



UiT The Arctic University of Norway

**Stability of space use in Svalbard coastal female polar bears:
Intra-individual variability and influence of kinship**

Master's Thesis

Clément Brun

Master's thesis in Biology: "Northern Populations and Ecosystems" BIO-3950 June 2020



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Cover photograph: Adult female polar bear captured on sea ice in spring 2019 (East Svalbard)

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Acknowledgments

I owe a debt of gratitude to many people for help with this project.

First, I would like to thank my two main supervisors, Jon Aars and Marie-Anne Blanchet, for their very helpful supervision over the last two years. I benefited from the many discussions and meetings we had together over these months and I am extremely grateful for their support and guidance.

I want to thank Rolf Ims for his helpful feedbacks on my manuscript and on the statistics of my thesis. I also thank him for his recommendations on the choice of my thesis subject, which has led me to use telemetry data and study polar bears with Jon, Marie-Anne and the Norwegian Polar Institute.

I would like to thank Jon Aars and Magnus Andersen to have given me the immense privilege of being part of their fieldwork in Svalbard in spring 2019. The very friendly and welcoming crew of the KV Svalbard added to this memorable expedition.

Many thanks to Ingrid Marie Garfelt Paulsen, for sharing her knowledge on telemetry data and helping me structuring my dataset. Thanks to Cuong for his precious tips during our meeting in the World Marine Mammal Science Conference in Barcelona. Good luck with your PhD! I also would like to thank my office friends and colleagues at the Norwegian Polar Institute, Vegard Stürzinger and Guillaume Mercier, for their great company at work, especially during the polar night.

I want to thank my friends and my family in France for the never-ending love and support I received during the last two years!

Finally, special thanks to Theresia who shared this two year journey with me in studying our Masters together at UiT. I am very grateful for her many pieces of advice, her helpful comments, her company and care during this project!

Abstract

Philopatry influences the distribution of animals and can lead to the formation of kinship-based population structures when relatedness among individuals is tightly linked to their proximity. Two different polar bear ecotypes exist in the Barents Sea sub-population: “coastal” bears and “offshore” bears. Coastal bears remain year-round within the Svalbard archipelago whereas offshore bears follow the ice edge. This study assessed the long-term stability of space use in 17 Svalbard coastal female polar bears using satellite telemetry data obtained from 2011 to 2019. Annual and seasonal home range (HR) sizes and locations were analysed in different years in order to assess the intra-individual variability in site fidelity. Additionally, HR sizes and locations of related females belonging to five different matrilineages were compared to explore the influence of kinship on site fidelity. The bears showed very stable movement patterns during the study period in both consecutive and non-consecutive years. All annual HRs belonging to the individual bears overlapped; intra-individual annual HR centroids were on average separated by only 15 km (range=2-63 km). Distances separating individual annual HRs were small and were independent of the time gap between two HRs. The number of years separating annual HRs was not correlated to an increase/decrease in overlap. Individual bears exhibited a long-term stability in HR size: the estimated intra-individual variance corresponded to a quarter of the total variance in annual HR size (range=96-22 545 km²). The close proximity of related females showed the presence of a female kin structure year-round. Related females (such as mothers/daughters or sisters) utilized similar areas of the archipelago; their annual HR centroids were on average only separated by 18.4 km (range=2-52 km) which is almost equal to the intra-individual variation. The results of this study are consistent with previous research that investigated site fidelity and kinship structure in polar bears of the Barents Sea sub-population. The bears of the Barents Sea region seem to exhibit a stronger site fidelity than reported from other parts of the species range. These findings enlighten the degree to which coastal female polar bears of the Svalbard archipelago are faithful to their local area and reveal the strong female kin structure present in this ecotype.

Key words: Space use; philopatry; site fidelity; matriline; kinship structure; female kin; *Ursus maritimus*

