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An Arctic predator–prey system in flux: Climate change impacts on coastal space use by polar bears and ringed seals

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Abstract

1. Climate change is impacting different species at different rates, leading to alterations in biological interactions with ramifications for wider ecosystem functioning. Understanding these alterations can help improve predictive capacity and inform management efforts designed to mitigate against negative impacts.
2. We investigated how the movement and space use patterns of polar bears (*Ursus maritimus*) in coastal areas in Svalbard, Norway, have been altered by a sudden decline in sea ice that occurred in 2006. We also investigated whether the spatial overlap between polar bears and their traditionally most important prey, ringed seals (*Pusa hispida*), has been affected by the sea-ice decline, as polar bears are dependent on a sea-ice platform for hunting seals.
3. We attached biotelemetry devices to ringed seals (n = 60, both sexes) and polar bears (n = 67, all females) before (2002–2004) and after (2010–2013) a sudden decline in sea ice in Svalbard. We used linear mixed-effects models to evaluate the association of these species to environmental features and an approach based on time spent in area to investigate changes in spatial overlap between the two species.
4. Following the sea-ice reduction, polar bears spent the same amount of time close to tidal glacier fronts in the spring but less time in these areas during the summer and autumn. However, ringed seals did not alter their association with glacier fronts during summer, leading to a major decrease in spatial overlap values between these species in Svalbard's coastal areas. Polar bears now move greater distances daily and spend more time close to ground-nesting bird colonies, where bear predation can have substantial local effects.
5. Our results indicate that sea-ice declines have impacted the degree of spatial overlap and hence the strength of the predator–prey relationship between polar bears and ringed seals, with consequences for the wider Arctic marine and terrestrial ecosystems. Shifts in ecological interactions are likely to become more widespread in many ecosystems as both predators and prey respond to changing environmental conditions induced by global warming, highlighting the importance of multi-species studies.

KEYWORDS
prey-shifting, *Pusa hispida*, sea-ice declines, spatial overlap, Svalbard, *Ursus maritimus*

1 | INTRODUCTION

Climate change is expected to have large consequences for the structure and function of ecosystems (IPCC 2014). Different species will be impacted at different rates, leading to temporal and spatial changes in biological interactions (Doney et al., 2012; Thackeray et al., 2010). The Arctic is warming at a rate three times greater than the global average and Arctic sea-ice extent is declining rapidly (Comiso & Hall, 2014). The Arctic Ocean is expected to be seasonally ice-free by as early as the 2030s (Wang & Overland, 2012). Altered trophic interactions may have particularly serious effects in highly seasonal environments, such as the Arctic, where important life cycle processes occur in a highly synchronised fashion during short time periods (Høye, Post, Meltofte, Schmidt, & Forchhammer, 2007).

The consequences of the large abiotic changes currently occurring in the Arctic are expected to be severe, especially for ice-associated species (IPCC 2014; Post et al., 2009). Arctic endemic marine mammals are dependent on sea ice and these species are sensitive to changes in this habitat (Kovacs, Lydersen, Overland, & Moore, 2011; Laidre, Stern et al. 2015). This is because of both the habitat loss issue and the sensitivity these species have to climate change due to their generally high trophic position(s) (see Doney et al., 2012; Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010). Sea-ice declines represent losses of shelter from inclement weather, protection from open-water predators (i.e. killer whales [*Orcinus orca*]) and many forms of human disturbance, foraging habitats, platforms for birthing, nursing, resting and moulting in the case of ice-associated seals and in a loss of hunting habitat and transport platforms for polar bears (*Ursus maritimus*; see Kovacs et al., 2011; Laidre, Stern et al. 2015: Stirling & Derocher, 2012; for more details).

Ringed seals (*Pusa hispida*) are one of the ice-obligate pinniped species that gives birth and nurses their young on sea ice. This species uses snow lairs constructed over breathing holes in sea ice to rear their offspring (Lydersen & Gjertz, 1986; Smith & Stirling, 1975). The lairs provide pups with thermal and predator protection and are vital for pup survival (Lydersen & Smith, 1989). Similar to the other Arctic seals, ringed seals use sea ice as a resting and moulting platform, and a high proportion of their diet is ice-associated prey (Reeves, 1998). Polar bears are a pinnacle predator in the Arctic. They are opportunistic feeders, but their primary prey in most areas is the ringed seal (Derocher, Wiig, & Andersen, 2002; Iversen et al., 2013; Thiemann, Iverson, & Stirling, 2008). Polar bears are dependent on a sea-ice platform for hunting seals effectively, with the primary hunting methods being stalking seals that are hauled out on sea ice or still-hunting at breathing holes (Stirling, 1974). Polar bears also eat terrestrial food sources, such as bird eggs, particularly when hunting opportunities for seals are reduced due to declines in sea ice (Iverson, Gilchrist, Smith, Gaston, & Forbes, 2014; Prop et al., 2015).

Both ringed seals and polar bears in the Svalbard Archipelago, Norway (10°–35°E, 74°–81°N) have two movement strategies. Individuals in both of these species either remain coastal throughout the year, with polar bears restricted to being on land if sea ice is absent, or they undergo seasonal movements that follow the summer retreat of the ice northward (Freitas, Kovacs, Ims, Fedak, & Lydersen, 2008; Hamilton, Lydersen, Ims, & Kovacs, 2015, 2016; Lydersen et al., 2014; Mauritzen et al., 2002). Coastal polar bears, especially females with dependent cubs, primarily occupy areas with land-fast ice near tidal glacier fronts in the spring, where they hunt ringed seals and their pups (Freitas et al., 2012).

Sea ice in the Barents Sea/Svalbard region is declining at a faster rate than other Arctic areas. This region has experienced the largest declines in seasonal sea-ice duration within the Arctic, with >20 weeks less sea-ice cover in 2013 compared to 1979 (two to four times the decrease compared to other Arctic areas; Laidre, Stern et al. 2015). In 2006, the sea-ice conditions in Svalbard changed dramatically. In addition to an ongoing northward retreat of the summer sea-ice extent, the amount of land-fast ice forming in the fjords of Svalbard, especially on the west coast of Spitsbergen, the largest island, declined sharply. This altered sea-ice regime has persisted to the present day (2016; Norwegian Ice Service, http://polarview.met.no/). Satellite tracking data for both polar bears and ringed seals in the Svalbard region have been collected from before and after the shift in sea-ice conditions; the effects the sea-ice changes have had on the behaviour, movement patterns and space use of ringed seals are reported elsewhere (Hamilton et al., 2015, 2016). The purpose of the present study was to investigate whether coastal polar bears have altered their hunting effort on ringed seals in areas near tidal glacier fronts following the decline in sea-ice conditions, given their dependence on sea-ice platforms for successful hunting. An increased use of areas close to glacier fronts could be expected if ringed seals have become less available due to less sea ice in other coastal areas. Alternatively, if ice conditions for seal hunting have also deteriorated near tidal glacial fronts, polar bears may have decreased the amount of time spent in these areas, in which case polar bears could be expected to increase their use of terrestrial resources, such as bird colonies. To assess these alternative hypotheses, the present study investigated the habitat and space use patterns of polar bears that remain in coastal areas in Svalbard during the spring, summer and autumn, specifically focusing on monthly home range size, the distance travelled per day and the association with environmental covariates such as tidal glacier fronts and bird colonies to determine whether the space use patterns of polar bears were affected by the sea-ice collapse. Potential changes in the polar bear–ringed seal predator–prey relationship were also investigated by assessing the spatial overlap between these two species before and after the change in sea-ice conditions occurred in Svalbard. The amount of spatial overlap was used as a proxy for the magnitude of the predator–prey relationship between polar bears and ringed seals.

2 | MATERIALS AND METHODS

2.1 | Polar bear and ringed seal locations

Sixty-seven adult female polar bears were captured and equipped with satellite collars (produced by Telonics [Mesa, AZ, USA], Advanced Telemetry Systems [ATS, Isanti, MN, USA] or SirTrack [Havelock North, Hawke's Bay, New Zealand]) in 2002–2004 (19 bears) and

2010–2013 (48 bears), around Svalbard, Norway (Tables S1 and S2, Supporting Information). For details on capture and handling, see Mauritzen et al. (2002). Mass and body condition index (bci) of the bears were calculated following Cattet, Caulkett, Obbard, and Stenhouse (2002).

A total of 60 ringed seals were captured and equipped with Satellite-Relay Data Loggers (SRDLs, Sea Mammal Research Unit Instrumentation, University of St Andrews, St Andrews, Scotland) in 2002–2004 (22 seals) and 2010–2012 (38 seals) around Svalbard. For details on capture and handling, see Hamilton et al. (2016). Because most of the polar bear data are from eastern Svalbard, only data from coastal ringed seals occupying this region during summer were included in the analyses herein ($N = 23$). All animal-handling protocols were approved by the Norwegian Animal Research Authority and the Governor of Svalbard.

Sixty-four of the polar bear collars calculated GPS locations that were transmitted by the Argos (System Argos, Toulouse, France) or the Iridium (Iridium Satellite Communications, McLean, VA, USA) satellite systems at least once every fourth hour. Locations for the remaining three polar bears and for the ringed seals were calculated by the Argos satellite system. Transmissions occurred whenever the antennae was exposed to the air (i.e. no duty cycle) for the ringed seals while the Argos tags for the three polar bears had a duty cycle of 6 hr on, 18 hr off. All polar bear locations in the first 3 days after capture were discarded to reduce potential effects on behaviour caused by drugging (Rode, Pagano et al. 2014). Maternity denning periods between October and April for polar bears were identified using both the location and temperature data measured by sensors on the collars. Thirteen bears were identified as having denned; locations from denning periods were removed from the analyses.

Polar bear and ringed seal locations were pre-filtered using a speed-distance-angle filter, using maximum speeds of 2.78 m/s (10 km/h) and 2 m/s respectively (Freitas, Lydersen, Fedak, & Kovacs, 2008). Locations were subsequently filtered using the CRAWL package in R 3.1.3, with a stopping model incorporated for ringed seals to account for time spent hauled out (Johnson, London, Lea, & Durban, 2008; R Core Team 2015). A position from every fourth hour was extracted from the CRAWL model for each animal.

Four seasons were delineated based on ringed seal and polar bear annual cycles, three of which were analysed in this study: spring (1 March to 31 May), summer (1 June to 31 August) and autumn (1 September to 30 November). Winter data (1 December to 28 February) were not analysed in the present study because of termination of data transmissions from some tags and because many of the bears entered dens (i.e. of the 16 bears still transmitting data in the winter in 2002–2004, nine entered a den). To account for potential effects of variable capture locations, polar bears were assigned to one of three spatial groups (S, NE or NW Svalbard, see Appendix S1 for further details).

Classification into the coastal and offshore strategies for each season was quite straightforward for most of the polar bears (55 of 67). They either stayed on or near land or they followed the retreat of the sea-ice edge. However, 12 bears were a little more challenging to classify. These bears were deemed to be offshore if an individual undertook directed movements away from the coast, resulting in the bear reaching a distance ≥50 km from the coastline; generally speaking, islands in the Archipelago are less than 100 km apart, so exceeding the 50-km limit takes them away from land-based areas. Some bears were classified as coastal in one season and offshore in another, depending on their locations. For example, two bears tagged in Svalbard travelled to Franz Josef Land, Russia (movements of between 500 and 700 km), and subsequently remained coastally there. The ringed seals were similarly classified into offshore and coastal strategies (see Hamilton et al., 2015 for details).

