s (n = 7)

| | 1990s | | | 2000s | | |
|---|---|---|---|---|---|---|
| Month | Median | SD | 90 % percentile | Median | SD | 90 % percentile |
| January | 2.8 | 8.5 | 17.8 | 5.2 | 8.5 | 18.4 |
| February | 1.8 | 11.8 | 16.3 | 4.5 | 10.8 | 28.2 |
| March | 4.9 | 9.7 | 21.1 | 10.0 | 10.7 | 25.4 |
| April | 8.7 | 8.9 | 24.7 | 18.6 | 13.4 | 41.3 |
| May | 9.2 | 7.9 | 21.1 | 17.6 | 14.1 | 42.7 |
| June | 10.1 | 7.3 | 17.8 | 15.1 | 11.1 | 31.3 |
| July | 9.1 | 10.4 | 22.0 | 11.7 | 10.2 | 27.5 |
| August | 11.5 | 9.7 | 21.2 | 10.6 | 8.3 | 24.3 |
| September | 8.4 | 34.7 | 21.3 | 10.2 | 10.2 | 27.1 |
| October | 6.7 | 10.6 | 16.1 | 6.2 | 12.0 | 31.1 |
| November | 6.3 | 5.8 | 15.7 | 2.7 | 12.3 | 27.0 |
| December | 8.6 | 6.4 | 16.2 | 1.8 | 9.9 | 22.3 |

latitude and longitude was calculated from the high-quality locations to identify the den location. The duration of individual denning periods was estimated as the time elapsed between the first and the last re-location at the denning site with a resolution of ±4 days.

Mann–Whitney *U* tests (Siegel 1956) were used to test for differences in den entry and exit dates and the duration of denning between the 1990s and 2000s. Day of assumed den entry was included in calculation of the duration of the denning period.

## Results

### Sea ice trends

The analysis of spring sea ice retreat and fall sea ice advance in the EG polar bear subpopulation region (depths $< 300$ m) resulted in significant trends during both seasons (Fig. 2). The trend in spring sea ice retreat was −4.0 (SD 1.4) days per decade ($p < 0.001$), and the trend in fall sea ice advance was +3.9 (SD 1.9) days per decade ($p < 0.001$). The trend in the length of the summer open water season (difference between spring retreat and fall advance) was +7.9 (SD 2.7) days per decade ($p < 0.001$).

### Movements and focal areas

Adult female polar bears tracked between March 2007 and 2010 (Table 1) were widely distributed along the northeast Greenland coast and in the offshore pack ice of the Fram Strait, the Greenland Sea, and the Denmark Strait (Fig. 1). Polar bears ranged up to 400 km offshore and over ca. 16° of latitude (66°–82°N). Adult females were tracked for up to 3 years and moved over 2,000 km annually. One collar stopped transmitting after 3 months and was not included in the habitat analyses. Of the remaining six adult female bears, five moved south of Scoresby Sound (into Denmark Strait) and one moved as far south as Tasiilaq (ca. 66°N). This southward movement occurred during winter and spring on the sea ice. None of the EG bears tracked during the 1990s and 2000s entered the Svalbard archipelago subpopulation region.

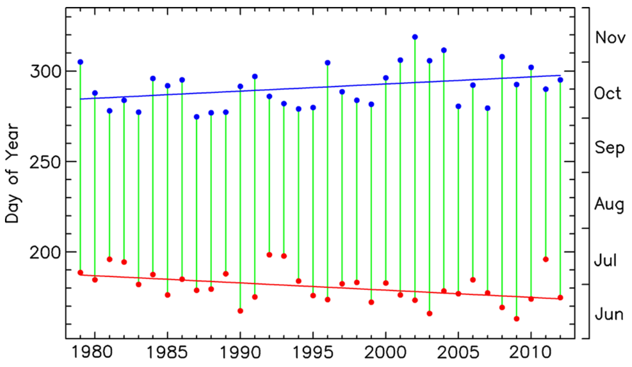


**Fig. 2** Spring retreat (*red*) and fall advance (*blue*) sea ice transition dates in the EG subpopulation boundary on shelf waters (<300 m), 1979–2012. *Red* and *blue lines* are least-squares fits. *Vertical green lines* indicate time intervals between spring and fall transition dates (i.e., the duration of the low sea ice period)

Focal area use (75 % kernel) across the three seasons in the 2000s was not significantly different (spring: 179,000 km$^2$, summer: 189,000 km$^2$, and winter: 204,000 km$^2$). In spring, the polar bears used a focal range along the pack ice edge between 70°N and 80°N (Fig. 3). As the sea ice receded in late spring and summer in the 2000s, polar bears shifted north and utilized two general strategies: (1) Some bears moved north on the offshore receding pack ice and remained on multi-year ice between 77° and 80°N or (2) some bears shifted onto land north of Scoresby Sound between 71° and 73° 30°N. In winter, bears were more widely distributed and used three regions: NE Greenland between 78° and 81°N, north of Scoresby Sound between 70° and 74° 30 N, and south of Scoresby Sound along the Blosseville Coast.

