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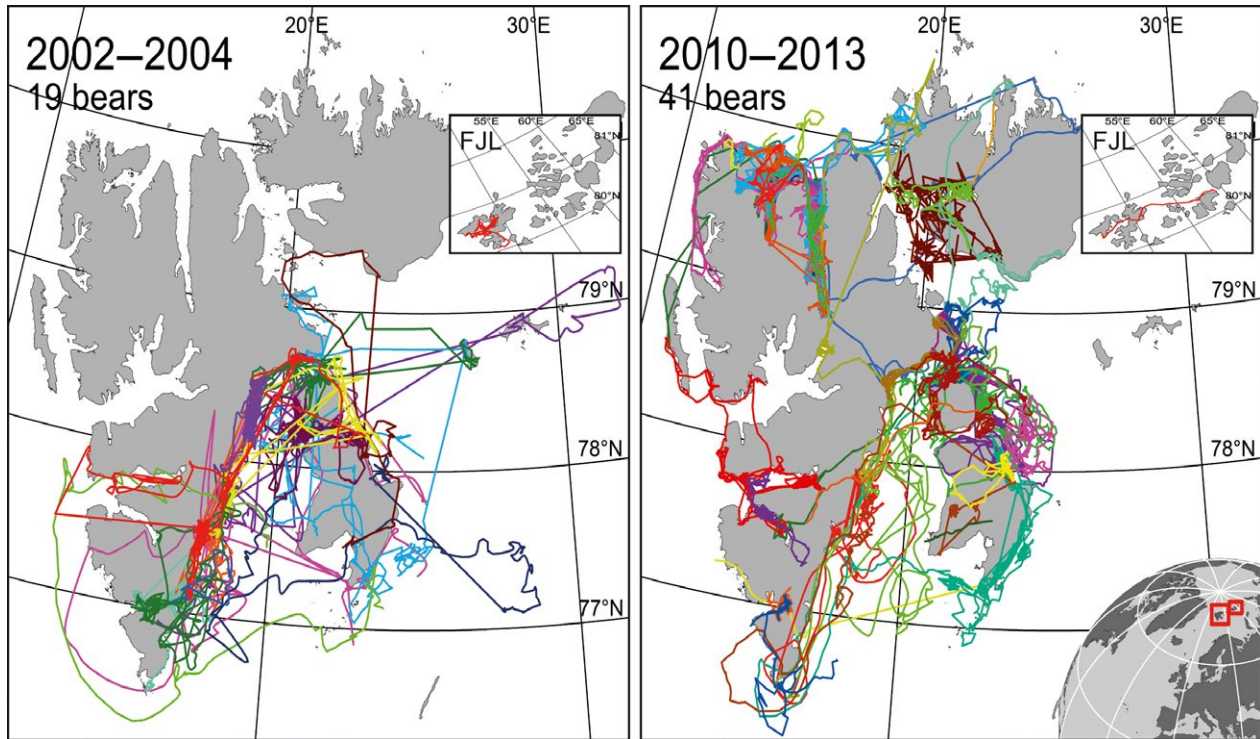
FIGURE 1 Tracks of the coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002–2004 and 2010–2013. The inset maps show two polar bears that moved to Franz Josef Land (FJL), Russia

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).
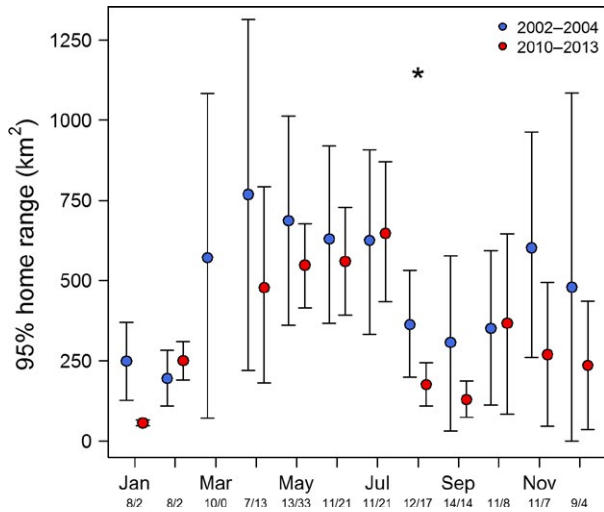
3.3 | Polar bear–ringed seal relationship