2.2 | Environmental variables

All analyses were conducted in R 3.1.3 (R Core Team 2015) and results are presented as mean ± 95% CI. Statistical explorations of all datasets were carried out following Zuur, Ieno, and Elphick (2010). Locations were compared to relevant environmental variables to define coastal polar bear habitats and to assess whether the association with these environmental features has been impacted by the change in sea-ice conditions. Environmental variables were selected a priori based on previous knowledge from the Barents Sea polar bear subpopulation and a literature review. Variables of interest included tidal glacier fronts, ground-nesting bird colonies, cliff-nesting bird colonies, the coastline, bathymetry and bathymetric slope. Cliff-nesting and ground-nesting bird colonies were treated separately because polar bears use quite different foraging strategies in the two types of colonies, which are occupied by different avian species groups (Iverson et al., 2014; Prop et al., 2015; see Appendix S1 for further details). Coastline and bird colony shapefiles for Svalbard and Franz Josef Land and the tidal glacier front shapefile for Svalbard were extracted from Norwegian Polar Institute databases (NPI, www.npolar.no, Strøm, Descamps, & Bakken, 2008). Glacier data for Franz Josef Land were retrieved from the Global Land Ice Measurements from Space (GLIMS, http://www.glims.org/) database and converted into tidal glacier fronts using ArcGIS (ESRI, Redlands, CA, USA). Bathymetry data, at a 500-m gridded surface resolution, were retrieved from the International Bathymetric Chart of the Arctic Ocean (IBCAO) version 3.0 (Jakobsson et al., 2012); these data were also used to calculate bathymetric slope (see Table S3 for the correlation coefficients between the environmental variables).

2.3 | Home range and movement analysis

Monthly 95% home ranges were calculated for each polar bear using the dynamic Brownian bridge movement model (Kranstauber, Kays, LaPoint, Wikelski, & Safi, 2012) to evaluate whether the amount of space used by individual bears had been affected by the decline in sea-ice conditions. This method expands the traditional Brownian bridge movement model, creating a utilisation distribution based on the movement path, by allowing changes in movement behaviour over time (Kranstauber et al., 2012). A bear had to transmit data for at least 20 days in a given month to be included; this resulted in the removal of 62 bear-months (13% of the total number of bear-months). The inputs to the Brownian bridge model were: hourly locations; grid cell size of 2.5 × 2.5 km; variable location error depending on collar type; window size of 47; and margin of 11 (Kranstauber et al., 2012). Errors of 500, 1,000 and 2,500 m were used for Telonics Iridium and ATS Iridium collars, Telonics GPS collars and SirTrack (Argos) collars, respectively, due to the varying location accuracy of these systems. Linear regression models, with the Gaussian family and identity link, were used to test for potential differences in home range size between the two periods. The response variable was transformed when necessary to fulfil model assumptions; residual plots were used to assess model assumptions (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The monthly home ranges were bootstrapped to obtain confidence intervals.

The distance between consecutive 4-hr locations was used to estimate the daily distance moved in order to assess whether polar bears altered their mobility patterns after the decline in sea-ice conditions. A linear mixed-effect model was used to model the daily distance moved for each season using the Gaussian family and identity link. The response variable was log-transformed to fulfil model assumptions. Possible predictor variables included period, capture location, month, bci and reproductive status of the polar bears (alone, with cubs of the year [COYs] or with second year cubs, i.e. yearlings). Bear id was included both as a random effect and as a grouping factor in the corAR1 temporal correlation term. Bayesian information criterion (BIC) was used for model selection; residual plots were used to assess model assumptions (Zuur et al., 2009).

2.4 | Association with environmental variables

Polar bear locations at 4-hr intervals were used to access the association with the environmental features listed above for each season. Distances to bird colonies were analysed only for the summer period. The proportion of bear locations within 5 km of a glacier front, and within 2 km of ground-nesting and cliff-nesting bird colonies, was also calculated. Linear models (proportion of location models) and linear mixed-effect models (other environmental variable models) were run for each environmental variable in each season using the Gaussian family and identity link. The response variable was transformed when necessary to fulfil model assumptions. Included variables, model selection and model validation took place as described above for the daily distance moved model.

Ringed seals on the east coast exhibited similar behavioural patterns during the two periods in terms of space use and haul out percentage (Hamilton et al., 2016). However, in order to explore potential impacts on polar bear hunting behaviour, the proportion of time ringed seals spent hauled out and their proximity to glacier fronts in summer were calculated.

2.5 | Polar bear–ringed seal predator–prey relationship

In order to assess the degree of spatial overlap between polar bears and ringed seals and whether the magnitude of overlap has been affected by the decline in sea-ice conditions, an approach similar to Hunsicker, Ciannelli, Bailey, Zador, and Stige (2013) was followed. Time spent in area (TSA) for the summer was calculated for each polar bear and each ringed seal over a 2.5 × 2.5 km grid (Sumner, 2014) on a monthly basis. A generalised additive mixed-effect model (GAMM) was run for each species and period using the Gaussian family and identity link with the R GAMM4 package (Wood & Scheipl, 2014). TSA was log-transformed to meet model assumptions (Zuur et al., 2009). Possible predictor variables included the environmental variables (see above), proportion of the grid cell on land (polar bears only), bci (polar bears only), reproductive status (polar bears only), capture location (polar bears in 2010–2013 only), body mass (ringed seals only) and sex (ringed seals only). Animal id was included as a random effect. BIC was used for model selection and residual plots were used to verify model assumptions (Zuur et al., 2009).

The models selected using BIC for each species and period were used to predict the TSA. These predicted TSA values were converted into proportion of time spent in each grid cell using the species and period specific sum. The ringed seal and polar bear proportions were multiplied for each period to estimate the degree of spatial overlap. The overlap values were rescaled between 1 (highest overlap value) and 0 (lowest overlap values) for graphical purposes. Cross-validation was performed to quantify the level of uncertainty in the spatial overlap estimates. A leave-one-out procedure was followed, where the percentage change in overlap in each grid cell was calculated after each individual was randomly removed from the analyses (Raymond et al., 2015).

3 | RESULTS

The polar bear collars transmitted data for 249 ± 151 days (mean ± *SD*). Sixty of the 67 tagged polar bears were classified as being coastal bears for at least one season (Figures 1 and S1). A summary of the number of locations and animals for each species and period are presented in Table 1.

3.1 | Polar bear home range and movements

Monthly 95% home range size for the polar bears was quite similar between the two periods (Figure 2). However, the 95% home range was significantly smaller in August ($t = -2.300$, $p = .029$) in 2010–2013 compared with 2002–2004.

In the spring, individual polar bears moved between 0.5 and 40 km/day on average (range of individual bears), with the daily distance moved increasing as the season progressed (Figure 3a, Tables S4 and S5). This pattern was similar for both periods. During the summer, individual polar bears moved between 0.3 and 19 km/day on average (range of individual bears), with the daily distance moved decreasing as the season progressed (Figure 3b, Tables S4 and S5). However, polar bears in 2010–2013 moved significantly larger distances per day, for all summer months, compared with bears in 2002–2004. In the autumn, individual polar bears moved between 1.4 and 22 km/day on average (range of individual bears), and there was a slight increase in

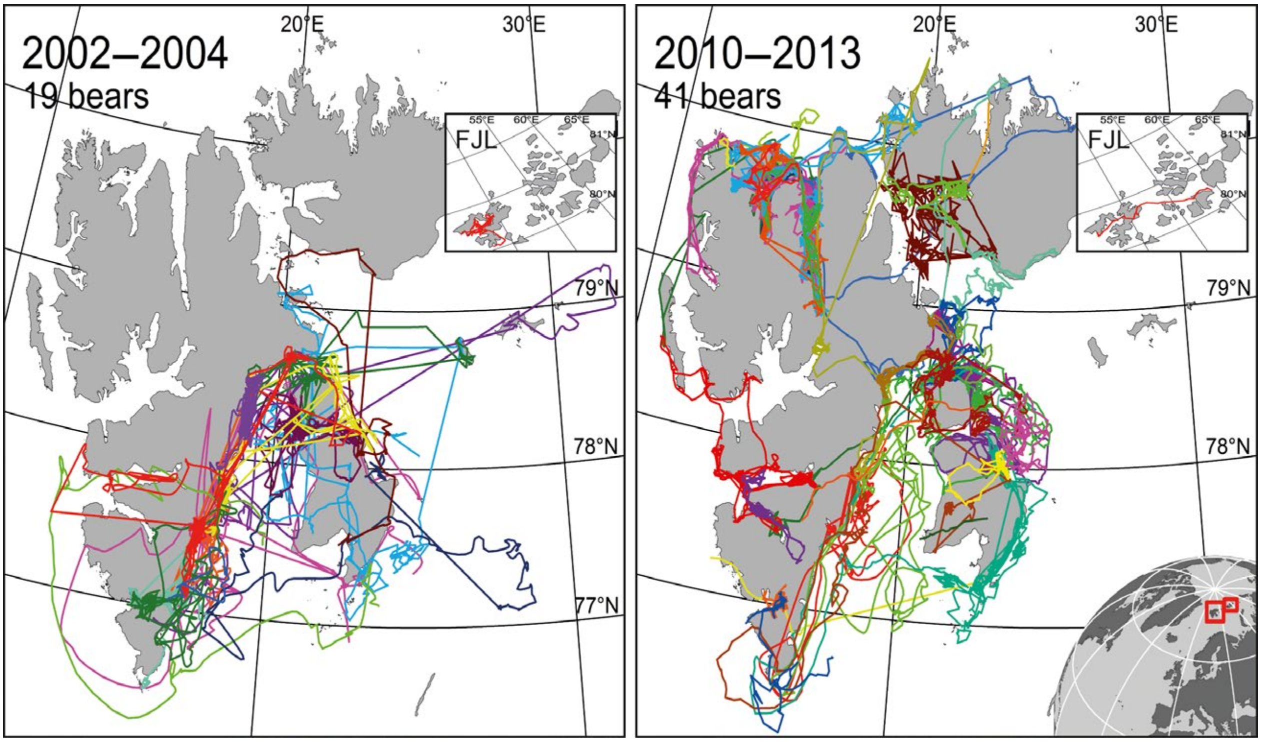

FIGURE 1 Tracks of the coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002–2004 and 2010–2013. The inset maps show two polar bears that moved to Franz Josef Land (FJL), Russia

TABLE 1 Number of coastal polar bears with biotelemetry devices in Svalbard, Norway, and the number of transmitted locations for each season. Similar ringed seal data are presented for the summer season—the period for which spatial overlap analyses (with the bears) were conducted

	Both time periods		2002–2004		2010–2013	
	Number of animals	Number of locations	Number of animals	Number of locations	Number of animals	Number of locations
Polar bears—spring	59	15,375	18	6,142	41	9,233
Polar bears—summer	38	16,476	15	5,997	23	10,470
Polar bears—autumn	36	12,227	15	6,694	21	5,533
Ringed seals—summer	23	4,560	14	3,210	9	1,350

distance moved as the season progressed. There was no significant difference in this pattern between the periods (Figure 3c, Tables S4 and S5).

3.2 | Association with environmental variables

Polar bears did not alter their association with glacier fronts during the spring between the two periods, but they did alter their association with glacier fronts during both the summer and autumn (Tables S6–S9). During the summer, the amount of time spent within 5 km of glacier fronts decreased significantly from 2002 to 2004 (63 ± 29%) to 2010–2013 (28 ± 28%), with the average distance from glacier fronts increasing from 3 km (95% CI: 2–5) in 2002–2004 to 8 km (95% CI: 5–12) in 2010–2013 (Tables 2, S6, S8, and S10). During the autumn, the percentage of time spent within 5 km of a glacier front also decreased significantly from 2002 to 2004 (71 ± 36%) to 2010–2013 (35 ± 35%) with the average distance from glacier fronts increasing from 2 km (95% CI: 1–3) in 2002–2004 to 7 km (95% CI: 4–11) in 2010–2013 (Tables 2, S6, and S9).

During the summer, ringed seals spent 68 ± 12% of their time within 5 km of a glacier front, with no change between the two periods (2002–2004: 65 ± 12%, 2010–2013: 74 ± 22%, $p = .487$). Ringed seals spent 12 ± 4% of their time hauled out in the summer during both periods (2002–2004: 12 ± 5%, 2010–2013: 12 ± 7%, $p = .920$).