Focal areas (75 % kernel) used by the four bears tagged in the pack ice in the 1990s (spring: 465,000 km$^2$, summer: 339,000 km$^2$, and winter: 631,000 km$^2$) were significantly larger than those in the 2000s (Fig. 3) ($p < 0.05$). Bears in the 1990s used the pack ice along entire continental shelf along the NE and east coast of Greenland in all three seasons.

### Interdecadal selection: Univariate habitat models 1990s–2000s

Median monthly movement rates for adult females in the 1990s ranged from 2.8 (in January) to 11.5 km/day (in August) (Table 2). Rates for adult females in the 2000s ranged from 1.8 (in February) to 18.6 km/day (in April). In general, rates were lowest in both decades during winter (November–February); however, adult females moved almost twice as fast in spring (April–June) in the 2000s than in the 1990s ($p < 0.001$) (Table 2).

There was a strong seasonal cycle to sea ice habitat use for adult females tagged in the 1990s and the 2000s. Bears used lower sea ice concentrations in late spring and summer and higher concentrations in early and late winter (Fig. 4), following the formation and recession of annual sea ice. There were significant differences in sea ice habitat availability between decades. Using all three scales of sea ice concentration, adult females used significantly lower (10–20 %) sea ice concentrations during winter months in the 2000s than in the 1990s (Tables 3, 4, Fig. 4). This pattern was most strongly influenced by the months in early winter (October–December). In general, seasonality of

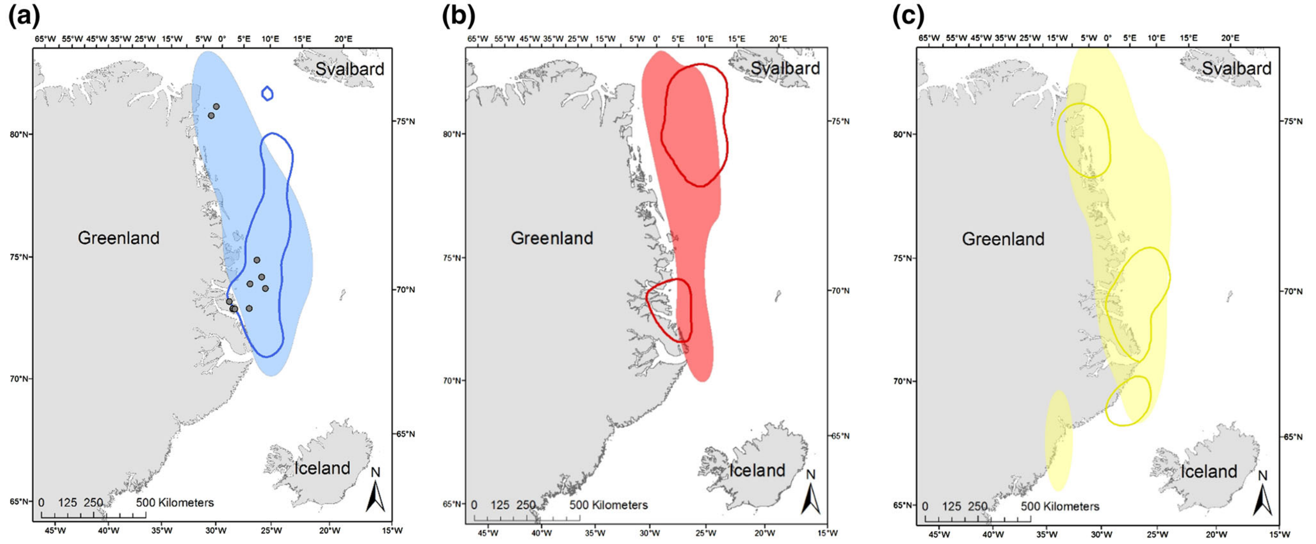
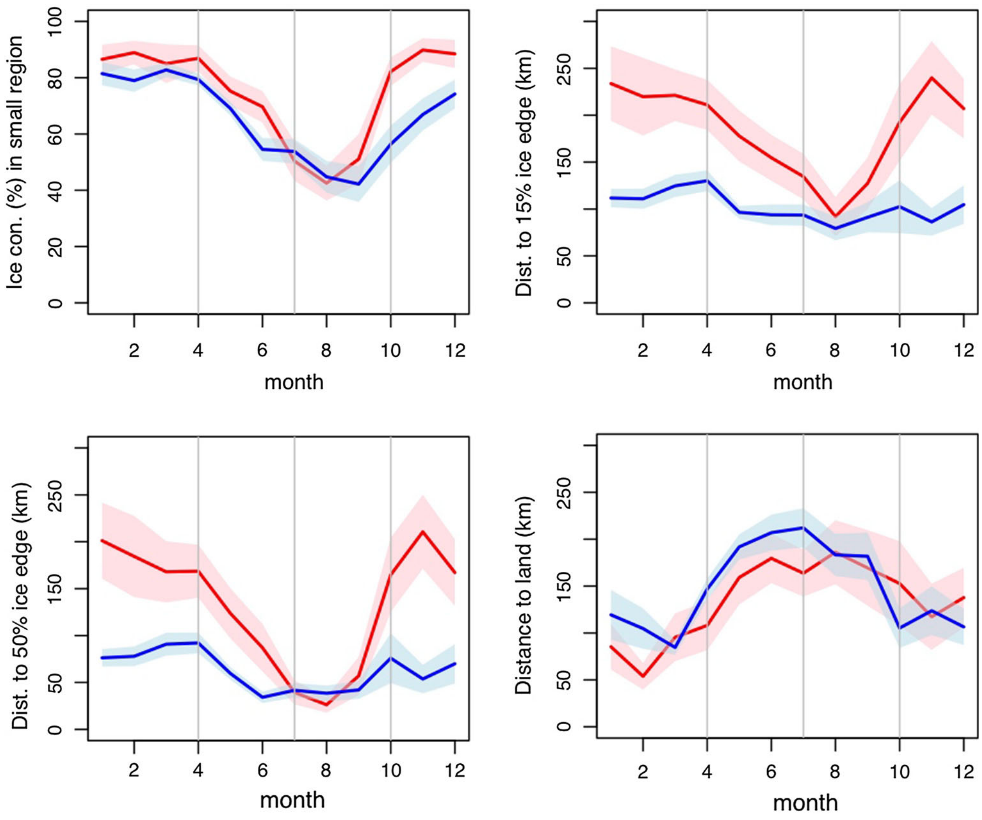