1 Introduction

Philopatry, also known as site fidelity, is common among mammals and refers to an individual's faithfulness to specific regions (Greenwood 1980, Rydell 1989). Philopatry affects the distribution and abundance of animals as many of them restrict their movement to particular home ranges (HR) that provide suitable habitats for survival and reproduction (Burt 1943, Clutton-Brock & Lukas 2012). In some cases, animals disperse far from their natal site. In others, they exhibit natal philopatry by remaining close to or within the region where they were born. In the case of migratory species, animals are philopatric when returning to specific stop-overs, breeding and feeding grounds (Greenwood 1980, Clutton-Brock & Lukas 2012, Baker et al. 2013, Horton et al. 2017). Animals move primarily in relation to the use of resources such as food, mates or shelters. Their movements are driven by the availability and variability of resources in space and time (Lewis & Murray 1993, Dingle & Drake 2007, Lawson Handley & Perrin 2007). Many factors influence philopatry and dispersal patterns such as inbreeding avoidance, competition for resources, habitat predictability or kin competition (Switzer 1993, Perrin & Mazalov 1999, Lawson Handley & Perrin 2007). Philopatry may be favoured when the costs of changing territories are high. Moving to suitable areas and familiarizing with new foraging places are examples of these costs (Johnson & Gaines 1990, Switzer 1993). In solitary mammalian species, contrasting philopatry and dispersal patterns have important consequences on kinship structures (Clutton-Brock & Lukas 2012). Kinship structures exist when the proximity between individuals is strongly associated with the degree of their relatedness (Maher 2009, Clutton-Brock & Lukas 2012). These structures influence the demography of populations, can increase reproductive success, and thereby the fitness of individuals (Lambin & Krebs 1993, Pope 2000). In mammals, philopatry is often sex biased. Females tend to be more philopatric than males, which favours female kin structures. The low-dispersal rate observed in females may result from the benefit of kin cooperation that provide competitive advantages for residents over immigrants (Greenwood 1980, Lawson Handley & Perrin 2007, Dobson et al. 2012). The direction of the sex-bias is thought to be primarily due to the mating system (Greenwood 1980). In polygynous species, females invest greatly in their offspring and are the limiting sex encouraging males to disperse. By dispersing, males increase their probability to mate with more than one female, which enhances their reproductive success. These attributes exist in the movement patterns of ursids such as the American black bear (*Ursus americanus*), the

brown bear (*Ursus arctos*) and the polar bear (*Ursus maritimus*) (Rogers 1987, Støen et al. 2005, Zeyl et al. 2009b).

The largest of all ursids, the polar bear, is a solitary predator endemic to the Arctic. Polar bears are usually found on sea ice most of the year and utilize land masses only for shorter periods of time (Amstrup 2003). The species has an estimated total population size of 26 000 individuals found in 19 different sub-populations (Regehr et al. 2016). The population density of bears differs across the Arctic with a relatively high density found in the Barents Sea region (Aars et al. 2009). In the Svalbard archipelago, polar bears belong to the Barents Sea sub-population, which includes the Norwegian Arctic and partly the western Russian Arctic (Mauritzen et al. 2002). The estimated abundance of this sub-population is approximately at 3 000 individuals (Aars et al. 2009). Within this sub-population, bears exhibit two distinct space-use strategies (Mauritzen et al. 2001) and therefore are divided into two different ecotypes hereafter termed “offshore bears” and “coastal” bears. Both strategies are thought to be stable over time (Mauritzen et al. 2001). These differing spatial patterns result in considerable variations in inter-individual HR sizes (Mauritzen et al. 2001, Aars et al. 2009, Obbard et al. 2010, Blanchet et al. 2020). Offshore bears typically travel large distances across the Barents Sea region. They are predominantly found along the marginal ice zone as they follow the sea ice advance and retreat. In contrast, coastal bears remain within the Svalbard archipelago year-round. They utilize primarily land-fast ice and glacier fronts rather than the drifting pack ice (Freitas et al. 2012). When sea ice is locally absent, these coastal bears travel by using land masses and open water (Freitas et al. 2012, Hamilton et al. 2017a). Both ecotypes ultimately depend on sea ice for survival as it provides a suitable habitat to move, hunt and reproduce (Stirling 1974, Amstrup 2003, Lone et al. 2018). Consequently, their movements are tightly linked to the phenology of sea ice, characterized by great inter-annual and seasonal variations retreating away from land in summer and freezing up early winter (Garner et al. 1990, Vinje & Kvambekk 1991, Amstrup 2003).

Seasons considerably influence the activity level and mobility of polar bears. A peak of activity is observed in spring and in summer followed by a less active period in fall and winter (Derocher & Stirling 1990, Messier et al. 1992, Ferguson et al. 1997, Amstrup et al. 2000). Spring is the mating season for polar bears. Adult males can reproduce every year, while females are available for reproduction every three years if cubs survive until weaning (Amstrup 2003). Pregnant females use maternity dens to give birth the following winter.

After a long fasting period, maternity dens are abandoned early April when mothers and their cubs start searching for food on sea ice (Hansson & Thomassen 1983, Andersen et al. 2012). Spring is a crucial hunting season for polar bears as prey abundance increases dramatically due to seal pupping (Messier et al. 1992, Lydersen 1998, Krafft et al. 2007). In this period, the coastal bears of Svalbard target glacier front and fast ice habitats where they mostly forage on ringed seals (*Phoca hispida*) and their pups (Freitas et al. 2012). In fall and winter, limited availability of food combined with harsh environmental conditions result in a lower level of activity (Messier et al. 1992).