There was a significant increase in the percentage of time polar bears spent within 2 km of ground-nesting birds from 2002 to 2004 (2 ± 3%) to 2010–2013 (7 ± 8%) during the summer (Tables 2, S6, and S8). There was no difference in the proximity of polar bears to cliff-nesting bird colonies between the two periods (Tables S6 and

S8). Reproductive status and bci were not retained in any of the BIC-selected models (Table S6). The decreased association with glacier fronts was similar for bears tagged in all three capture locations, while the increased association with ground-nesting bird colonies was greatest for bears tagged in NW Svalbard, although increased association with this type of bird colony was also exhibited by bears tagged in southern Svalbard (Tables S11–S13).

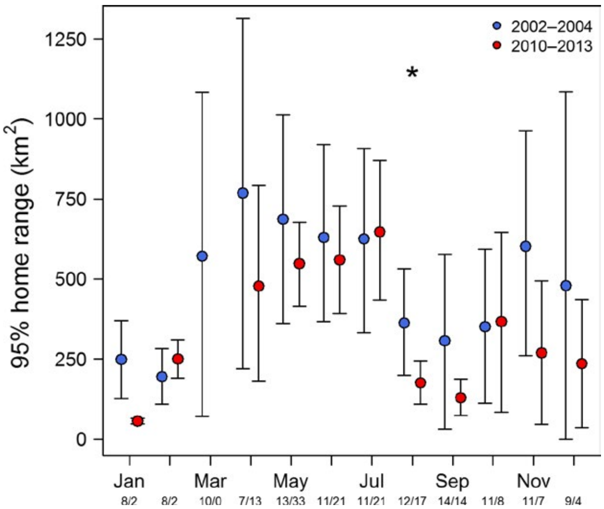

FIGURE 2 95% home range size (km^2, mean ± 95% CI) for 60 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002–2004 and 2010–2013 by month. Significant differences between the two periods are indicated by *. Values underneath the *x*-axis indicate the number of bears included for each period and month

3.3 | Polar bear–ringed seal relationship

The highest values of spatial overlap between the two species were seen in 2002–2004; the maximum values were *c*. 150% higher than the maximum values for 2010–2013 (Figures 4, 5a and c). The relative change in summer spatial overlap between the polar bears and ringed seals during the two periods showed large and widespread changes (Figure 5, Table S14). The spatial overlap values decreased greatly in 2010–2013 compared to 2002–2004 in areas close to glacier fronts, with small increases in coastal areas where no glacier fronts occur (Figure 5e). A cross-validation procedure showed that uncertainty (the percentage change) in the overlap values after each individual was randomly left out were generally small, with means less than 8% (Figure 5b and d). Analyses using only bears tagged in the southern area (in both periods) showed that the decrease in spatial overlap between polar bears and ringed seals on the eastern side of Svalbard was intensified compared to analyses using all bears tagged in 2010–2013 (Figures 5 and S2).

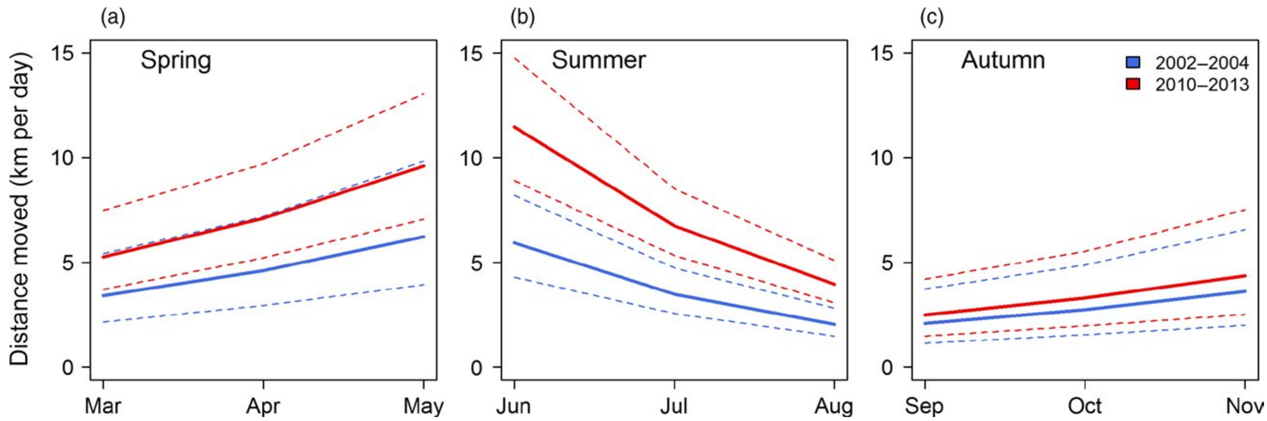

FIGURE 3 Distance moved (km/day, mean ± 95% CI) during spring (a), summer (b) and autumn (c) by 60 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002–2004 and 2010–2013

TABLE 2 Proportion of time (mean ± *SD*) spent within a certain number of km of an environmental feature for each season for the 60 coastal polar bears equipped with satellite collars in Svalbard, Norway, for all bears and for each period and the *p*-value for the difference between the periods. Significant *p*-values (<.05) are presented in bold font

Season	Environmental variable	All bears	2002–2004	2010–2013	*p*-value
Spring	Glacier front (5 km)	31 ± 30	37 ± 30	29 ± 30	.3280
	Coast (5 km)	75 ± 28	69 ± 28	77 ± 29	.3380
Summer	Glacier front (5 km)	42 ± 33	63 ± 29	28 ± 28	**.0007**
	Bird colony (2 km)	12 ± 12	9 ± 13	14 ± 11	.0555
	Ground-nesting birds (2 km)	5 ± 7	2 ± 3	7 ± 8	**.0050**
	Cliff-nesting birds (2 km)	9 ± 10	7 ± 12	9 ± 9	.1540
	Coast (5 km)	86 ± 19	91 ± 10	83 ± 23	.2250
Autumn	Glacier front (5 km)	50 ± 39	71 ± 36	35 ± 35	**.0054**
	Coast (5 km)	91 ± 18	94 ± 10	89 ± 22	.4150

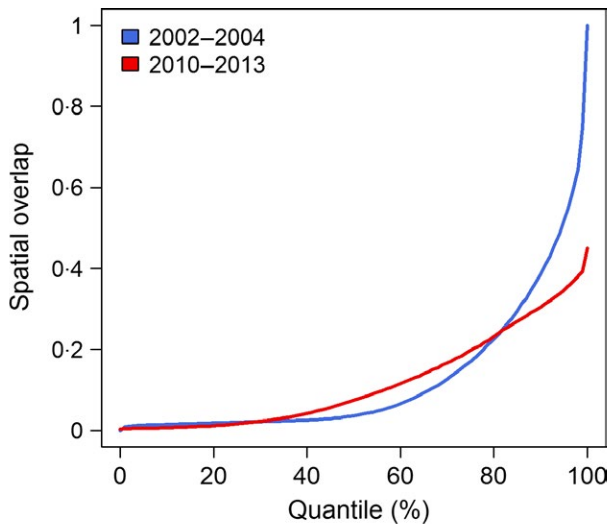

FIGURE 4 Quantiles of the spatial overlap values for the summer months for 2002–2004 and 2010–2013 between the 38 coastal polar bears and 23 coastal ringed seals equipped with biotelemetry devices in Svalbard, Norway. The overlap values were rescaled between 0 (lowest overlap value) and 1 (highest overlap value) for graphical purposes

4 | DISCUSSION

Remaining coastal, when the sea ice retreats away from land each year, is one of the two movement strategies exhibited by polar bears in Svalbard, the alternative strategy being use of offshore sea ice (Mauritzen et al., 2002). The strategy followed by individuals appears to be individually specific, with bears preferentially following the same strategy every year if conditions allow (Mauritzen, Derocher, & Wiig, 2001; J. Aars, unpublished data). Most bears (60 of 67) in this study had at least one season in which they were classified as being coastal, likely reflecting the fact that denning areas in Svalbard are located on land, and coastal areas provide food that is readily available in spring (Lydersen et al., 2014).

Spring is a critical hunting period for polar bears; after the long dark winter when many female bears have been in the den rearing young and fasting, finding food quickly to replenish depleted energy stores is important. During this period, polar bears in most Arctic regions primarily hunt ringed seals and their pups (Stirling & Derocher, 2012). During the spring, coastal polar bears in Svalbard concentrate their hunting activities at tidal glacier fronts (Freitas et al., 2012; Lydersen et al., 2014); this behaviour remained consistent in the two periods indicating that the overall declines in sea ice have not yet been severe enough to cause polar bears to alter their hunting strategy during spring. Tidal glacier fronts are particularly important pupping areas for ringed seals in Svalbard because the archipelago is an Arctic desert, which has little snow fall. In this region, calved pieces of glacier ice frozen into the annual land-fast ice accumulate snow to sufficient depths for ringed seals to build snow lairs over their breathing holes, which are vital for pup survival (Lydersen & Gjertz, 1986; Lydersen & Smith, 1989).

Tidal glacier fronts have high concentrations of invertebrate and fish prey during the open-water season because they are upwelling areas; subsurface glacial river run-off entrains large volumes of intermediate depth water masses and its production as it rises to the surface. Invertebrates and fish either become stunned or die due to osmotic shock or become trapped in a water layer below the glacier river run-off. These concentrations of biomass make tidal glacier front areas important foraging hotspots for both sea birds and marine mammals (see Lydersen et al., 2014 for details). Additionally, calved pieces of glacier ice and the enduring land-fast ice deep inside fjords (at least before the change in sea-ice conditions occurred) provide haul-out platforms for seals (Freitas, Kovacs, et al., 2008; Hamilton et al., 2016; Lydersen et al., 2014). The association of coastal ringed seals with glacier fronts in eastern Svalbard in the summer has not yet been affected by the overall reductions that have taken place in annually formed ice. East coast ringed seals spent 68% of their time close to glacier fronts both before and after the change in sea-ice conditions. Interestingly, on the west coast of Svalbard where the reduction in sea-ice conditions has been much more severe than on the east coast, ringed seals in 2010–2012 spent the majority of their time (72%–100%) close to glacier fronts (Hamilton et al., 2016). There was also no change in the fraction of time that coastal ringed seals in eastern Svalbard spent hauled out on ice (i.e. most exposed to polar bear predation) between the periods. However, behaviour patterns of coastal bears in the summer and autumn have changed following the major reduction in annually-formed coastal sea ice. The amount of time polar bears spent in close proximity to glacier fronts decreased significantly in both summer and autumn between the two periods. These changes in polar bear behaviour are not apparently directly linked to changes in the presence of their primary prey, ringed seals. However, the early break-up and complete seasonal disappearance of land-fast ice means that ringed seals must increasingly use calved pieces of glacier ice as resting platforms in summer and autumn. Polar bears normally hunt ringed seals by stalking them on sea ice or by still-hunting at breathing holes (Stirling, 1974; Stirling & Archibald, 1977). But in areas with broken glacier ice, polar bears must do aquatic approaches, sneaking in on seals and then bursting onto the ice to capture their prey. This hunting technique has been suggested to be a ‘specialty’ hunting strategy, only used by some bears (Stirling, 1974). Concordantly, only 5 of the 23 bears (22%) in the recent period that were coastal during the summer spent more than 50% of their time within 5 km of glacier fronts, whereas in the earlier period, when land-fast or broken first-year sea ice was present during summer, 11 out of 15 bears (73%) spent over 50% of their time within 5 km of a glacier front. The shift in the type of ice used as a haul out platform by the seals may have resulted in a decrease in the intensity of the predator–prey relationship between polar bears and ringed seals, with reduced spatial overlap occurring between these two species in summer.