**Fig. 3** Focal areas used by adult female polar bears in EG in **a** spring, **b** summer, and **c** winter in the 1990s and 2000s defined by 75 % kernel probability contours based on one location per fourth day per bear. *Shaded colored areas* are those used in the 1990s, and outlined areas are those used in the 2000s. Capture locations are shown on 3a with *gray dots*. Note some captures occurred in the same geographic location; thus, they overlap

**Fig. 4** 1990s and 2000s adult female polar bear habitat use for each of four sea ice habitat variables: sea ice concentration in small buffer, distance to 15 % sea ice, distance to 50 % sea ice, and distance to land. Data from 1990s are shown in *red*, 2000s in *blue*. *Shaded regions* represent two SE of the mean. *Vertical lines* indicate monthly boundaries for seasons (winter, spring summer). SSM/I sea ice concentration is used in both decades. Sample sizes for each are shown in Table 3



habitat use was more muted in the 2000s and bears used lower sea ice concentrations for longer periods. Polar bears in the 2000s used <60 % sea ice for an additional 2 months (June–October) when compared to polar bears in the 1990s (July–September) (Fig. 4). Models using sea ice concentration values at the bear's location and within the large ice area (85 km radius) also demonstrated these patterns, though not shown in Fig. 4.

**Table 3** Statistics for sea ice habitat use by adult female polar bears in EG

| Season | Decade | N bears | N obs. | Ice con. (%) at pixel | Ice con. (%) within 45 km | Ice con. (%) within 85 km | Distance to 15 % ice (km) | Distance to 50 % ice (km) | Distance to land (km) |
|---|---|---|---|---|---|---|---|---|---|
| Spring | 1990s | 4 | 100 | 75.0, 80.8 (21.0) | 74.3, 78.6 (20.9) | 72.9, 78.1 (20.2) | 165.7, 158.9 (81.4) | 113.6, 100.7 (79.2) | 168.0, 162.2 (81.0) |
| | 2000s | 7 | 483 | 71.0, 73.6 (18.9) | 69.3, 71.7 (18.6) | 65.3, 66.2 (17.9) | 103.5, 92.9 (54.3) | 60.5, 48.1 (50.2) | 186.0, 175.7 (91.8) |
| Summer | 1990s | 4 | 89 | 48.3, 50.4 (20.0) | 47.9, 51.4 (19.5) | 46.6, 48.7 (19.3) | 124.2, 115.3 (72.9) | 37.4, 16.5 (44.6) | 177.8, 165.0 (91.6) |
| | 2000s | 6 | 242 | 51.4, 57.6 (25.5) | 50.1, 54.9 (24.9) | 47.3, 49.6 (23.0) | 93.0, 83.8 (67.4) | 42.6, 27.2 (45.4) | 208.0, 220.6 (100.9) |
| Winter | 1990s | 4 | 110 | 84.6, 87.4 (16.9) | 84.4, 87.7 (16.6) | 83.2, 86.6 (16.9) | 207.1, 213.4 (92.8) | 168.8, 160.4 (95.2) | 119.9, 114.8 (74.0) |
| | 2000s | 7 | 301 | 73.5, 80.0 (23.4) | 72.0, 78.8 (23.0) | 67.8, 72.9 (21.8) | 103.7, 95.4 (66.1) | 72.0, 61.4 (62.4) | 109.3, 103.4 (68.6) |

Data are reported for two study periods (1990s and 2000s) and in each of three seasons (spring, summer and winter, defined in text). Mean, median, and standard deviation (SD) are reported