Site fidelity of polar bears belonging to the Barents Sea sub-population has been previously documented revealing a high degree of philopatry year-round (Wiig 1995, Mauritzen et al. 2001, Zeyl et al. 2010, Lone et al. 2013). For instance, Mauritzen et al. (2001) used satellite telemetry to track females of the Barents Sea region throughout the year. They found that individuals of both ecotypes were philopatric with a season-specific fidelity. Studies based on telemetry data are restricted to female individuals because the shape of the neck and head of male polar bears prevents collar attachment. This results in a lower knowledge of male's movement patterns. However, the movement behaviour of both sexes can be studied with other methods like capture-recapture techniques which were used by Lone et al. (2013). They investigated site fidelity of male and female polar bears in Svalbard during spring and showed that individuals of both sexes are faithful to specific areas. Females exhibited a higher degree of site fidelity than males. They also observed a recapture bias for females suggesting that long-term philopatry might occur in females as an individual space-use strategy. Mark-recapture methods combined with genetic analysis revealed that during winter, adult females of the archipelago are faithful to their denning area and that daughters are denning in close proximity to their mothers' denning site (Zeyl et al. 2010). In spring, during the breeding season, Zeyl et al. (2009a) showed that polar bears of the Barents Sea region exhibit a significant kinship structure which suggest that offspring remain close to their mothers' area at adulthood.

Even though philopatry has been studied in polar bears of the Barents Sea region, there is little knowledge of the degree to which the Svalbard female polar bears of the coastal ecotype exhibit long-term philopatry and of the variability of site fidelity at the individual level. This study used high-resolution GPS telemetry data over an eight-year period to investigate long-term philopatry on coastal female polar bears. Annual and seasonal HR sizes and locations were analysed to further understand variability in site fidelity throughout the

year. In addition, the space use of related bears was examined to explore the following question: to what extent is there a correlation between relatedness of the coastal female polar bears and their HR proximity?

2 Material and methods

2.1 Study site

The high Arctic archipelago of Svalbard encompasses 62 000 km² and is located between 74°-81°N and 10°-35°E. Seasonal average temperatures typically do not exceed 6°C in summer and do not fall below -20°C in winter, making it the warmest region of the high Arctic (Przybylak et al. 2014). Atlantic water flows northwards and enters the Arctic Ocean through Fram Strait to the west of Svalbard and the Barents Sea to the east (Loeng 1991, Piechura & Walczowski 2009, Przybylak et al. 2014). The amount of heat transported by the West Spitsbergen Current (WSC) has been increasing in the last 20 years, negatively