Bearded seals (*Erignathus barbatus*) are also an important prey species for polar bears in Svalbard (Derocher et al., 2002; Iversen et al., 2013). Satellite tracking has shown that during the summer and autumn, bearded seals return to glacier fronts from their foraging areas to haul out on calved pieces of glacier ice (Lydersen et al., 2014). Unfortunately, no tracking data are available for this species from the east coast of Svalbard to explore possible shifts in their spatial overlap with bears.

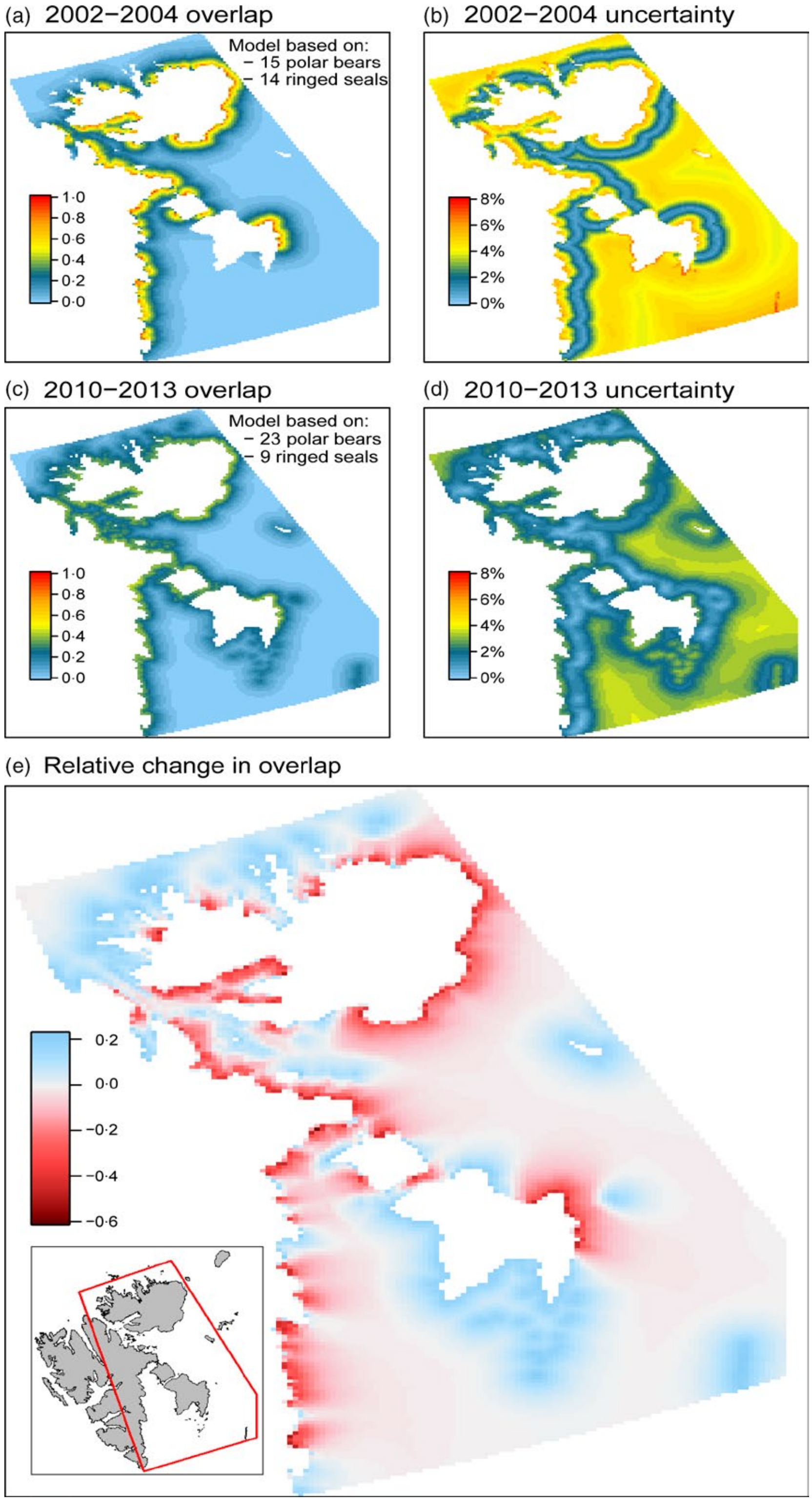

FIGURE 5 Spatial overlap values (rescaled between 1 [highest overlap value] and 0 [lowest overlap value]) for the summer period (June-August) for 2002–2004 (a) and 2010–2013 (c) for the 38 coastal polar bears and 23 coastal ringed seals equipped with biotelemetry devices in Svalbard, Norway. Cross-validation showed the percentage change in overlap values when an individual was left out for 2002–2004 (b) and 2010–2013 (d). The relative change in overlap values between the two periods (e) with negative values indicating less overlap and positive values indicating more overlap in 2010–2013 compared to 2002–2004

The decreased accessibility of ringed seals to polar bears due to the decrease in sea ice and the resulting changes in the two species biological interactions has had effects on other parts of the ecosystem. Following the alteration in the sea-ice regime, polar bears moved greater distances per day in the summer months, but had smaller home ranges in August, suggesting that polar bears are searching more for food but are restricted in the area that they search, potentially due to reductions in sea ice. Movement rates of offshore female polar bears in the spring in East Greenland have also increased in 2007–2010 compared to the 1990s, potentially as a result of the decreased sea-ice concentrations and increased sea-ice mobility (Laidre, Born, et al., 2015).

Following the reduction in sea ice, coastal polar bears in Svalbard spent more time close to ground-nesting bird colonies, suggesting that they are utilising this alternative food source to a larger degree. The occurrence of polar bears at ground-nesting bird colonies has increased in western Svalbard in recent decades, concurrent with the decreased duration of the sea-ice season (Prop et al., 2015). The large population increases in pink-footed geese (*Anser brachyrhynchus*) and barnacle geese (*Branta leucopsis*) in Svalbard over the last decades have probably enhanced the supply of terrestrially-based summer food for bears (Goosemap, 2012; Madsen & Williams, 2012). Polar bear predation within ground-nesting bird colonies can be severe and have strong local impacts, with predation levels over 90% recorded at some colonies in Svalbard (Prop et al., 2015). This phenomenon has also been observed in the Canadian Arctic, concomitant with longer ice-free seasons (Iverson et al., 2014).

Cliff-nesting seabird colonies were not visited more by bears after the change in the sea-ice regime in Svalbard. This is perhaps because ground-nesting bird colonies are more easily accessible, have experienced large population increases and demand less specialised feeding techniques (i.e. cliff climbing). However, in other areas of the Arctic, the frequency of polar bear visitation at cliff-nesting seabird colonies has increased (Iverson et al., 2014), suggesting that cliff-nesting seabird colonies in Svalbard have the potential to be utilised to a larger degree in the future as sea-ice declines continue.

Other alternative food resources, such as Svalbard reindeer (*Rangifer tarandus platyrhynchus*) carcasses and whale carcasses, are important food resources for polar bears in Svalbard (Derocher, Wiig, & Bangjord, 2000; Iversen et al., 2013). It is possible that use of these types of food resources (in addition to ground-nesting bird colonies) has increased following the sea-ice collapse, but biotelemetry data in isolation only permit assessment of polar bears' affinity with features that are spatially fixed over long time periods. The greater mobility of polar bears on land during the more recent study period could be a result of searching for carrion and other alternative prey.

Polar bears throughout their range are increasingly spending more time on land, which has been linked to declines in body condition, lower rates of survival and declines in abundance for some subpopulations (Atwood et al., 2016; Bromaghin et al., 2015; Rode, Wilson, et al., 2015; Stirling & Derocher, 2012). Body condition and cub production of Svalbard polar bears do not show significant declining trends at this time, although interannual variation in these metrics have been linked to Arctic Oscillation patterns (Andersen & Aars, 2016). Declines of sea ice in coastal areas has decreased the ability of polar bears to hunt traditional, ice-associated prey during summer and autumn in Svalbard, leading to increased usage of alternative prey resources to meet energy demands. This appears to be the case elsewhere in the Arctic as well, with reports of increased predation on avian food types from various locales (Iverson et al., 2014; Prop et al., 2015). Increases in the number of human–bear conflicts also suggest that more bears are on shore or that changes in their movement patterns are bringing them into contact with people more frequently (Towns, Derocher, Stirling, Lunn, & Hedman, 2009). There is currently some debate about whether terrestrial food sources can compensate for the reduced ice-based hunting opportunities in an energetic or nutritional sense (Gormezano & Rockwell, 2015; Rode, Robbins, Nelson, & Amstrup, 2015). Additionally, increased movement rates will likely increase the energetic needs of coastal bears as sea ice-free periods become longer.

The summer and early autumn are likely critical periods for polar bears as these are the seasons where sea-ice loss is occurring disproportionally, impacting the ability of polar bears to hunt ice-associated prey (Rode, Regehr, et al., 2014; Stroeve et al., 2012). Coastal polar bears in Svalbard have changed their habitat use as a result of the decreased sea ice, resulting in reduced spatial overlap with ringed seals and presumably concomitant increases in use of alternative prey. However, ringed seals did not change the amount of time they spent hauled out despite the change in sea-ice conditions. Therefore, there is the potential for more polar bears to learn the aquatic hunting strategy (i.e. sneaking up on hauled out seals in the water) which previously was viewed as a specialty hunting technique (Stirling, 1974). However, this option will only be available to bears in Arctic regions where calved pieces of glacier ice or drifting sea ice pieces are present to be used by the seals as haul-out platforms. Offshore polar bears in the Chukchi Sea are also being impacted disproportionally in the summer by the decline in sea-ice conditions. Bears in this region have not changed their habitat selection patterns, which has led to a 75% decrease in the amount of key habitat available to them during the summer (Wilson, Regehr, Rode, & St. Martin, 2016).

Reproductive status did not influence space use of female polar bears in this study. Females with COYs in Svalbard are more dependent on land-fast ice in front of glacier fronts than other females, as COYs quickly become hypothermic if they must swim in cold water (Blix & Steen, 1979; Freitas et al., 2012). However, less than half of the polar bears (27 of 61) in this study had COYs or yearlings; this may have reduced the ability of the statistical models to detect potential differences due to reproductive status. There are no telemetry data available from Svalbard to evaluate whether male polar bears have similar movement strategies to those of females. However, tracking data from east Greenland during the breeding season indicates that male and female polar bears have different movement patterns although they use the same type of sea-ice habitat (Laidre et al., 2013).

The expanded capture area for polar bears in the second period did not significantly impact the changes detected in the relationship between polar bears and ringed seals in the two periods (Figure S2, Tables S12–S16), suggesting that coastal polar bears across Svalbard use the same basic hunting strategies and have been affected in a similar way by sea-ice declines.

5 | CONCLUSION

This study documented how sea-ice declines in Svalbard have altered the behaviour of polar bears. During spring, which is the most important hunting period for polar bears, polar bears both before and after a major sea-ice collapse that occurred in 2006 occupied areas in front of tidal glaciers along the east coast of Svalbard; in these areas, they prey on ringed seal pups born in snow lairs constructed on top of breathing holes in the land-fast ice. However, during summer and autumn, polar bears spent less time associated with tidal glacier fronts following the sea-ice collapse, while ringed seal spatial behaviour remained unchanged in these same coastal areas. Ringed seals use glacier ice pieces for hauling out when land-fast ice is not available, but bears do not seem to hunt them as readily in this type of ice. The dichotomy in these species' responses to the environmental change that has taken place has altered the amount of spatial overlap between the two members of this Arctic predator–prey relationship in the summer months. Deprived of their traditionally most important food source (Iversen et al., 2013), polar bears moved greater distances daily and spent more time in close proximity to ground-nesting bird colonies following the sea-ice decline. This shift to avian prey is having substantial local effects on ground-nesting bird colonies (Prop et al., 2015), and it highlights the linkage between the marine and terrestrial systems in many Arctic regions. Higher predation pressure from bears on duck and goose populations in Svalbard could also have effects in other areas along the various bird species' migratory routes.