**Table 4** Summary statistics and inference using generalized estimating equations for environmental characteristics at locations where adult female polar bears in EG were present

| | Season | Mean value 1990s | SE | Mean value 2000s | SE | p value |
|---|---|---|---|---|---|---|
| Ice con. (%) at bear | Spring | 75.0 | 3.3 | 71.0 | 1.6 | 0.264 |
| | Summer | 48.3 | 2.7 | 51.4 | 3.2 | 0.460 |
| | Winter | 84.6 | 2.5 | 73.5 | 2.4 | 0.001 |
| Ice con. (%) in small region | Spring | 74.3 | 3.2 | 69.3 | 1.6 | 0.160 |
| | Summer | 47.9 | 2.7 | 50.1 | 3.1 | 0.597 |
| | Winter | 84. 4 | 2.5 | 72.0 | 2.5 | <0.001 |
| Ice con. (%) in large region | Spring | 72.9 | 3.1 | 65.3 | 1.6 | 0.031 |
| | Summer | 46.6 | 2.8 | 47.3 | 3.0 | 0.854 |
| | Winter | 83.2 | 2.6 | 67.8 | 2.4 | <0.001 |
| Distance to 15 % ice edge (km) | Spring | 165.7 | 12.9 | 103.5 | 5.3 | <0.001 |
| | Summer | 124.2 | 11.4 | 93.0 | 8.2 | 0.025 |
| | Winter | 207.1 | 15.2 | 103.7 | 6.4 | <0.001 |
| Distance to 50 % ice edge (km) | Spring | 113.6 | 12.5 | 60.5 | 4.5 | <0.001 |
| | Summer | 37.4 | 5.3 | 42.6 | 5.0 | 0.478 |
| | Winter | 168.8 | 16.3 | 72.0 | 6.1 | <0.001 |
| Distance to land (km) | Spring | 168.0 | 14.7 | 186.0 | 12.6 | 0.352 |
| | Summer | 177.8 | 15.9 | 208.0 | 13.1 | 0.144 |
| | Winter | 119.9 | 11.9 | 109.3 | 9.1 | 0.478 |

Decade refers to 1990s and 2000s, sea ice concentration is in (%), and all distance metrics are in km

The most striking results were the decadal differences in distance from polar bears' locations to the sea ice edge (15 and 50 % sea ice concentrations) over the annual cycle (Fig. 4). In all three seasons, the adult females in the 2000s were located significantly closer (50–100 km) to 15 % sea ice (open water) than bears in the 1990s, although individual months varied within season (Fig. 4, Table 4). This was in contrast to a clear seasonal pattern in the 1990s where adult females were located >100 km away from open water (i.e., 15 % ice) outside of the summer season. In the 2000s, this seasonal cycle was nearly absent. There were no significant differences between decades for the distance of polar bears to the coastline.

## Interdecadal selection: Multivariate habitat models 1990s–2000s

Multivariate conditional logistic regression models determined the suite of sea ice habitat covariates preferred by adult female polar bears between decades and seasons (Table 5). Sea ice concentration at the bear location was the strongest predictor of bear presence for all seasons and in both decades. In some cases, a quadratic rather than a linear term provided the best model fit for sea ice concentration (Table 5). In spring and winter, distance to 15 % sea ice concentration and distance to the coastline also explained bear presence. In summer, the only predictor common to both decades was sea ice concentration at the bear location. In general, there was not a great difference in the habitat parameters preferred by adult female polar bears between the two decades. Polar bears in the 2000s had a strong and statistically significantly preference for higher sea ice concentrations (Fig. 5), which was most pronounced in winter. Bears in the 1990s showed similar patterns but less significant associations with sea ice (Table 5). There was a common preference for polar bears to be closer to land in winter in both decades (Fig. 5). Sea ice concentration, regardless of scale (i.e., bear location, small buffer, large buffer), was the top predictor in all models; however, it was not possible to determine the best sea ice scale (e.g., combine them into a multi-scale sea ice concentration multivariate model) because the three scales were nested and colinear.

## Maternity denning: 1990s–2000s

During the 1990s and the 2000s, all polar bears used land as a denning substrate, irrespective of whether the individual was tagged on (or had a general preference for) the fast ice or pack ice. Hence, to increase sample size in the denning comparison between decades, all polar bears tracked in the 1990s (Born et al. 1997; Wiig et al. 2003) were included in the denning analysis.