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).
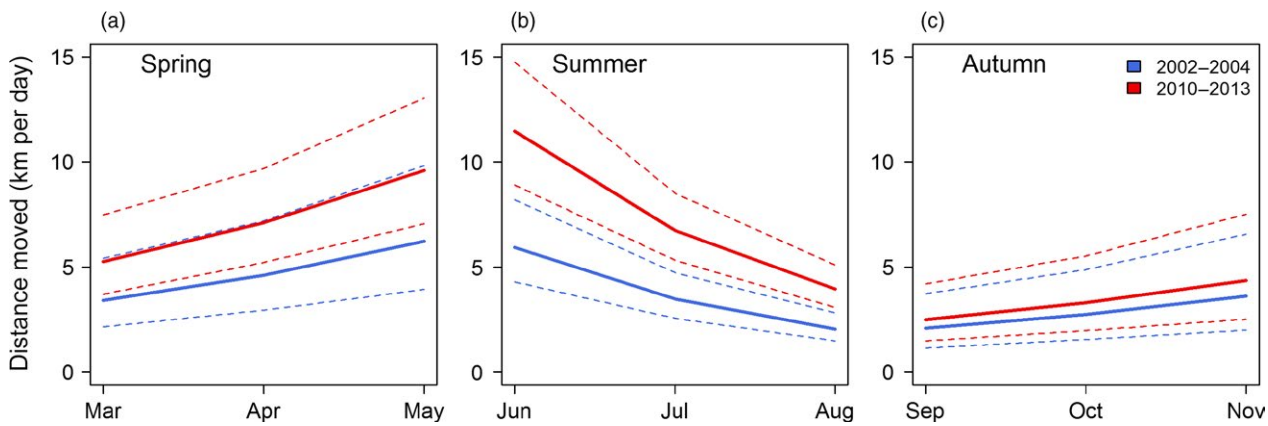

FIGURE 2 95% home range size (km², mean ± 95% CI) for 60 coastal polar bears equipped with satellite collars in Svalbard, Norway in 2002–2004 and 2010–2013 by month. Significant differences between the two periods are indicated by *. Values underneath the *x*-axis indicate the number of bears included for each period and month