This study demonstrates the importance of considering multiple species when investigating the impacts of climate change. Changes in biological interactions with resultant consequences for marine and terrestrial food webs are likely to become more widespread in many ecosystems due to differential responses of species to changing environmental conditions induced by global warming. Improved understanding of how climate change has altered biological interactions will increase predictive capacity regarding future ecosystem changes and potentially help improve amelioration efforts.

AUTHORS' CONTRIBUTIONS

K.M.K., C.L., J.A. and C.D.H. conceived the study; K.M.K., C.L. and J.A. conducted the fieldwork; C.D.H. and R.A.I. led the analyses. All authors took part in interpreting the data and writing the manuscript. All authors gave final approval for publication.

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DATA ACCESSIBILITY

The data are available at the Norwegian National Polar Data Centre https://doi.org/10.21334/npolar.2017.132248b4 (Lydersen, Kovacs, Aars, Hamilton, & Ims, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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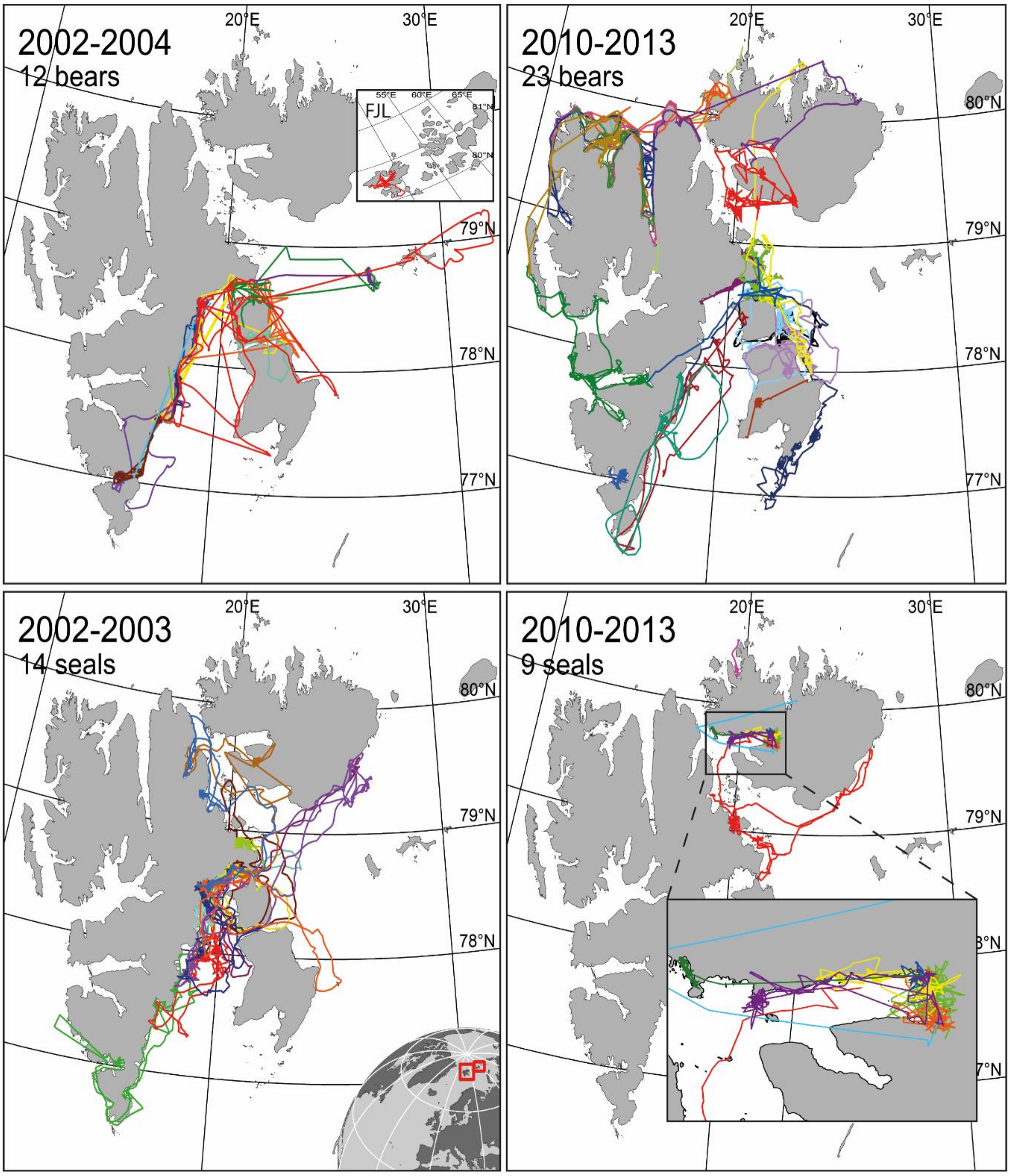

Figure S1.

Tracks of the coastal polar bears and coastal ringed seals equipped with biotelemetry devices during the summer (Jun-Aug) in Svalbard, Norway in each period. The inset map for 2002-2004 bears shows the polar bear that moved to Franz Josef Land (FJL), Russia.

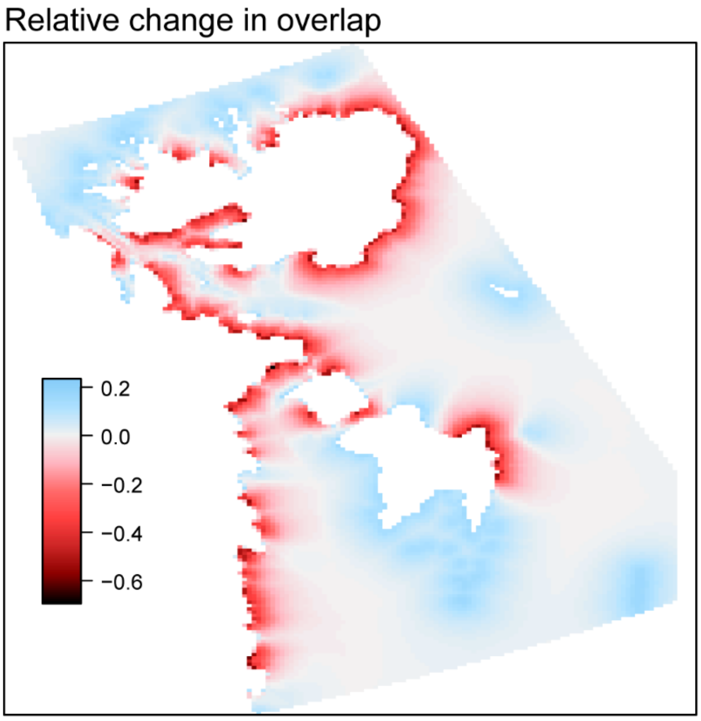

Figure S2.

Relative change in overlap for the summer period (Jun-Aug) between 23 coastal ringed seals and 30 coastal polar bears equipped with biotelemetry devices in Svalbard, Norway. Negative values indicate less overlap and positive values indicate more overlap in 2010-2013 than 2002-2004. This figure is similar to figure 5e, except that here only bears that were captured in southern Svalbard are included. Comparison of the two figures shows that the decrease in overlap in 2010-2013 compared to 2002-2004 is intensified in coastal areas near glacier fronts when the analyses are run using only bears captured in southern Svalbard compared to the analyses using bears captured in all three capture-location groups.

Table S1.

Information on the 19 polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004. Mass and body condition index are calculated as per Cattet et al. (2002). “N”, “c”, and “y” in cub status stand for no cub, cub(s) and yearling(s), respectively.

Bear ID	Tagging date	Tag duration (d)	Cub status	Mass (kg)	Standard length (cm)	Body condition index	Capture Latitude	Capture Longitude	Denning period	Tag type
9679,23691	2002-08-19	530	n	239.5	205	-0.473	77.7	18.3	Yes	Telonics GPS
9695,7822	2002-08-19	366	n	207.3	196	-0.5047	78	18.5	Yes	Telonics GPS
9683,7805	2002-08-20	233	n	166.7	190	-1.143	78.34	18.81	Yes	Telonics GPS
9685,23693	2002-08-20	73	n	156.6	188	-1.207	78.3	18.5	No	Telonics GPS
9678,23105	2002-08-21	446	n	195.8	196	-0.7669	77.95	21.27	Yes	Telonics GPS
9690,23343	2002-08-21	294	n	206.1	194	-0.3853	78.55	19.17	No	Telonics GPS
9692,23694	2002-08-21	607	n	205.6	198	-0.6855	78.7	21.1	Yes	Telonics GPS
2172,7757	2003-04-05	373	c	201.7	190	-0.0411	76.81	16.8	No	Telonics GPS
9684,23699	2003-04-10	397	y	170.1	198	-1.557	77.38	17.61	Yes	Telonics GPS
2185,23701	2003-04-15	423	n	153.6	188	-1.297	77.34	20.75	Yes	Telonics GPS
9696,23703	2003-04-15	406	y	198.1	189	-0.199	78.19	20.35	No	Telonics GPS
2175,23705	2003-04-16	569	n	185.2	196	-1.021	77.42	21	Yes	Telonics GPS
2166,23715	2003-04-19	333	c	177.6	195	-1.144	77.52	17.7	No	Telonics GPS
2170,23714	2003-04-19	542	n	NA	191	NA	77.52	17.82	Yes	Telonics GPS
2174,7815	2003-04-19	369	y	176.9	200	-1.516	77.65	18.37	No	Telonics GPS
2178,23357	2003-04-19	364	c	152.4	195	-1.847	77.5	17.78	No	Telonics GPS
2182,7805	2003-04-21	337	c	166.7	191	-1.143	78.34	18.81	No	Telonics GPS
2183,7757	2004-04-12	379	n	201.7	188	-0.0411	77.05	17.25	No	Telonics GPS
2165,23742	2004-04-15	426	n	220.7	195	-0.1449	77.31	22.58	No	Telonics GPS

Table S2.

Information on the 48 polar bears equipped with satellite collars in Svalbard, Norway in 2010-2013. Mass and body condition index are calculated as per Cattet et al. (2002). “N”, “c”, and “y” in cub status stand for no cub, cub(s) and yearling(s), respectively.