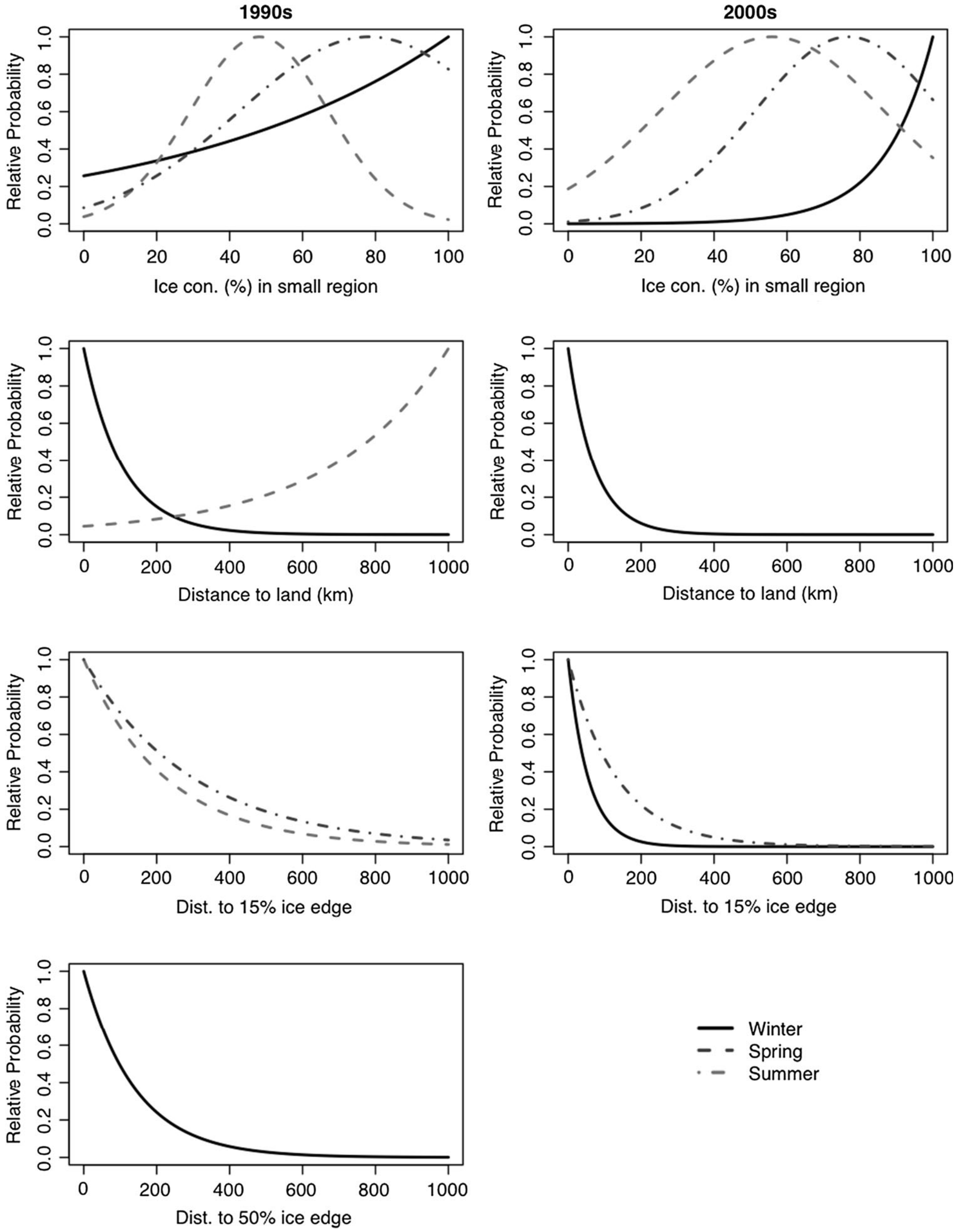
Between 1993 and 1997, six individual bears were tracked to seven maternity dens in NE Greenland between 72°N and 81°N. Between 2007 and 2010, six individual bears were tracked to eight maternity dens between 71°N and 81°N (Fig. 1, Table 6). In one of these cases, transmissions stopped during the denning period and data were not included in summary statistics. Two female bears denned twice during the 2007–2010 period, and in both cases, the dens were located on the shore of the Northeast

**Table 5** Top multivariate logistic regression models for resource selection by adult female polar bears in the 1990s and 2000s in three seasons

| | Estimate | SE | p |
|---|---|---|---|
| 1990s spring | | | |
| Mean sea ice concentration | 0.63 | 0.244 | 0.01 |
| Ice concentration squared | −0.040 | 0.021 | 0.06 |
| Distance to 15 % sea ice | −0.334 | 0.215 | 0.12 |
| 1990s summer | | | |
| Mean sea ice concentration | 1.216 | 0.245 | <0.001 |
| Ice concentration squared | −0.121 | 0.025 | <0.001 |
| Distance to 15 % sea ice | 0.447 | 0.29 | 0.001 |
| Distance to land | 0.311 | 0.222 | 0.16 |
| 1990s winter | | | |
| Mean sea ice concentration | 0.136 | 0.083 | 0.10 |
| Distance to 50 % sea ice | −0.711 | 0.276 | 0.01 |
| Distance to land | −0.949 | 0.271 | <0.001 |
| 2000s spring | | | |
| Mean sea ice concentration | 1.179 | 0.135 | <0.001 |
| Ice concentration squared | −0.077 | 0.011 | <0.001 |
| Distance to 15 % sea ice | −0.752 | 0.165 | <0.001 |
| 2000s summer | | | |
| Mean sea ice concentration | 0.60 | 0.116 | <0.001 |
| Ice concentration squared | −0.054 | 0.013 | <0.001 |
| 2000s winter | | | |
| Mean sea ice concentration | 0.757 | 0.123 | <0.001 |
| Ice concentration squared | −0.045 | 0.0117 | 0.001 |
| Distance to 15 % sea ice | −1.823 | 0.296 | <0.001 |
| Distance to land | −1.40 | 0.222 | <0.001 |

Specific model coefficients are scaled, so that they show the increase in preference per 10 % increase in sea ice concentration or per 100-km increase in distance. Stepwise AIC was used to determine best model for each season/decade. Models are reported for small buffer only

**Fig. 5** Covariate relationships in multivariate habitat selection models developed for adult female polar bears in EG in the 1990s and 2000s. RSF predictions were scaled, so the maximum prediction was 1.0 for each season. Sea ice concentration is in small buffer region. SSM/I sea ice concentration was used in both decades



Water Polynya (NEW). Irrespective of tagging location, 11 (ca. 73 %) of the 15 maternity dens were located along the coast of the NEW (Fig. 1).