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
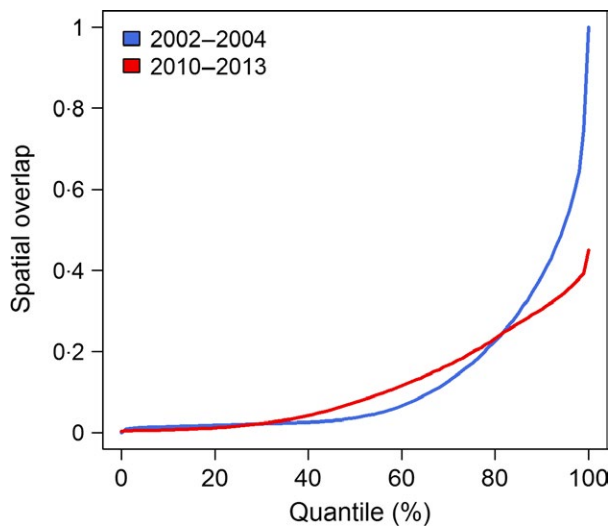
FIGURE 4 Quantiles of the spatial overlap values for the summer months for 2002–2004 and 2010–2013 between the 38 coastal polar bears and 23 coastal ringed seals equipped with biotelemetry devices in Svalbard, Norway. The overlap values were rescaled between 0 (lowest overlap value) and 1 (highest overlap 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.
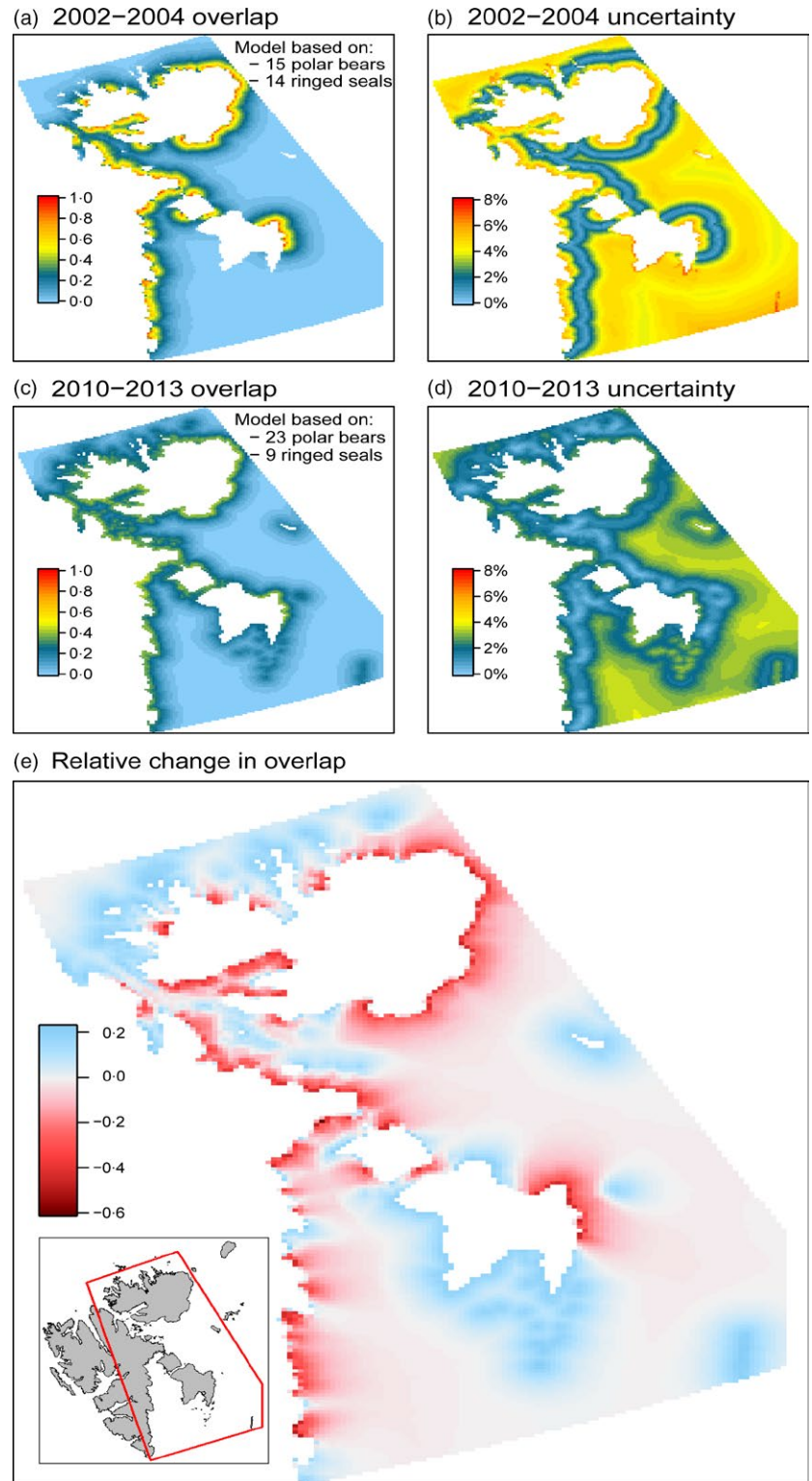
FIGURE 5 Spatial overlap values (rescaled between 1 [highest overlap value] and 0 [lowest overlap value]) for the summer period (June-August) for 2002–2004 (a) and 2010–2013 (c) for the 38 coastal polar bears and 23 coastal ringed seals equipped with biotelemetry devices in Svalbard, Norway. Cross-validation 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).