Bear ID	Tagging date	Tag duration (d)	Cub status	Mass (kg)	Standard length (cm)	Body condition index	Capture Latitude	Capture Longitude	Denning period	Tag type
37171,23425	2010-04-18	527	n	223.2	190	0.275	77.8	17.06	Yes	Telonics GPS
37175,23944	2010-04-18	489	n	206.1	196	-0.5298	77.45	16.45	Yes	Telonics GPS
37172,23831	2011-04-07	40	c	188.3	200	-1.23	79.6	12.34	No	Telonics GPS
49824,23939	2011-04-08	155	n	210.7	198	-0.9241	79.45	15.45	No	Telonics GPS
50752,23688	2011-04-08	173	c	198.8	203	-1.19	79.71	14.16	No	Telonics GPS
52032,23937	2011-04-08	175	n	217.5	203	-0.7771	79.43	15.51	No	Telonics GPS
49887,26047	2011-04-10	171	n	209.3	197	-0.5318	80.4	22.18	No	Telonics GPS
50830,26044	2011-04-10	266	c	176.4	196	-1.246	80.4	22.23	Yes	Telonics GPS
50102,26018	2011-04-19	163	c	256.8	199	-0.0839	78.46	18.92	No	Telonics GPS
50754,26050	2011-04-19	164	n	168.4	197	-1.532	78.21	20.42	No	Telonics GPS
50762,26054	2011-04-19	116	n	251.4	204	-0.1814	78.58	21.09	No	Telonics GPS
49851,23732	2011-04-23	239	c	167.2	190	-1.055	77.01	16.42	No	Telonics GPS
50755,23423	2011-04-23	157	n	182.5	195	-1.018	78.59	21.56	No	Telonics GPS
52501,23966	2011-04-26	226	c	206.6	198	-0.6633	77.56	15.82	No	SirTrack
52499,26068	2012-04-04	288	c	187	190	-0.5397	79.56	21.25	No	SirTrack
52502,26066	2012-04-04	184	n	206.5	188	0.0662	79.57	20.47	No	SirTrack
31321,7753	2012-04-05	267	y	185.4	192	-0.7277	79.53	21.15	No	ATS Iridium
31311,26077	2012-04-07	44	y	179.4	186	-0.4312	79.73	21.14	No	ATS Iridium
31306,23939	2012-04-08	32	n	210.7	203	-0.9241	79.49	13.79	No	ATS Iridium
31312,23989	2012-04-08	346	n	202	207	-1.392	79.53	15.23	Yes	ATS Iridium
31324,7951	2012-04-08	222	n	243.1	205	-0.4037	79.31	14.04	No	ATS Iridium
31309,23906	2012-04-09	345	c	143.3	191	-1.839	79.47	13.69	No	ATS Iridium
31310,23980	2012-04-14	302	n	217.8	192	-0.4916	77.78	14.62	No	ATS Iridium
31313,26025	2012-04-17	99	n	213.2	197	-0.4471	78.52	20.21	No	ATS Iridium
31305,23347	2012-04-18	172	n	198.1	193	-0.4947	78.56	20.7	No	ATS Iridium
31307,26084	2012-04-18	288	n	241.7	200	-0.0838	78.59	21.18	No	ATS Iridium
31304,23719	2012-04-19	30	c	162.3	189	-1.119	78.53	20.35	No	ATS Iridium
31317,26088	2012-04-19	246	c	250.1	199	0.1442	77.32	23.03	No	ATS Iridium
31314,26095	2012-04-20	294	n	175.2	193	-1.56	78.15	19.17	No	ATS Iridium
31315,26009	2012-04-20	35	c	193.4	191	-0.4583	78.51	18.83	No	ATS Iridium
31319,26018	2012-04-20	149	y	256.8	204	-0.0839	78.06	18.93	No	ATS Iridium
31308,23479	2012-04-21	161	c	170.1	191	-1.05	78.48	19.08	No	ATS Iridium
31322,26098	2012-04-24	71	n	246	204	-0.281	77.94	23.59	No	ATS Iridium
31323,26103	2012-04-27	156	n	232.3	203	-0.4755	77.74	18.48	No	ATS Iridium
31327,26102	2012-04-27	245	n	156.2	183	-0.8392	78.66	20.23	No	ATS Iridium
30535,26129	2012-09-22	153	c	153.1	187	-1.237	78.02	22.07	No	ATS Iridium
669450,23980	2013-04-06	274	n	217.8	199	-0.4916	77.52	14.71	No	Telonics Iridium
669452,26132	2013-04-06	61	y	190.4	192	-0.6037	77.4	15.59	No	Telonics Iridium
659123,23637	2013-04-08	272	n	250.7	215	-0.9328	77	16.41	No	Telonics Iridium
666177,26135	2013-04-09	283	n	233.8	208	-0.7887	77.03	16.93	No	Telonics Iridium
659121,26095	2013-04-10	336	n	175.2	200	-1.56	77.93	24.22	No	Telonics Iridium
669539,26137	2013-04-10	376	c	157.2	196	-1.776	77.03	22.85	No	Telonics Iridium
659122,26141	2013-04-11	37	n	203.1	192	-0.3071	76.68	25.48	No	Telonics Iridium
669532,26143	2013-04-11	111	n	219.5	197	-0.3129	76.61	22.9	No	Telonics Iridium
669536,23881	2013-04-13	18	n	168.9	200	-1.731	79.83	11.83	No	Telonics Iridium
669454,7951	2013-04-14	117	n	243.1	205	-0.4037	79.67	13.66	No	Telonics Iridium
669455,23882	2013-04-14	358	y	185.2	198	-1.164	79.65	13.37	No	Telonics Iridium
669533,26153	2013-04-15	48	c	185.2	191	-0.6574	79.54	13.82	No	Telonics Iridium

Table S3.

Correlation coefficients for the environmental variables assigned to locations between March and November for 60 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013.

	Bathymetry (m)	Bathymetric slope (deg)	Distance to ground-nesting birds (km)	Distance to cliff-nesting birds (km)	Distance to bird colony (km)	Distance to glacier front (km)	Distance to the coast (km)	Body condition index
Bathymetry (m)	1							
Bathymetric slope (deg)	0.561	1						
Distance to ground-nesting birds (km)	-0.066	-0.004	1					
Distance to cliff-nesting birds (km)	-0.267	-0.105	0.603	1				
Distance to bird colony (km)	-0.214	-0.157	0.701	0.786	1			
Distance to glacier front (km)	-0.261	-0.109	0.133	0.023	0.072	1		
Distance to the coast (km)	-0.296	-0.259	0.379	0.310	0.474	0.509	1	
Body condition index	0.027	-0.063	0.017	-0.091	-0.055	-0.001	-0.033	1

Table S4.

BIC model selection tables for the linear mixed-effects models (LME) run for distance moved (km/d) for each season showing the BIC, change in BIC and BIC weight for the 60 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013. The top three models for each season are shown; the BIC selected model is bolded. Month(num) and month(fac) indicate whether month is included as a numeric or factor variable, respectively. Period is a factor variable denoting if bears were tagged in 2002-2004 or 2010-2013.

Season	**Model**	**BIC**	**ΔBIC**	**BICw**
Spring	**Month(num)**	**6569.02**	**0.00**	**0.46**
(Mar-May)	Month(fac)	6569.05	0.04	0.45
	Month(fac)*Period	6572.89	3.88	0.07
Summer	**Month(num)+Period**	**7877.64**	**0.00**	**0.61**
(Jun-Aug)	Month(num)	7879.10	1.46	0.29
	Month(fac)+Period	7882.11	4.47	0.07
Autumn	**Month(num)**	**5795.82**	**0.00**	**0.68**
(Sep-Nov)	Month(fac)	5797.49	1.68	0.29
	Month(num)+Period	5803.24	7.43	0.02

Table S5.

Model results from the linear mixed-effects models selected by BIC for the distance moved (km/d) for each season for the 60 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013.

Season	Variable/Factor level	Coefficient	Std. Error	t-value	p-value
Spring	Intercept	7.496	0.282	26.620	<0.001
(Mar-May)	Month	0.309	0.056	5.465	<0.001
Summer	Intercept	11.877	0.385	30.842	<0.001
(Jun-Aug)	Month	-0.531	0.050	-10.702	<0.001
	2010-2013	0.657	0.196	3.359	0.002
Autumn	Intercept	5.260	0.684	7.694	<0.001
(Sep-Nov)	Month	0.276	0.067	4.100	<0.001

Table S6.

BIC model selection tables for the linear mixed-effects models run for each environmental variable in each season showing the BIC, change in BIC and BIC weight for the 60 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013. The top three models for each variable are shown; the BIC selected model is bolded. Month(num) and month(fac) indicate whether month is included as a numeric or factor variable, respectively, Period is a factor variable denoting if bears were tagged in 2002-2004 or 2010-2013, CL is a factor variable denoting capture location (south, NE or NW), PeriodCL stands for a factor variable incorporating the period and capture location, and cub indicates whether the female had a cub(s), yearling(s) or was unaccompanied.

Season	Variable	Model	BIC	ΔBIC	BICw
Spring (Mar-May)	Distance to glacier front (km)	**Month(fac)**	**11308.74**	**0.00**	**0.97**
		Month(fac)*Cub	11316.51	7.77	0.02
		Period*Month(fac)	11317.40	8.66	0.01
	Distance to the coast (km)	**Month(num)+CL**	**42929.54**	**0.00**	**0.62**
		Month(num)	42931.77	2.23	0.20
		CL	42932.1	2.56	0.17
	Bathymetry (m)	Month(fac)*PeriodCL+Cub	161217.00	0.00	0.64
		Month(fac)*PeriodCL	**161218.40**	**1.40**	**0.32**
		Period*Month(fac)	161222.50	5.50	0.04
	Bathymetric slope (deg)	**Period*Month(fac)**	**34623.74**	**0.00**	**0.98**
		Month(num)	34632.12	8.38	0.02
		Month(fac)	34640.28	16.54	0.00
Summer (Jun-Aug)	Distance to ground-nesting birds (km)	**Period**	**8433.42**	**0.00**	**0.95**
		CL	8440.33	6.91	0.03
		Month(num)	8440.93	7.51	0.02
	Distance to glacier front (km)	**Period**	**27744.93**	**0.00**	**0.92**
		Month(num)	27750.79	5.86	0.05
		CL	27751.90	6.97	0.03
	Distance to cliff-nesting birds (km)	Period	10750.06	0.00	0.70
		Month(num)	**10751.81**	**1.75**	**0.29**
		CL	10759.64	9.58	0.01
	Distance to bird colony (km)	**Month(num)**	**16424.36**	**0.00**	**0.93**
		Month(fac)	16429.86	5.50	0.06
		Period+Month(num)	16434.56	10.20	0.01
	Distance to the coast (km)	Month(fac)	48517.09	0.00	0.57
		Month(num)	**48517.67**	**0.58**	**0.42**
		CL+Month(fac)	48525.51	8.42	0.01
	Bathymetry (m)	**Period*Month(fac)**	**170744.00**	**0.00**	**0.56**
		Period*Month(fac)+Cub	170745.10	1.10	0.33
		CL*Month(num)	170747.30	3.30	0.11
	Bathymetric slope (deg)	**Month(num)**	**-52874.80**	**0.00**	**1.00**
		Month(fac)	-52862.20	12.60	0.00
		Period+Month(num)	-52859.68	15.12	0.00
Autumn (Sep-Nov)	Distance to glacier front (km)	CL*Month(num)	27737.43	0.00	0.70
		Period*Month(num)	**27739.22**	**1.79**	**0.29**
		Period	27745.67	8.24	0.01
	Distance to the coast (km)	**Month(num)**	**33884.77**	**0.00**	**0.97**
		Month(num)*Cub	33891.94	7.17	0.03
		Period+Month(num)	33895.01	10.24	0.01
	Bathymetry (m)	**PeriodCL*Month(fac)**	**128468.2**	**0**	**0.99**
		CL*Month(fac)	128477.9	9.7	0.01
		PeriodCL*Month(num)	128478.1	9.9	0.01
	Bathymetric slope (deg)	**Period*Month(num)**	**18372.75**	**0.00**	**0.95**
		Period*Month(fac)	18378.62	5.87	0.05
		Period*Month(num)+Cub	18391.22	18.47	0.00

Table S7.

Model results from the linear mixed-effects models selected by BIC for the association between polar bear locations and environmental variables during the spring (Mar-May) for the 59 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013.