During the 1990s, mean den entry date was 26 October (mean day of year = 299, SD = 21, range 29 September–24 November, $n = 7$). Mean exit date was 1 April (mean day of year = 91, SD = 16, range 26 February–28 April, $n = 7$). Duration of maternity den occupancy in the 1990s averaged 158 days (SD = 22, $n = 7$). In the 2007–2010 period, mean entry date was 6 October (mean day of year = 279, SD = 7, range 22 September–17 October, $n = 8$), mean exit date was 29 March (mean day of year = 88, SD = 8, range 19 March–4 April, $n = 7$), and duration of maternity den occupancy averaged 174 days (SD = 11, $n = 7$).

Exit date and duration of den occupancy during the two periods (1990s vs. 2000s) were not significantly different (exit date: $z = -0.511$, $p = 0.609$; occupancy: $z = -1.661$, $p = 0.097$). However, on average, the mean den entry date in the 2000s was nearly 3 weeks earlier than in the 1990s though not statistically significant at the 5 % level ($z = -1.852$, $p = 0.064$). Entry date for the four maternity dens in the southern range (south of 75°N) did not differ statistically from entry dates into the 11 dens in

**Table 6** Dates for entry and emergence from polar bear maternity dens and duration of den occupancy in EG during two time periods: 1993–1997 (seven dens and six individual bears) and 2007–2010 (n = 8 dens and 6 bears)

| Tagging year | Bear no | Date entry | Date exit | Days in den |
|---|---|---|---|---|
| 1993 | D7125 | 10/20/94 | 4/28/95 | 191 |
| 1993 | D7127 | 10/7/93 | 3/24/94 | 169 |
| 1993 | D7133 | 11/17/94 | 4/16/95 | 151 |
| 1993 | D7351 | 11/8/93 | 4/19/94 | 163 |
| 1994 | D7356 | 11/24/94 | 3/26/95 | 123 |
| 1994 | D7356 | 10/16/96 | 3/21/97 | 156 |
| 1994 | D7357 | 9/29/95 | 2/26/96 | 151 |
| 2007 | D7360 | 10/7/07 | 3/31/08 | 176 |
| 2007 | D7363 | 10/3/07 | 4/4/08 | 184 |
| 2007 | D7364 | 10/7/07 | 4/4/08 | 180 |
| 2007 | D7250 | 10/11/07 | 3/19/08 | 160 |
| 2007 | D7251 | 10/9/08 | 4/3/09 | 177 |
| 2008 | D7260 | 10/17/08 | 3/22/09 | 157 |
| 2008 | D7260 | 9/22/09 | 3/21/10 | 182 |

the north ($p = 0.433$) (Fig. 1). Overall, bears spent little time on land outside of time for denning. On average, only 16 % of all bear locations were on land during 2007–2010.

## Discussion

### Importance of sea ice to EG polar bears

Despite the presence of pack ice year round in offshore EG, the area undergoes a pronounced annual cycle which has a major influence on the annual movements of polar bears (Fig. 1). Outside of the summer period, polar bears tracked in EG in 2007–2010 had a remarkable affinity for relatively dense offshore pack ice. This was consistent with resource selection models for both 2000s and 1990s, where sea ice concentration was the single most important predictor of selection in all seasons. This also follows well with Wiig et al. (2003) who reported polar bears in EG in 1994 showed a preference for areas with ≥70 % ice cover.

An analysis of a subset of adult female and male polar bear movement during spring in East Greenland showed that the two sexes selected for the same habitat and sea ice concentrations (Laidre et al. 2012). Hence, the habitat selection results in this study may also apply to adult males in the EG subpopulation.

### Changes in sea ice habitat availability and selection

We report striking differences in sea ice habitat used by adult female polar bears between the 1990s and 2000s (Fig. 4). Regression models for sea ice concentration demonstrated that adult females in the 2000s use significantly lower sea ice concentrations (10–15 % lower) during nearly all seasons, with an extended summer period using ice habitat <60 % concentration and significantly lower concentrations in winter. This pattern is most strongly influenced by the period between October and December, indicating a late sea ice advance (freeze-up) which results in delayed access to the sea ice platform. This may be most important to the fraction of the EG subpopulation that is on land waiting for freeze-up, rather than bears using the offshore multi-year pack ice during summer. Adult female polar bears consistently select for higher sea ice concentrations in EG among available options, although availability changed between the 1990s and 2000s.