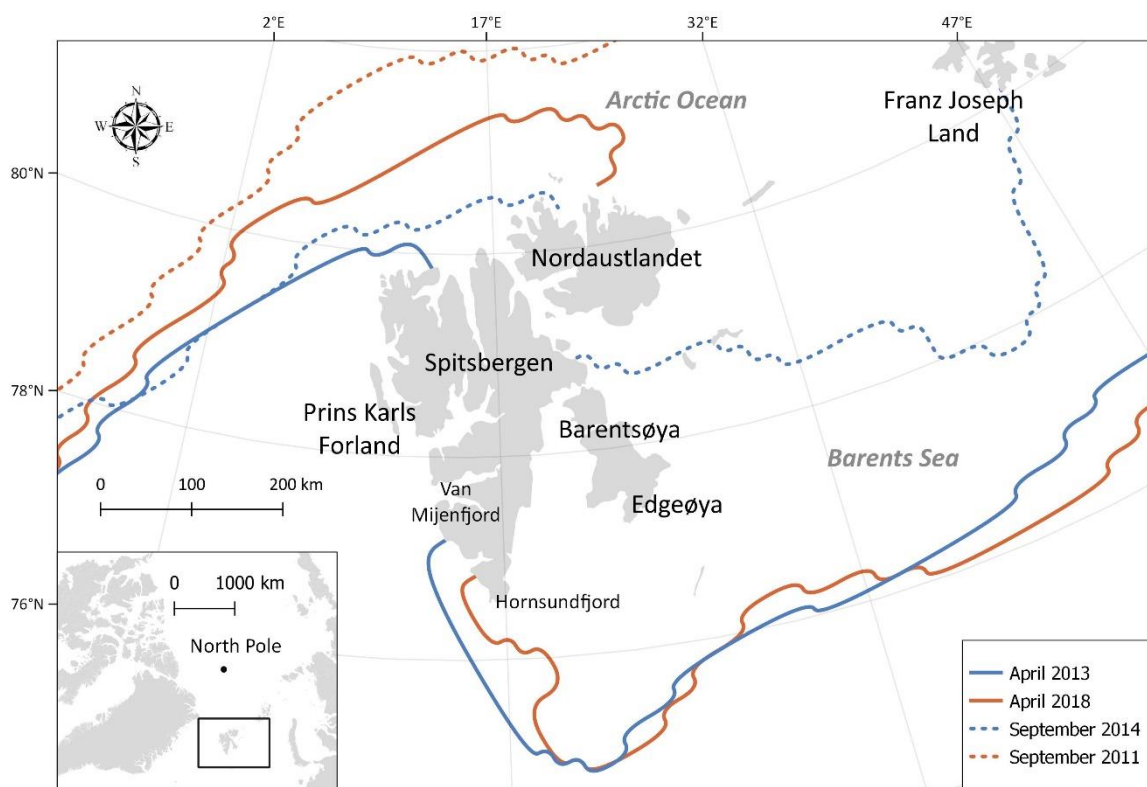


Figure 1. Map of the Barents Sea region: the high Arctic archipelago of Svalbard and part of the western Russian Arctic. The inset displays the Barents Sea region in a circumpolar perspective. The lines represent the annual maximum (solid lines, April) and minimum (dotted lines, September) sea ice extents (15% concentration threshold). The color scheme corresponds to extremes in sea ice extent observed during the 2011-2019 study period (red = minimum, blue = maximum) in April and September. The most extreme years are displayed to show the inter-annual variability during the study period. Note that the lines correspond to different years, as the observed extremes did not occur within the same year

impacting the seasonal sea ice cover as well as the thickness of the ice found around the archipelago (Gerland et al. 2008, Piechura & Walczowski 2009). The warming of the WSC can locally prevent ice formation. A lack of fast ice in the west of Svalbard was observed in the years 2005-2006 compared to the preceding decade (Cottier et al. 2007). Since 2006, the fjord systems went from an Arctic state to a more Atlantic state along the west coast of Spitsbergen (Cottier et al. 2007, Muckenhuber et al. 2016). Around the Svalbard archipelago, maximum sea ice extent typically occurs in March or April, while minimum extent occurs in September or October (Løset & Carstens 1996, Muckenhuber et al. 2016).

2.2 Capture and instrumentation

Satellite telemetry data was collected over an 8-year period (2011-2019) as part of an ongoing research program on the ecology of polar bears led by the Norwegian Polar Institute since 1988. Capture of polar bears followed the standard protocols (Stirling et al. 1989). Adult females that appeared healthy were equipped with Global Positioning System (GPS) satellite transmitters from Telonics (www.telonics.com, type Telonics TGW4678-3 or TGW-4678-4). Seventeen out of the 89 adult female polar bears that were equipped with a GPS collars in the high Arctic archipelago of Svalbard from 2011 to 2019 were selected for this study. This subset included females that were tracked for at least 2 full years as well as related females (mothers-daughters or sisters) tracked for at least 1 full year each. Most of the captures took place in April (n=34) but some collars were also fitted in March (n=1) and September (n=2). Morphometric measurements as well as the presence and age of cubs were recorded. The Norwegian Animal Research Authority approved all animal handling and protocols. The work was carried out in accordance with the relevant guidelines and regulations under permits issued by the Governor of Svalbard.

2.3 Analysis of spatial data

2.3.1 Data processing

All numerical analyses were performed using the software R (R Core Team, 2020). Location estimates were obtained by GPS via the ARGOS (Collecte Localisation Satellites, Toulouse, France) or IRIDIUM systems (Iridium Satellite Communications, McLean, VA, USA). Instruments were programmed to transmit every two hours with no duty cycle. Satellite signals can be affected by physical constraints and be altered when the individuals are denning or in water resulting in gaps in the data stream. This occurred rarely as the time step between two consecutive GPS locations was less than 4 hours 90% of the time (total number

of locations recorded = 95 271). The data was processed with a Kalman filter under a state-space model framework using the R package “crawl” (Johnson et al. 2008). Modelled locations were predicted every two hours. A full year started from 1 June and ended 31 May the following year. When collars stopped recording before 31 May, only years of at least nine months of records were included in the analysis. Seasons were defined as follows: Spring (1 June-31 July), Summer (1 August-30 September), Fall (1 October-30 November) and Winter (1 December-30 May).

2.3.2 Dataset structure

The dataset was divided into two different subsets: a first subset of female bears used to assess the intra-individual variability in site fidelity (Table 1); as well as a second subset of related females used to explore the influence of kinship on site fidelity (Table 2). Note that 7 out of the 17 females were used in both analyses, and that all individual bears belonged to the coastal ecotype.