REFERENCES

Andersen, M., & Aars, J. (2016). Barents Sea polar bears (*Ursus maritimus*): Population biology and anthropogenic threats. *Polar Research*, *35*, 26029.

Atwood, T. C., Peacock, E., McKinney, M. A., Lillie, K., Wilson, R., Douglas, D. C., ... Terletzky, P. (2016). Rapid environmental change drives increased land use by an Arctic marine predator. *PLoS ONE*, *11*, e0155932.

Blix, A. S., & Steen, J. B. (1979). Temperature regulation in newborn polar homeotherms. *Physiological Reviews*, *59*, 285–304.

Bromaghin, J. F., McDonald, T. L., Stirling, I., Derocher, A. E., Richardson, E. S., Regehr, E. V., ... Amstrup, S. C. (2015). Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. *Ecological Applications*, *25*, 634–651.

Cattet, M. R. L., Caulkett, N. A., Obbard, M. E., & Stenhouse, G. B. (2002). A body-condition index for ursids. *Canadian Journal of Zoology*, *80*, 1156–1161.

Comiso, J. C., & Hall, D. K. (2014). Climate trends in the Arctic as observed from space. *WIREs Climate Change*, *5*, 389–409.

Derocher, A. E., Wiig, Ø., & Andersen, M. (2002). Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biology*, *25*, 448–452.

Derocher, A. E., Wiig, Ø., & Bangjord, G. (2000). Predation of Svalbard reindeer by polar bears. *Polar Biology*, *23*, 675–678.

Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., ... Talley, L. D. (2012). Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, *4*, 11–37.

Freitas, C., Kovacs, K. M., Andersen, M., Aars, J., Sandven, S., Skern-Mauritzen, M., ... Lydersen, C. (2012). Importance of fast ice and glacier fronts for female polar bears and their cubs during spring in Svalbard, Norway. *Marine Ecology Progress Series*, *447*, 289–304.

Freitas, C., Kovacs, K. M., Ims, R. A., Fedak, M. A., & Lydersen, C. (2008). Ringed seal post-moulting movement tactics and habitat selection. *Oecologia*, *155*, 193–204.

Freitas, C., Lydersen, C., Fedak, M. A., & Kovacs, K. M. (2008). A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science*, *24*, 315–325.

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology and Evolution*, *25*, 325–331.

Goosemap. (2012) Site-specific information for geese occurring on Svalbard. Retrieved from http://goosemap.nina.no

Gormezano, L. J., & Rockwell, R. F. (2015). The energetic value of land-based foods in western Hudson Bay and their potential to alleviate energy deficits of starving adult male polar bears. *PLoS ONE*, *10*, e0128520.

Hamilton, C. D., Lydersen, C., Ims, R. A., & Kovacs, K. M. (2015). Predictions replaced by facts: A keystone species' behavioural responses to declining Arctic sea-ice. *Biology Letters*, *11*, 20150803.

Hamilton, C. D., Lydersen, C., Ims, R. A., & Kovacs, K. M. (2016). Coastal habitat use by ringed seals *Pusa hispida* following a regional sea-ice collapse: Importance of glacial refugia in a changing Arctic. *Marine Ecology Progress Series*, *545*, 261–277.

Høye, T. T., Post, E., Meltofte, H., Schmidt, N. M., & Forchhammer, M. C. (2007). Rapid advancement of spring in the High Arctic. *Current Biology*, *17*, R449–R451.