Furthermore, adult females in the 2000s were located significantly closer to open water ($\sim$15 % ice) in all seasons (spring, summer, and winter) than in the 1990s. The seasonal cycle present in the 1990s, where adult females moved >100 km away from poorer habitat in spring and winter, was completely absent in the 2000s. Instead, adult females were located consistently 100 km from the 15 % sea ice edge. This pattern was also present when 50 % sea ice concentration was used to define ice edge. This threshold has been considered the threshold for poor polar bear habitat (Stirling and Parkinson 2006).

The decadal comparison reported here must be considered in terms of the relatively small sample size of adult females. Only four of nine adult female polar bears tracked in 1990s were included in the comparative analyses of habitat selection. These four bears were included because they were tagged in the pack ice and utilized the pack ice during their tracking period. When the full sample of nine adult female bears from the 1990s was included in the models (regardless of pack or fast ice use), larger and more significant differences between the 2000s for all covariates were obtained (not reported here). Of note, the bears tracked in the 2000s rarely used the fast ice. There may be some ecological separation between polar bears in the pack ice and fast ice of EG, though more data are needed to explore this.

In winter in both decades, there was a common preference for polar bears to be closer to land than in summer, a pattern also found in Durner et al. (2009) (Fig. 5). In winter, ice drift speeds in EG are highest and bears locating themselves close to land may minimize passive transport southward. Summer preference to be farther from land may be due to some polar bears staying on the multi-year sea ice as it recedes far from the coast.

The model for polar bear distance to land did not reveal any significant differences between decades, suggesting bears have maintained a similar movement pattern of shifting offshore in late winter and early spring as the sea ice forms and moving east toward land (or north on the receding ice) in late summer (Fig. 4). We attribute the differences observed in distance to 15 and 50 % sea ice to the loss of the sea ice platform (Fig. 2), not bears shifting away from the coastline.

Durner et al. (2009) forecasted that optimal polar bear habitat in EG will decrease substantially during the next 50–100 years using ten IPCC sea ice scenarios. The decrease in optimal habitat in EG was predicted to be most pronounced during spring and summer. In this study, we found the greatest change in EG polar bear habitat use was in the fall and early winter even though habitat changes are occurring in both spring and fall. Given projections of sea ice loss through mid-century (e.g., Overland and Wang 2013), changes in EG polar bear habitat use may extend to other seasons in the future.

### Focal areas

Generally, polar bears inhabiting active offshore ice make use of larger home ranges than bears in landfast ice (Ferguson et al. 1999; Amstrup et al. 2000; Mauritzen et al. 2002). Previous satellite telemetry studies in EG indicated that the range of polar bears in the offshore pack ice is, on average, approximately five times larger than that for polar bears in coastal habitat (Born et al. 1997; Wiig et al. 2003). In 2007–2010, polar bears exploited vast areas of the offshore pack ice in Fram Strait, the Greenland Sea, and the Denmark Sea. The seasonal 75 % kernel areas used by bears during this period ranged between 180,000 and 204,000 km$^2$, comparable to ranges reported by Ferguson et al. (1999) for polar bears in other areas with dynamic pack ice (e.g., Davis Strait = 228,300 km$^2$ and Baffin Bay = 192,000 km$^2$). The areas used by bears in this study were generally concentrated in northeast Greenland, north of 68° N, and only a few bears ranged into Southeast Greenland. The focal areas were smaller than those in the 1990s ($\sim$340,000 to 630,000 km$^2$) suggesting seasonal ranges may have contracted. However, sample sizes were twice as large in the 2000s making it difficult to make comparisons.

Polar bears are generally solitary and independent predators, continuously searching for food throughout the year (Ramsay and Stirling 1986) including the spring breeding season (Laidre et al. 2012). Polar bears, especially females with cubs, must prioritize nutritional gain in spring to improve body condition before the summer sea ice minimum. Ringed seals (*Phoca hispida*) are the principal prey for polar bears in EG (McKinney et al. 2013), although this appears to vary annually and seasonally and their importance relative to other seal species may be decreasing. EG polar bear also prey on bearded (*Erignathus barbatus*) (Dietz et al. 1985), harp (*Pagophilus groenlandicus*), and hooded (*Cystophora cristata*) seals during whelping and molting (Wiig et al. 2003; Øigård et al. 2010). In particular, harp and hooded seals are possibly becoming more important in their diet (McKinney et al. 2013). Recent estimates of harp sea seals in the Greenland Sea indicate over 600,000 animals and a stable population (Øigård et al. 2013; Laidre et al. 2015). Additionally, polar bears in EG may occasionally feed on narwhals (*Monodon monoceros*) and walrus (*Odobenus rosmarus*) (Sandell et al. 2001).

Although the polar bears roamed vast areas of comparable size during all seasons, the general patterns of seasonal variation followed well with access to prey or good habitat. The spring distribution likely reflected an affinity to the whelping patches of harp and hooded seals or the ice edge where there is access to immature ringed seals. The distribution of bears during summer reflected strong affinity to the northward retreat of the pack ice, where seals may also be available during summer. In winter, the bears remained in the vicinity of denning areas or closer to the coast, or moved south into Denmark Strait.