2.3.2.1 Intra-individual variability analysis

Thirteen female polar bears were included in the intra-individual analysis (Table 1). The number of years of data per individual varied from 2 to 4 and the total number of years in the dataset was 31. For distance and overlap analyses, 9 comparisons were between consecutive years while 15 were between non-consecutive years. On average, the gap between non-consecutive years was 2 years with a maximum gap of 4 years.

Table 1. Summary of the biological data of Svalbard coastal female polar bears of the intra-individual analysis

IDs	Recorded years	Number of collars	Total duration (days)
A	11-12 15-16	3	676
B	14-15 17-18	2	645
Ba	14-15 15-16 18-19	3	1095
C	11-12 15-16	2	690
Da	15-16 17-18	3	701
Ea	17-18 18-19	3	728
Eb	11-12 15-16	2	605
F	14-15 15-16 17-18	4	1095
G	13-14 17-18	3	688
H	14-15 15-16 17-18 18-19	2	1409
I	17-18 18-19	1	730
J	15-16 16-17 17-18	1	1095
K	14-15 15-16	1	694

2.3.2.2 Kinship analysis

Eleven females belonging to 5 different matriline were included in the kinship analysis (Table 2). The relatedness of the females was identified using the extensive database of the Norwegian Polar Institute. Cubs are fitted with a permanent ear tag while captured with their mother and can be instrumented as adults with a satellite transmitter. Daughters were given 2 letters coding for identification with the first letter referencing to their mother (i.e. mother A, daughter Aa). The number of years of data per individual varied from 1 to 3 and the total number of years was 19. For distance and overlap analyses, three comparisons were between records of the same year. Three were between consecutive years and 15 were between non-consecutive years. The dataset corresponded to 3 mother and daughter pairs: A-Aa, C-Ca, D-Da; 1 mother with 2 daughters from different litters: B-Ba-Bb; and 2 sisters from different litters: Ea-Eb (Table 2).

Table 2. Summary of the biological data of Svalbard coastal female polar bears of the kinship analysis. Eleven female polar bears form 5 matriline named from A to E. Unique capital letters refer to mothers, double letters to daughters/sisters with the first letter referring to the mother identification. Year of birth assuming birth occurred after January first

IDs	Year of birth	Recorded years	Number of collars	Total duration (days)
A	1995	11-12 15-16	3	676
Aa	2002	15-16	2	365
B	1993	14-15 17-18	2	730
Ba	2008	14-15 15-16 18-19	3	1074
Bb	2012	18-19	1	312
C	1991	11-12 15-16	2	690
Ca	2011	18-19	1	365
D	1996	15-16	1	365
Da	2006	15-16 17-18	3	670
Ea	2006	17-18 18-19	3	728
Eb	2003	11-12 15-16	2	664

2.3.3 Space use analysis

2.3.3.1 Home ranges

Home ranges represent defined areas in which animals forage and reproduce (Burt 1943). Annual and seasonal HRs were obtained using the minimum convex polygon method (Mohr 1947). This non-parametric method consists of the calculation of the smallest convex polygon capturing all the locations of an animal. This method is simple, easy to implement and widely

used to define species HRs. Because convex polygons are formed using the extreme locations in space, unusual long excursions undertaken by females affect to a large extent the size of the polygons. To minimize this bias, the analysis was run with polygons enclosing 50% of the locations to focus on the core regions occupied by the individuals. For HR polygons to reflect the spatial use of the individuals, GPS locations during the denning periods were removed (extended periods during which the bears are stationary). A female polar bear was identified to be in den by the combination of high temperature, low activity, and no spatial movement (based on GPS positions). Seventeen denning periods identified from 2011-2019 for 12 individuals were removed. The azimuthal equidistant projection was used for the minimum convex polygon analysis. The main feature of this projection is that all distances and directions of the globe are correct from its centre point. The centre point of the projection corresponded to the median of all latitudes and longitudes of all GPS locations of the dataset. Annual and seasonal HRs were calculated.

To estimate the proportion of variance in annual HR size that occurs within individuals relatively to the total variance, that is the variance that occurs within individuals added to the variance that occurs between individuals, a one-way ANOVA test with one random factor (i.e. individuals ID) was performed using the lmer function from the R package “lme4” (Bates et al. 2015).

To determine intra-individual variations in annual HR size, relative differences in percentages as well as the differences in km² were calculated between the largest and the smallest individual’s HRs.

To determine inter-individual variations in annual HR size within matriline, relative differences in percentages as well as the differences in km² were calculated between the largest and the smallest HRs of related females. When an individual had more than one annual HR value, the mean between HR sizes was calculated to obtain a single HR value for each bear.