Hunsicker, M. E., Ciannelli, L., Bailey, K. M., Zador, S., & Stige, L. C. (2013). Climate and demography dictate the strength of predator-prey overlap in a subarctic marine ecosystem. *PLoS ONE*, *8*, e66025.

IPCC. (2014). *Summary for policymakers. Climate change 2014: Impacts, adaptation, and vulnerability*. Cambridge and New York: Cambridge University Press.

Iversen, M., Aars, J., Haug, T., Alsos, I. G., Lydersen, C., Bachmann, L., & Kovacs, K. M. (2013). The diet of polar bears (*Ursus maritimus*) from Svalbard, Norway, inferred from scat analysis. *Polar Biology*, *36*, 561–571.

Iverson, S. A., Gilchrist, H. G., Smith, P. A., Gaston, A. J., & Forbes, M. R. (2014). Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. *Proceedings of the Royal Society B*, *281*, 20133128.

Jakobsson, M., Mayer, L., Coakley, B., Dowdeswell, J. A., Forbes, S., Fridman, B., ... Weatherall, P. (2012). The International Bathymetric Chart of the Arctic Ocean (IBCAO) version 3.0. *Geophysical Research Letters*, *39*, L12609.

Johnson, D. S., London, J. M., Lea, M.-A., & Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology*, *89*, 1208–1215.

Kovacs, K. M., Lydersen, C., Overland, J. E., & Moore, S. E. (2011). Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity*, 41, 181–194.

Kranstauber, B., Kays, R., LaPoint, S. D., Wikelski, M., & Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, 81, 738–746.

Laidre, K. L., Born, E. W., Gurarie, E., Wiig, Ø., Dietz, R., & Stern, H. (2013). Females roam while males patrol: Divergence in breeding season movements of pack-ice polar bears (*Ursus maritimus*). *Proceedings of the Royal Society B*, 280, 20122371.

Laidre, K. L., Born, E. W., Heagerty, P., Wiig, Ø., Stern, H., Dietz, R., … Andersen, M. (2015). Shifts in female polar bear (*Ursus maritimus*) habitat use in East Greenland. *Polar Biology*, 38, 879–893.

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., … Ugarte, F. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology*, 29, 724–737.

Lydersen, C., Assmy, P., Falk-Petersen, S., Kohler, J., Kovacs, K. M., Reigstad, M., … Zajączkowski, M. (2014). The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. *Journal of Marine Systems*, 129, 452–471.

Lydersen, C., & Gjertz, I. (1986). Studies of the ringed seal (*Phoca hispida* Schreber 1775) in its breeding habitat in Kongsfjorden, Svalbard. *Polar Research*, 4, 57–63.

Lydersen, C., Kovacs, K. M., Aars, J., Hamilton, C., & Ims, R. (2017). An Arctic predator-prey system in flux: Climate change impacts on coastal space use by polar bears and ringed seals [Data set]. Norwegian Polar Institute. Retrieved from https://doi.org/10.21334/npolar.2017.132248b4

Lydersen, C., & Smith, T. G. (1989). Avian predation on ringed seal *Phoca hispida* pups. *Polar Biology*, 9, 489–490.

Madsen, J., & Williams, J. H. (2012). *International species management plan for the Svalbard population of the pink-footed goose Anser brachyrhynchus*. AWEA Technical Series No. 48. Bonn.

Mauritzen, M., Derocher, A. E., & Wiig, Ø. (2001). Space-use strategies of female polar bears in a dynamic sea ice habitat. *Canadian Journal of Zoology*, 79, 1704–1713.

Mauritzen, M., Derocher, A. E., Wiig, Ø., Belikov, S. E., Boltunov, A. N., Hansen, E., & Garner, G. W. (2002). Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. *Journal of Applied Ecology*, 39, 79–90.

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., … Aastrup, P. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325, 1355–1358.

Prop, J., Aars, J., Bårdsen, B.-J., Hanssen, S. A., Bech, C., Bourgeon, S., … Moe, B. (2015). Climate change and the increasing impact of polar bears on bird populations. *Frontiers in Ecology and Evolution*, 3, 33.