### Movement rates

The EG offshore polar bear habitat is highly influenced by the EG current flowing south year round. This current transports multi-year pack ice from the Arctic Ocean as well as annual sea ice in the Greenland Sea with an average speed of 7–13 km/day (Aagaard and Coachman 1968; Martin and Wadhams 1999) or up to 85 km/day at the eastern edge of the pack ice (Rigor and Ortmeyer 1999).

Observations made by Inuit in coastal EG suggest a general 'passive' transport of polar bears south with the current on the drifting sea ice and an 'active' movement of bears north along the coast (Dietz et al. 1985; Sandell et al. 2001). However, this study and others (Larsen et al. 1983; Born et al. 1997; Wiig et al. 2003) have shown that EG polar bears are able to move in the pack ice irrespective of the southward movement of the EG Current. Wiig et al. (2003) suggested that the distribution of polar bears in the EG pack ice likely reflects behavioral rather than physical processes, similar to the case of the polar bears in the Barents Sea (Mauritzen et al. 2003).

Movement rates in the pack ice for adult female polar bears in the 2000s were higher and more seasonally variable than those in the 1990s. Polar bear movement rates may increase as sea ice concentrations are reduced and ice becomes more mobile, so bears must move actively to maintain their position against the direction of sea ice drift (Stirling and Derocher 2012).

### Maternity denning sites

No statistically significant difference was found for observed maternal den entry or exit timing between decades; however, the duration of denning was longer during the 2000s (Fig. 2). Our study reports a small sample size, and the mean date in the 1990s was partly affected by one very late den entry (11 November) in 1994.

Miscellaneous observations of maternity dens and family groups with 0-year-old cubs indicate that maternity dens occur along the entire EG coast with an apparent higher density north of 68°N where ice and weather conditions are generally more stable (Pedersen 1945; Vibe 1967; Born 1983; Dietz et al. 1985; Born and Rosing-Asvid 1989; Glahder 1995; Born et al. 1997; Sandell et al. 2001; Wiig et al. 2003). Areas regularly used for EG denning include Kangerlussuaq, the Blosseville Coast, inner parts of Scoresby Sound fjord, the areas between Kong Oscars Fjord and Kejser Franz Joseph Fjord, and the coast at the NEW. The ranges for maternity entry and exit dates observed in EG area are similar to other polar bear subpopulations (Messier et al. 1994; Amstrup and Gardner 1994; Wiig 1998; Derocher et al. 2011; Andersen et al. 2012).

Amstrup and Gardner (1994) suggested that polar bears using drifting pack ice in late summer have a less predictable choice of denning location than bears on stable ice. It is possible that den site choice for polar bears in EG depends on the extension of the pack ice just before den entry. The majority of dens in this study were located at the NEW irrespective of tagging location. Sea ice was present in the NEW in September and October, and pregnant females likely used this as a platform for hunting before den entry. Hence, at the time of den site selection, all adult females that used the NEW for denning were already in the NEW region. A forecast decrease in polar bear habitat in EG (Durner et al. 2009) will likely increase the tendency of adult females to den in the NEW area given its northern location.

Larsen et al. (1983) noted that approximately 90 % of the polar bear tracks observed during the FRAM I expedition (83°N off northeast Greenland) were adult females with small cubs. Based on the distance of these tracks from the coast and the resemblance to the ice situation off the northern coast of Alaska (where polar bears use maternity dens in offshore pack ice), Amstrup and DeMaster (1988) suggested that maternity dens may also be found on the multi-year pack ice in northeast Greenland. This study and previous tracking studies did not observe offshore denning in the multi-year pack ice in EG (Born et al. 1997; Wiig et al. 2003; this study).

## Conclusions

Vongraven et al. (2012) characterized the EG subpopulation as being at high risk from impacts of climate change (Durner et al. 2009), a high pollution load (Dietz et al. 2012), and an unknown harvest rate due to the lack of data on subpopulation size and growth rate. The EG subpopulation was also characterized as having a low quality of baseline data. This study contributes to new knowledge on the ecology of the EG subpopulation of polar bears and documents shifts in habitat use and habitat availability over a period of sea ice loss. Future research on body condition, demography, and subpopulation size is needed to contribute to the conservation and management of the EG subpopulation.

**Acknowledgments** Funding was provided by the Bureau of Mineral and Petroleum (Nuuk, Greenland), the Danish Ministry of the Environment (Copenhagen, Denmark), and the Greenland Institute of Natural Resources (Nuuk). All permits for the study were provided by the Greenland Institute of Natural Resources and the Government of Greenland. We thank the Norwegian Polar Institute (NPI; Tromsø, Norway) and in particular Drs. Kit M. Kovacs and Christian Lydersen (NPI) and the Institute of Marine Research (Tromsø) and Dr. Tore Haug for valuable help during field work in 2007 and 2008. The field work in 1993 and 1994 was made possible by logistical support from Alfred Wegener Marine Research Institute (AWI, Bremerhaven and Potsdam). Thanks are due to the crew of RV "Polarstern" (AWI), MV "Nordsyssel" (IMR), and RV "Lance" (NPI). Support for K. L. and H. S. was provided by NASA (NNX11AO63G and NNX13AN28G) and the Greenland Institute of Natural Resources. Three anonymous reviewers improved the paper.

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