2.3.3.2 Centroid distances and home range overlaps

A centroid or geometric centre of a plane figure refers to the arithmetic mean of all the points in the HR polygon. The R function gCentroid from the package “rgeos” determined the position of annual and seasonal HR centroids (Bivand & Rundel 2018). These centroid positions were used to calculate distances between HRs. Matrix of distances between all

centroids were computed using the pointDistance function from the R package “geosphere” (Hijmans, 2019). Inter-individual and intra-individual distances between annual and seasonal HRs were calculated.

To determine if the HR sizes and the distances between centroids differed between seasons, a Kruskal-Wallis test was computed. If significant, the use of pairwise Wilcoxon signed-rank tests revealed which seasons differed from others significantly.

Percentages of HR overlaps were calculated for intra-individual comparisons and between related bears. The percentage of overlap for each HR pair of polygons was calculated using the following equation:

$$\frac{(\text{area of overlap between polygons A \& B})}{(\text{area A} + \text{area B} - \text{area of overlap between A \& B})} \times 100$$

A Spearman’s Rank Coefficient was calculated to determine whether differences in HR overlap were dependent on the time gap between 2 HRs, that is whether the percentage of overlap between annual HRs tends to increase/decrease with increasing time between compared years.

3 Results

3.1 Intra-individual variability

3.1.1 Annual variability

Annual HR sizes of the Svalbard coastal female polar bears varied from 96 to 22 545 km² (Fig. 2, Table 3). Female C had the 2 largest annual HRs with 21 371 and 22 545 km² in 2011-2012 and 2015-2016 respectively (Fig. 2). Female Eb had the two smallest annual HRs with 105 km² and 96 km² in 2011-2012 and 2015-2016 respectively (Fig. 2). Intra-individual annual HR sizes varied between years (Fig. 2 & 3). The relative decrease in percentage from the largest HRs to the smallest HRs were between 5 to 50% for 9 females (Fig. 3a). Four individuals had a higher decrease in HR in percentage with the highest percentage reaching 91.8% for the female F (Fig. 3a). This variation corresponded to a decrease of 17 939 km² from her HR size in year 2014-2015 and her HR size in year 2017-2018 (Fig. 3b).

The estimated variance in annual HR size that occurred within individuals corresponded to 24.7% of the total variance (Fig. 2b). GPS tracks of female J and female Eb

Table 3. Summary of the analysis in annual and seasonal home ranges (HR) of Svalbard coastal female polar bears instrumented from 2011 to 2019. Intra-individual analysis: distances between HR centroids and percentages of HR overlaps were calculated using the same individuals. Kinship analysis: distances between HR centroids and percentages of HR overlaps were calculated using related bears belonging to the same matriline

		Intra-individual (n _{collars} =29; n _{bears} =13; n _{years} =31)			Kinship (n _{collars} =23; n _{bears} =11; n _{years} =19)		
		Mean	Median	Range	Mean	Median	Range
	Annual tracking duration (days)	353.3	365	299 - 365	348.9	365	299 - 365
Year	HR size (km ²)	3273	1097	96 - 22 545	3456	1097	96 - 22 545
	Distances HR centroids (km)	15	7.7	2 - 63	18.4	15	2.4 - 52.4
	HR Overlap (%)	44.2	44.4	8.5 - 95.8	23.8	24.9	0 - 66
Spring	HR size (km ²)	2915	1349	36 - 22 648	3215	1741	36 - 22 648
	Distances HR centroids (km)	29.7	17.7	1.9 - 172	38	29	9.9 - 109.3
	HR Overlap (%)	25.2	23.8	0 - 79	9.2	4.5	0 - 35
Summer	HR size (km ²)	792	325	12 - 9 522	905	279	27 - 9 522
	Distances HR centroids (km)	17.8	9.7	2.3 - 72.1	23	9.8	1.2 - 138.4
	Overlap of HR (%)	20.5	22.6	0 - 50	15	7.8	0 - 69.7
Fall	HR size (km ²)	268	204	3 - 1 311	270	203	22 - 945
	Distances HR centroids (km)	14	12	1.8 - 50.5	19.6	17.7	2.6 - 54.8
	Overlap of HR (%)	12.5	5.4	0 - 67.5	7.2	0	0 - 51.4
Winter	HR size (km ²)	1284	833	0.8 - 6 390	1241	833	0.8 - 6 390
	Distances HR centroids (km)	16.3	12.5	2.4 - 44.4	19.8	21	1.5 - 34
	Overlap of HR (%)	25.3	23	0 - 63.3	12.7	7.8	0 - 76