R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Raymond, B., Lea, M.-A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.-B., … Hindell, M. A. (2015). Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography*, 38, 121–129.

Reeves, R. R. (1998). Distribution, abundance and biology of ringed seals (*Phoca hispida*): An overview. *NAMMCO Scientific Publications*, 1, 9–45.

Rode, K. D., Pagano, A. M., Bromaghin, J. F., Atwood, T. C., Durner, G. M., Simac, K. S., & Amstrup, S. C. (2014). Effects of capture and collaring on polar bears: Findings from long-term research on the southern Beaufort Sea population. *Wildlife Research*, 41, 311–322.

Rode, K. D., Regehr, E. V., Douglas, D. C., Durner, G., Derocher, A. E., Thiemann, G. W., & Budge, S. M. (2014). Variation in the response of an Arctic top predator experiencing habitat loss: Feeding and reproductive ecology of two polar bear populations. *Global Change Biology*, 20, 76–88.

Rode, K. D., Robbins, C. T., Nelson, L., & Amstrup, S. C. (2015). Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities. *Frontiers in Ecology and the Environment*, 13, 138–145.

Rode, K. D., Wilson, R. R., Regehr, E. V., StMartin, M., Douglas, D. C., & Olson, J. (2015). Increased land use by Chukchi Sea polar bears in relation to changing sea ice conditions. *PLoS ONE*, 10, e0142213.

Smith, T. G., & Stirling, I. (1975). The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. *Canadian Journal of Zoology*, 53, 1297–1305.

Stirling, I. (1974). Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). *Canadian Journal of Zoology*, 52, 1191–1198.

Stirling, I., & Archibald, W. R. (1977). Aspects of predation of seals by polar bears. *Journal of the Fisheries Research Board of Canada*, 34, 1126–1129.

Stirling, I., & Derocher, A. E. (2012). Effects of climate warming on polar bears: A review of the evidence. *Global Change Biology*, 18, 2694–2706.

Stroeve, J. C., Kattsov, V., Barrett, A., Serreze, M., Pavlova, T., Holland, M., & Meier, W. N. (2012). Trends in Arctic sea ice extent from CMIP5, CMIP3 and observations. *Geophysical Research Letters*, 39, L16502.

Strøm, H., Descamps, S., & Bakken, V. (2008). *Sea bird colonies by the Barents Sea, White Sea and Kara Sea*. Tromsø: Norwegian Polar Institute. Retrieved from https://data.npolar.no/dataset/fd4fd3aa-7249-53c9-9846-6e28c5a42587

Sumner, M. D. (2014). trip: spatial analysis of animal track data. R package version 1.1-19. Retrieved from http://CRAN.R-project.org/package=trip

Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., … Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16, 3304–3313.

Thiemann, G. W., Iverson, S. J., & Stirling, I. (2008). Polar bear diets and Arctic marine food webs: Insights from fatty acid analysis. *Ecological Monographs*, 78, 591–613.

Towns, L., Derocher, A. E., Stirling, I., Lunn, N. J., & Hedman, D. (2009). Spatial and temporal patterns of problem polar bears in Churchill, Manitoba. *Polar Biology*, 32, 1529–1537.

Wang, M., & Overland, J. E. (2012). A sea ice free summer Arctic within 30 years: An update from CMIP5 models. *Geophysical Research Letters*, 39, L18501.

Wilson, R. R., Regehr, E. V., Rode, K. D., & St. Martin, M. (2016). Invariant polar bear habitat selection during a period of sea ice loss. *Proceedings of the Royal Society B*, 283, 20160380.

Wood, S., & Scheipl, F. (2014). gamm4: generalized additive mixed models using mgcv and lme4. R package version 0.2-3. Retrieved from http://CRAN.R-project.org/package=gamm4

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer-Verlag.

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