Response variable	**Predictor variable/ Factor level**	**Coefficient**	**Std. Error**	**t-value**	**p-value**
sqrt(distance to glacier front (km))	Intercept	3.902	0.204	19.094	<0.001
	Month – Apr	-0.570	0.078	-7.347	<0.001
	Month – May	-0.463	0.078	-5.928	<0.001
log(distance to the coast (km))	Intercept	-0.474	0.495	-0.957	0.339
	Month	0.165	0.040	4.116	<0.001
	CL – NW	-0.868	0.527	-1.645	0.106
	CL – South	0.588	0.484	1.216	0.229
Bathymetry (m)	Intercept	23.485	16.804	1.398	0.162
	2002-2004 –South – Apr	12.286	8.568	1.434	0.152
	2002-2004 – South – May	-33.518	8.298	-4.039	<0.001
	2010-2013 – NE – Apr	6.866	38.984	0.176	0.860
	2010-2013 – NE – May	-58.776	39.530	-1.487	0.137
	2010-2013 – NW – Mar	160.240	32.489	4.932	<0.001
	2010-2013 – NW – Apr	3.388	25.616	0.132	0.895
	2010-2013 – NW – May	-6.098	25.550	-0.239	0.811
	2010-2013 – South – Mar	176.872	35.790	4.942	<0.001
	2010-2013 – South – Apr	7.128	22.543	0.316	0.752
	2010-2013 – South – May	3.091	21.995	0.141	0.888
log(bathymetric slope + 0.0001 (deg))	Intercept	-3.840	0.246	-15.629	<0.001
	2002-2004 – Apr	-0.131	0.105	-1.248	0.212
	2002-2004 – May	-0.455	0.098	-4.663	<0.001
	2010-2013 – Mar	1.519	0.351	4.329	<0.001
	2010-2013 – Apr	-0.237	0.295	-0.804	0.422
	2010-2013 – May	-0.394	0.293	-1.343	0.179

Table S8.

Model results from the linear mixed-effects models selected by BIC for the association between polar bear locations and environmental variables during the summer (Jun-Aug) for the 38 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013.

Response variable	Predictor variable/ Factor level	Coefficient	Std. Error	t-value	p-value
log(distance to ground-nesting birds (km))	Intercept	2.724	0.143	19.102	<0.001
	2010-2013	-0.371	0.181	-2.054	0.047
log(distance to glacier front (km))	Intercept	1.043	0.290	3.593	<0.001
	2010-2013	0.997	0.370	2.695	0.011
log(distance to cliff-nesting birds (km))	Intercept	2.596	0.232	11.172	<0.001
	Month	-0.056	0.030	-1.891	0.059
log(distance to bird colony (km))	Intercept	2.744	0.229	11.997	<0.001
	Month	-0.123	0.030	-4.097	<0.001
log(distance to the coast (km))	Intercept	2.523	0.264	9.573	<0.001
	Month	-0.379	0.032	-11.980	<0.001
Bathymetry (m)	Intercept	37.033	18.433	2.009	0.045
	2002-2004 – Jul	62.405	7.890	7.909	<0.001
	2002-2004 – Aug	68.003	8.293	8.200	<0.001
	2010-2013 – Jun	-9.016	23.403	-0.385	0.700
	2010-2013 – Jul	15.612	23.369	0.668	0.504
	2010-2013 – Aug	56.343	23.440	2.404	0.016
sqrt(bathymetric slope (deg))	Intercept	-0.092	0.019	-4.860	<0.001
	Month	0.042	0.002	17.246	<0.001

Table S9.

Model results from the linear mixed-effects models selected by BIC for the association between polar bear locations and environmental variables during the autumn (Sep-Nov) for the 36 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013.

Response variable	Predictor variable/ Factor level	Coefficient	Std. Error	t-value	p-value
log(distance to glacier front (km))	Intercept	-0.784	0.658	-1.192	0.234
	2010-2013	6.248	0.981	6.366	<0.001
	Month	0.145	0.059	2.444	0.015
	2010-2013*Month	-0.517	0.092	-5.599	<0.001
log(distance to the coast (km))	Intercept	-2.103	0.370	-5.688	<0.001
	Month	0.198	0.036	5.549	<0.001
Bathymetry (m)	Intercept	123.460	15.013	8.223	<0.001
	2002-2004 – South – Oct	-10.209	7.167	-1.424	0.154
	2002-2004 – South – Nov	-49.418	8.464	-5.839	<0.001
	2010-2013 – NE – Sep	-121.075	59.040	-2.051	0.040
	2010-2013 – NE – Oct	-56.998	58.565	-0.973	0.330
	2010-2013 – NE – Nov	-35.187	59.040	-0.596	0.551
	2010-2013 – NW – Sep	25.327	28.296	0.895	0.371
	2010-2013 – NW – Oct	12.213	29.901	0.409	0.683
	2010-2013 – NW – Nov	74.885	31.292	2.393	0.017
	2010-2013 – South – Sep	1.020	22.562	0.045	0.964
	2010-2013 – South – Oct	9.893	23.535	0.420	0.674
	2010-2013 – South – Nov	12.891	23.934	0.539	0.590
log(bathymetric slope (deg))	Intercept	-0.775	0.374	-2.074	0.038
	2010-2013	-3.827	0.558	-6.855	<0.001
	Month	-0.240	0.034	-6.999	<0.001
	2010-2013*Month	0.418	0.053	7.834	<0.001

Table S10.

Percentage of locations within 5 km of a glacier front during the summer (Jun-Aug) for the 38 coastal polar bears equipped with a biotelemetry device in Svalbard, Norway in 2002-2004 and 2010-2013.

ID	Period	Locations within 5 km of a glacier front (%)
2166,23715	2002-2004	56.88
2170,23714	2002-2004	25.18
2172,7757	2002-2004	96.01
2174,7815	2002-2004	84.96
2175,23705	2002-2004	63.89
2178,23357	2002-2004	66.67
2182,7805	2002-2004	77.17
9678,23105	2002-2004	25.00
9679,23691	2002-2004	55.58
9683,7805	2002-2004	100.00
9685,23693	2002-2004	100.00
9690,23343	2002-2004	97.18
9692,23694	2002-2004	50.44
9695,7822	2002-2004	24.28
9696,23703	2002-2004	29.17
31305,23347	2010-2013	4.89
31307,26084	2010-2013	44.02
31308,23479	2010-2013	90.96
31309,23906	2010-2013	0.00
31310,23980	2010-2013	14.93
31312,23989	2010-2013	8.88
31313,26025	2010-2013	57.93
31314,26095	2010-2013	54.35
31317,26088	2010-2013	5.95
31319,26018	2010-2013	6.55
31321,7753	2010-2013	15.50
31323,26103	2010-2013	2.70
31324,7951	2010-2013	5.07
31327,26102	2010-2013	26.63
37175,23944	2010-2013	72.63
49824,23939	2010-2013	13.22
49851,23732	2010-2013	98.07
50102,26018	2010-2013	19.86
50752,23688	2010-2013	9.78
50754,26050	2010-2013	18.70
52032,23937	2010-2013	37.14
52499,26068	2010-2013	24.46
52501,23966	2010-2013	4.53

Table S11.

Model results from the linear mixed-effects models for the association between polar bear locations and environmental variables fitted using the interaction of capture location and period as predictor variables during the spring (Mar-May) for the 59 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013. The reference level for the capture location and period interaction is 2002-2004 – South.

Response variable	Factor level	Coefficient	Std. Error	t-value	p-value
log(proportion of time within 5 km of a glacier front)	Intercept	0.371	0.071	5.201	<0.001
	2010-2013 – NE	0.043	0.167	0.255	0.800
	2010-2013 – NW	-0.138	0.110	-1.254	0.215
	2010-2013 – South	-0.076	0.094	-0.800	0.427
log(proportion of time within 5 km of the coast)	Intercept	0.692	0.060	11.456	<0.001
	2010-2013 – NE	0.172	0.142	1.217	0.229
	2010-2013 – NW	0.287	0.093	3.080	0.003
	2010-2013 – South	-0.051	0.080	-0.643	0.523
sqrt(distance to glacier front (km))	Intercept	3.332	0.329	10.121	<0.001
	2010-2013 – NE	-0.772	0.798	-0.966	0.338
	2010-2013 – NW	0.657	0.514	1.277	0.207
	2010-2013 – South	0.018	0.444	0.041	0.967
log(distance to the coast (km))	Intercept	0.910	0.215	4.229	<0.001
	2010-2013 – NE	-0.657	0.514	-1.278	0.207
	2010-2013 – NW	-1.519	0.334	-4.549	<0.001
	2010-2013 – South	-0.115	0.287	-0.402	0.690
Bathymetry (m)	Intercept	18.078	15.296	1.182	0.237
	2010-2013 – NE	-16.337	36.925	-0.442	0.660
	2010-2013 – NW	9.870	23.799	0.415	0.680
	2010-2013 – South	10.830	20.528	0.528	0.600
log(bathymetric slope + 0.0001 (deg))	Intercept	-4.046	0.236	-17.163	<0.001
	2010-2013 – NE	-0.037	0.561	-0.066	0.948
	2010-2013 – NW	0.264	0.365	0.724	0.472
	2010-2013 – South	0.308	0.314	-0.981	0.331

Table S12.

Model results from the linear-mixed effects models for the association between polar bear locations and environmental variables fitted using the interaction of capture location and period as predictor variables during the summer (Jun-Aug) for the 38 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013. The reference level for the capture location and period interaction is 2002-2004 – South.

Response variable	Factor level	Coefficient	Std. Error	t-value	p-value
log(proportion of time within 5 km of a glacier front)	Intercept	0.635	0.072	8.787	<0.001
	2010-2013 – NE	-0.435	0.211	-2.066	0.047
	2010-2013 – NW	-0.511	0.135	-3.783	0.001
	2010-2013 – South	-0.277	0.102	-2.703	0.011
log(proportion of time within 2 km of ground-nesting birds)	Intercept	0.078	0.034	2.321	0.026
	2010-2013 – NE	0.138	0.098	1.410	0.168
	2010-2013 – NW	0.265	0.063	4.197	<0.001
	2010-2013 – South	0.089	0.048	1.876	0.069
log(proportion of time within 2 km of cliff-nesting birds)	Intercept	0.197	0.043	4.633	<0.001
	2010-2013 – NE	0.128	0.124	1.033	0.309
	2010-2013 – NW	0.103	0.080	1.300	0.202
	2010-2013 – South	0.061	0.060	1.015	0.317
log(proportion of time within 2 km of a bird colony)	Intercept	0.224	0.046	4.865	<0.001
	2010-2013 – NE	0.152	0.135	1.128	0.267
	2010-2013 – NW	0.204	0.086	2.364	0.024
	2010-2013 – South	0.079	0.065	1.205	0.237
log(proportion of time within 5 km of the coast)	Intercept	0.953	0.033	28.502	<0.001
	2010-2013 – NE	-0.092	0.097	-0.947	0.350
	2010-2013 – NW	0.042	0.063	0.669	0.508
	2010-2013 – South	-0.089	0.047	-1.875	0.070
log(distance to ground-nesting birds (km))	Intercept	2.723	0.139	19.559	<0.001
	2010-2013 – NE	-0.250	0.389	-0.641	0.526
	2010-2013 – NW	-0.721	0.249	-0.290	0.007
	2010-2013 – South	-0.238	0.194	-1.225	0.229
log(distance to glacier front (km))	Intercept	1.046	0.282	3.714	<0.001
	2010-2013 – NE	1.286	0.801	1.605	0.118
	2010-2013 – NW	1.660	0.514	3.226	0.003
	2010-2013 – South	0.677	0.395	1.716	0.095
log(distance to cliff-nesting birds (km))	Intercept	2.351	0.168	14.021	<0.001
	2010-2013 – NE	-0.358	0.469	-0.762	0.451
	2010-2013 – NW	-0.294	0.300	-0.981	0.333
	2010-2013 – South	-0.204	0.234	-0.871	0.390
log(distance to bird colony (km))	Intercept	1.982	0.142	13.981	<0.001
	2010-2013 – NE	-0.155	0.395	-0.393	0.697
	2010-2013 – NW	-0.441	0.253	-1.745	0.090
	2010-2013 – South	-0.055	0.198	-0.277	0.784
log(distance to the coast (km))	Intercept	-0.074	0.203	-0.363	0.716
	2010-2013 – NE	0.378	0.575	0.658	0.515
	2010-2013 – NW	-1.030	0.369	-2.789	0.009
	2010-2013 – South	0.174	0.284	0.612	0.545
Bathymetry (m)	Intercept	82.140	18.109	4.536	<0.001
	2010-2013 – NE	-60.870	51.222	-1.188	0.243
	2010-2013 – NW	-32.368	32.886	-0.984	0.332
	2010-2013 – South	-16.926	25.331	-0.668	0.509
sqrt(bathymetric slope (deg))	Intercept	0.219	0.012	18.475	<0.001
	2010-2013 – NE	-0.082	0.033	-2.489	0.018
	2010-2013 – NW	0.018	0.021	0.862	0.395
	2010-2013 – South	-0.034	0.016	-2.047	0.049

Table S13.