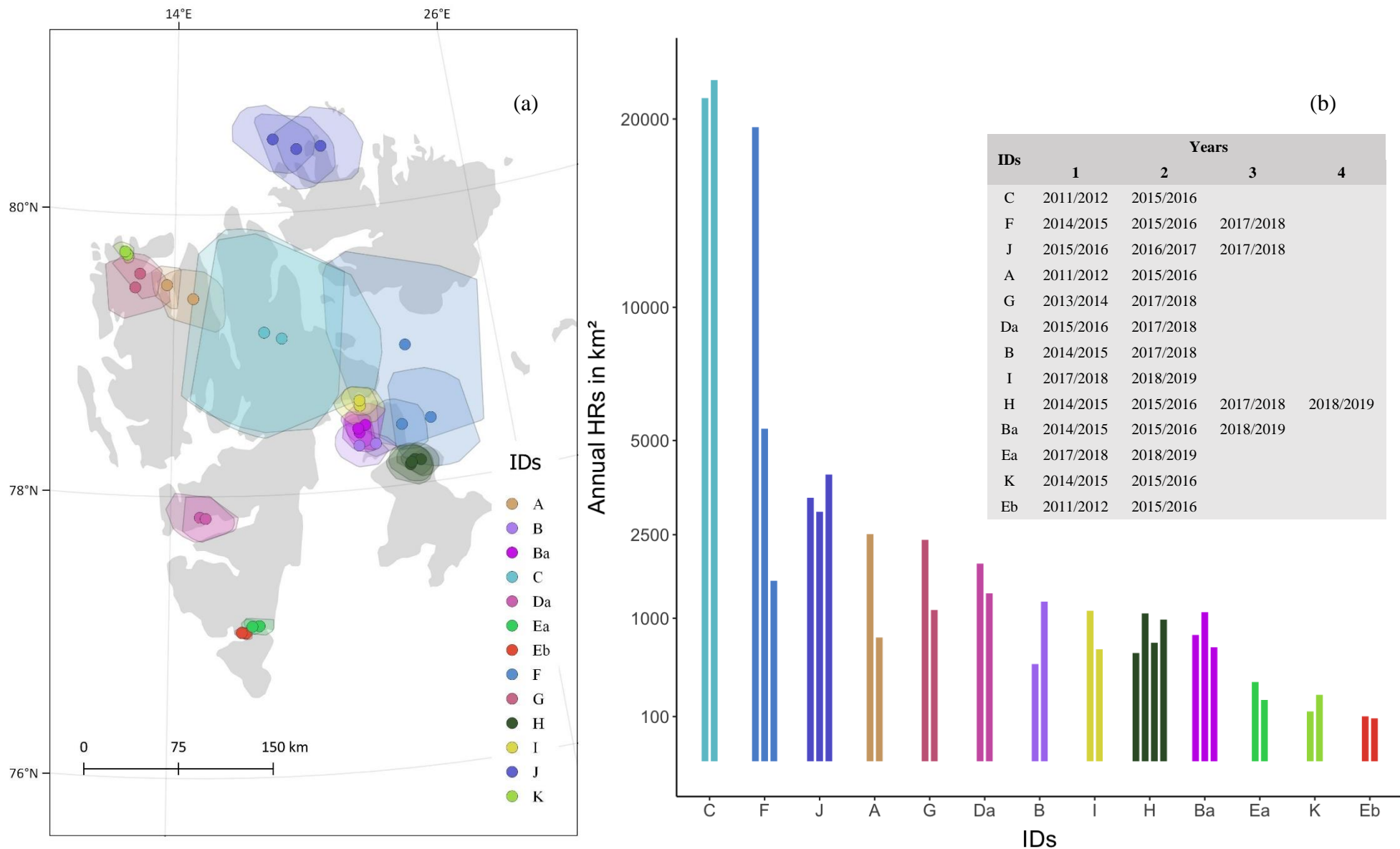


Figure 2. (a) Annual home ranges (HR) defined as 50% minimum convex polygons for 13 coastal female polar bears instrumented in the Archipelago of Svalbard between 2011 and 2019. Each polygon is colour coded per individual. The points represent the centroids for each polygon. (b) Areas of annual HRs for the same female polar bears in km². The number of bars depends on the number of full years an individual was tracked for. Individual's bars are organized chronologically (see explanatory table). Each bar is colour coded per individual as on a). Note that the scale of the Y-axis was square root transformed

illustrate the long-term intra-individual stability in annual HR size and location (Fig. 4).