Model results from the linear mixed-effects models for the association between polar bear locations and environmental variables fitted using the interaction of capture location and period as predictor variables during the autumn (Sep-Nov) for the 36 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013. The reference level for the capture location and period interaction is 2002-2004 – South.

Response variable	**Factor level**	**Coefficient**	**Std. Error**	**t-value**	**p-value**
log(proportion of time within 5 km of a glacier front)	Intercept	0.708	0.090	7.827	<0.001
	2010-2013 – NE	-0.204	0.362	-0.564	0.577
	2010-2013 – NW	-0.512	0.169	-3.029	0.005
	2010-2013 – South	-0.293	0.130	-2.249	0.032
log(proportion of time within 5 km of the coast)	Intercept	0.940	0.048	19.603	<0.001
	2010-2013 – NE	0.011	0.192	0.056	0.956
	2010-2013 – NW	0.008	0.090	0.088	0.931
	2010-2013 – South	-0.081	0.069	-1.170	0.250
log(distance to glacier front (km))	Intercept	0.647	0.303	2.135	0.033
	2010-2013 – NE	0.764	1.201	0.637	0.529
	2010-2013 – NW	1.773	0.573	3.095	0.004
	2010-2013 – South	1.044	0.448	2.331	0.026
log(distance to the coast (km))	Intercept	-0.132	0.189	-0.696	0.487
	2010-2013 – NE	-0.321	0.746	-0.430	0.670
	2010-2013 – NW	-0.688	0.359	-1.919	0.064
	2010-2013 – South	0.216	0.282	0.763	0.451
Bathymetry (m)	Intercept	106.477	14.177	7.510	<0.001
	2010-2013 – NE	-54.102	55.338	-0.978	0.336
	2010-2013 – NW	46.351	27.125	1.709	0.097
	2010-2013 – South	21.764	21.389	1.018	0.317
log(bathymetric slope (deg))	Intercept	-3.155	0.126	-25.057	<0.001
	2010-2013 – NE	-0.250	0.494	-0.507	0.616
	2010-2013 – NW	0.847	0.240	3.532	0.001
	2010-2013 – South	0.011	0.189	0.056	0.955

Table S14.

BIC model selection tables for generalized additive mixed-effect models (GAMM) run on the time spent in area (TSA) values for the summer (Jun-Aug) showing the BIC, change in BIC and BIC weight for the 38 coastal polar bears and 23 coastal ringed seals equipped with biotelemetry devices in Svalbard, Norway in 2002-2004 and 2010-2013. The top three models for each variable are shown: the BIC selected model is bolded. Glac, Coast, Bath, Slope, Land, GroundBird, CliffBird, CL and cub stand for distance to glacier front, distance to coastline, bathymetry, bathymetric slope, proportion of the TSA grid cell on land, distance to ground-nesting bird colony, distance to cliff-nesting bird colony, capture location and whether a polar bear had a cub(s), yearling(s) or was unaccompanied, respectively.

Period	**Species**	**Model**	**BIC**	**ΔBIC**	**BIC w**
2002-2004	Ringed seals	**s(Glac)+s(Bath)+Slope**	**17326.55**	**0.00**	**0.98**
		s(Coast)+s(Glac)+s(Bath)+Slope	17334.73	8.18	0.02
		s(Glac)+s(Bath)+Slope+Sex	17336.83	10.25	0.01
2010-2013	Ringed seal	**s(Coast)+s(Glac)**	**6271.01**	**0.00**	**0.79**
		s(Coast)	6273.92	2.91	0.19
		s(Coast)+s(Glac)+sex	6278.03	7.02	0.02
2002-2004	Polar bear	**s(Glac)+s(Bath)+s(Land)**	**9623.08**	**0.00**	**0.94**
		GroundBird+s(Glac)+s(Bath)+s(Land)	9628.49	5.40	0.06
		s(Glac)+s(Bath)+s(Land)+Cub	9638.51	15.42	0.00
2010-2013	Polar bear	GroundBird+CliffBird+s(Coast, by=CL)	21460.53	0.00	0.48
		GroundBird+CliffBird+s(Coast)	**21460.62**	**0.09**	**0.46**
		CliffBird+s(Coast)	21464.79	4.26	0.06

Table S15.

Output of the linear models for monthly home range size (km^2) fitted using the interaction of capture location and period as predictor variables for the 60 coastal polar bears equipped with satellite collars between 2002-2004 and 2010-2013. The number of bears in each capture location that transmitted locations for at least 20 days for each month is also included. The reference level for the capture location and period interaction is 2002-2004 – South.

Month	Transformation	Factor level	Number of bears	Coefficient	Std. Error	t-value	p-value
January	None	Intercept	8	248.440	63.550	3.909	0.006
		2010-2013 – NE	0	-	-	-	-
		2010-2013 – NW	1	-198.440	190.650	-1.041	0.333
		2010-2013 – South	1	-185.940	190.650	-0.975	0.362
February	None	Intercept	8	195.310	49.100	3.978	0.005
		2010-2013 – NE	0	-	-	-	-
		2010-2013 – NW	1	98.440	147.290	0.668	0.525
		2010-2013 – South	1	10.940	147.290	0.074	0.943
March	-	Intercept	10	-	-	-	-
		2010-2013 – NE	0	-	-	-	-
		2010-2013 – NW	0	-	-	-	-
		2010-2013 – South	0	-	-	-	-
April	Log	Intercept	7	6.246	0.317	19.736	<0.001
		2010-2013 – NE	2	-0.152	0.671	-0.226	0.824
		2010-2013 – NW	6	-0.616	0.466	-1.323	0.205
		2010-2013 – South	5	-0.291	0.490	-0.593	0.562
May	Square root	Intercept	13	9.469	1.005	9.422	<0.001
		2010-2013 – NE	2	1.337	2.752	0.486	0.630
		2010-2013 – NW	9	-1.253	1.571	-0.797	0.430
		2010-2013 – South	22	-0.526	1.268	-0.415	0.680
June	Log	Intercept	11	4.325	0.233	18.562	<0.001
		2010-2013 – NE	1	1.155	0.807	1.431	0.163
		2010-2013 – NW	6	-0.038	0.392	-0.098	0.923
		2010-2013 – South	14	-0.189	0.311	-0.606	0.549
July	Square root	Intercept	11	8.979	1.177	7.629	<0.001
		2010-2013 – NE	1	8.854	4.077	2.172	0.039
		2010-2013 – NW	6	-0.192	1.981	-0.097	0.924
		2010-2013 – South	14	0.207	1.573	0.131	0.897
August	Log	Intercept	12	3.741	0.259	14.430	<0.001
		2010-2013 – NE	1	-0.307	0.935	-0.329	0.745
		2010-2013 – NW	6	-0.464	0.449	-1.033	0.311
		2010-2013 – South	11	-0.968	0.375	-2.581	0.016
September	Log	Intercept	14	3.313	0.251	13.206	<0.001
		2010-2013 – NE	1	-0.055	0.972	-0.057	0.955
		2010-2013 – NW	5	-0.207	0.489	-0.424	0.675
		2010-2013 – South	8	-0.999	0.416	-2.400	0.025
October	Log	Intercept	11	3.591	0.247	14.541	<0.001
		2010-2013 – NE	1	1.839	0.856	2.149	0.048
		2010-2013 – NW	3	-0.124	0.534	-0.232	0.819
		2010-2013 – South	4	-0.189	0.478	-0.395	0.698
November	Log	Intercept	11	4.064	0.288	14.101	<0.001
		2010-2013 – NE	1	1.024	0.998	1.025	0.323
		2010-2013 – NW	1	-1.867	0.998	-1.870	0.083
		2010-2013 – South	5	-0.900	0.516	-1.746	0.103
December	Log	Intercept	9	3.320	0.447	7.436	<0.001
		2010-2013 – NE	1	1.111	1.412	0.787	0.451
		2010-2013 – NW	1	-1.528	1.412	-1.082	0.307
		2010-2013 – South	2	-0.420	1.047	-0.401	0.698

Table S16.

Model results from the linear mixed-effects models for the distance moved (km/d) for each season fitted using the interaction of capture location and time period as predictor variables for the 60 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002-2004 and 2010-2013. The reference level for the capture location and period interaction is 2002-2004 – South.

Season	Variable/ Factor level	Coefficient	Std. Error	t-value	p-value
Spring (Mar-May)	Intercept	7.227	0.326	22.179	<0.001
	Month	0.302	0.057	5.323	<0.001
	2010-2013 – NE	0.864	0.551	1.569	0.122
	2010-2013 – NW	0.562	0.355	1.580	0.120
	2010-2013 – South	0.289	0.308	0.939	0.352
Summer (Jun-Aug)	Intercept	11.861	0.387	30.671	<0.001
	Month	-0.530	0.050	-10.669	<0.001
	2010-2013 – NE	1.033	0.438	2.360	0.024
	2010-2013 – NW	0.697	0.279	2.495	0.018
	2010-2013 – South	0.599	0.221	2.714	0.010
Autumn (Sep-Nov)	Intercept	5.153	0.730	7.064	<0.001
	Month	0.277	0.067	4.098	<0.001
	2010-2013 – NE	1.319	1.155	1.142	0.262
	2010-2013 – NW	0.403	0.562	0.717	0.479
	2010-2013 – South	-0.017	0.441	-0.038	0.970

Appendix S1

Materials & Methods

(a) Polar bear and ringed seal locations

Polar bears were assigned to one of three capture location groupings. Bears tagged on Nordaustlandet were assigned to the "NE" grouping, bears tagged in north-western Spitsbergen (north of 79°N) were assigned to the "NW" grouping and bears tagged in southern Svalbard (south of 79°N) were assigned to the "south" grouping. All bears tagged in 2002-2004 were from the "south". For the bears tagged in 2010-2013, 30, 12 and 6 bears were assigned to the "south", "NW", and "NE", grouping, respectively.

Ringed seals were tagged in two different areas in the two periods. Ringed seals in 2002-2004 were tagged in southern Spitsbergen (78.68°N, 20.22°E) while ringed seals in 2010-2013 were tagged in three locations on Nordaustlandet (79.77°N, 21.67°E; 80.16°N, 23.21°E, 80.12°N, 23.09°E; see Hamilton *et al.* 2016). Previous analyses showed that the ringed seals tagged in these two areas on eastern Svalbard showed similar patterns in terms of space use and association with environmental variables (Hamilton *et al.* 2016); they were thus treated as belonging to the same "capture location grouping" in the analyses within the current study.

(b) Environmental variables

A bird colony shapefile for Svalbard and Franz Josef Land was obtained from the Norwegian Polar Institute (NPI, www.npolar.no, Strøm, Descamps & Bakken 2008). Bird colonies were split into two groups because bears use quite different foraging strategies in the two types of colonies, which are occupied by different avian species groups (Iverson *et al.* 2014; Prop *et al.* 2015). Ground-nesting birds included the common eider (*Somateria mollissima*), barnacle geese (*Branta leucopsis*), pink-footed geese (*Anser brachyrhynchus*), brent geese (*Branta bernicla*), king eiders (*Somateria spectabilis*) and Arctic terns (*Sterna paradisaea*). Cliff-nesting seabirds included the black-legged kittiwake (*Rissa tridactyla*), Brunnich's guillemots (*Uria lomvia*), Atlantic puffins (*Fratercula arctica*) and the northern fulmar (*Fulmarus glacialis*).

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