HRs belonging to the same individuals were much closer together than HRs belonging to different animals: an average of 172.8 km (SD=88.7, range=7.4-392.1 km) separated locations between inter-individual HR centroids while an average of 15 km (SD=16.9, range=2-63 km) separated locations between intra-individual HR centroids (Fig. 2a, Table 3).

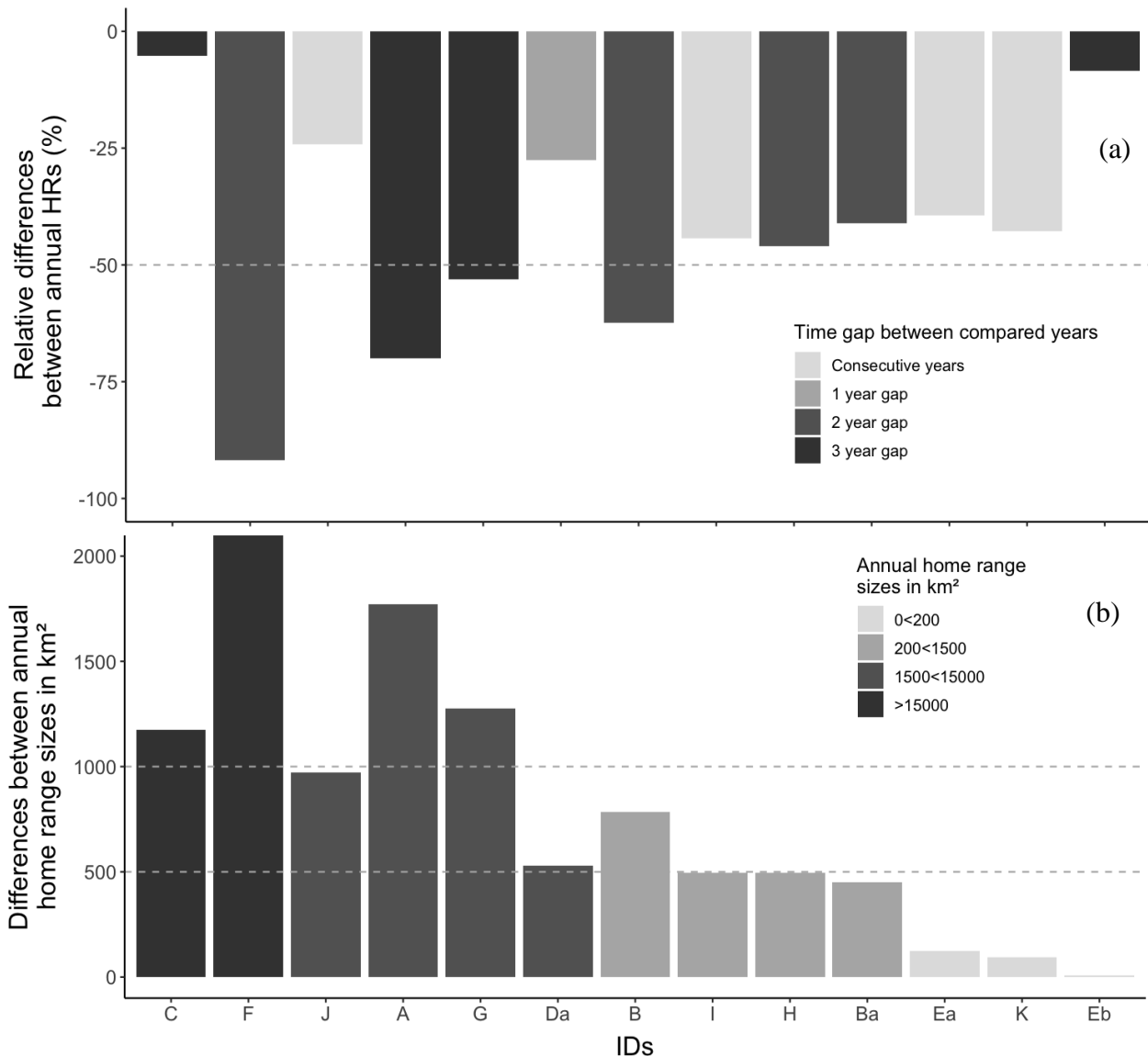


Figure 3. (a) Relative variation between the largest and the smallest annual home ranges (HR) for 13 female polar bears instrumented in the Archipelago of Svalbard between 2011 and 2019. The shades of grey represent the time gap between the HRs. The darker the hue the larger the time gap. (b) Variation between the largest and the smallest annual HR areas for 13 female polar bears instrumented in the Archipelago of Svalbard between 2011 and 2018. The shades of grey represent the size of the largest individual HR. Value for ID F is not shown due to difference is size; the value is 17 939 km²

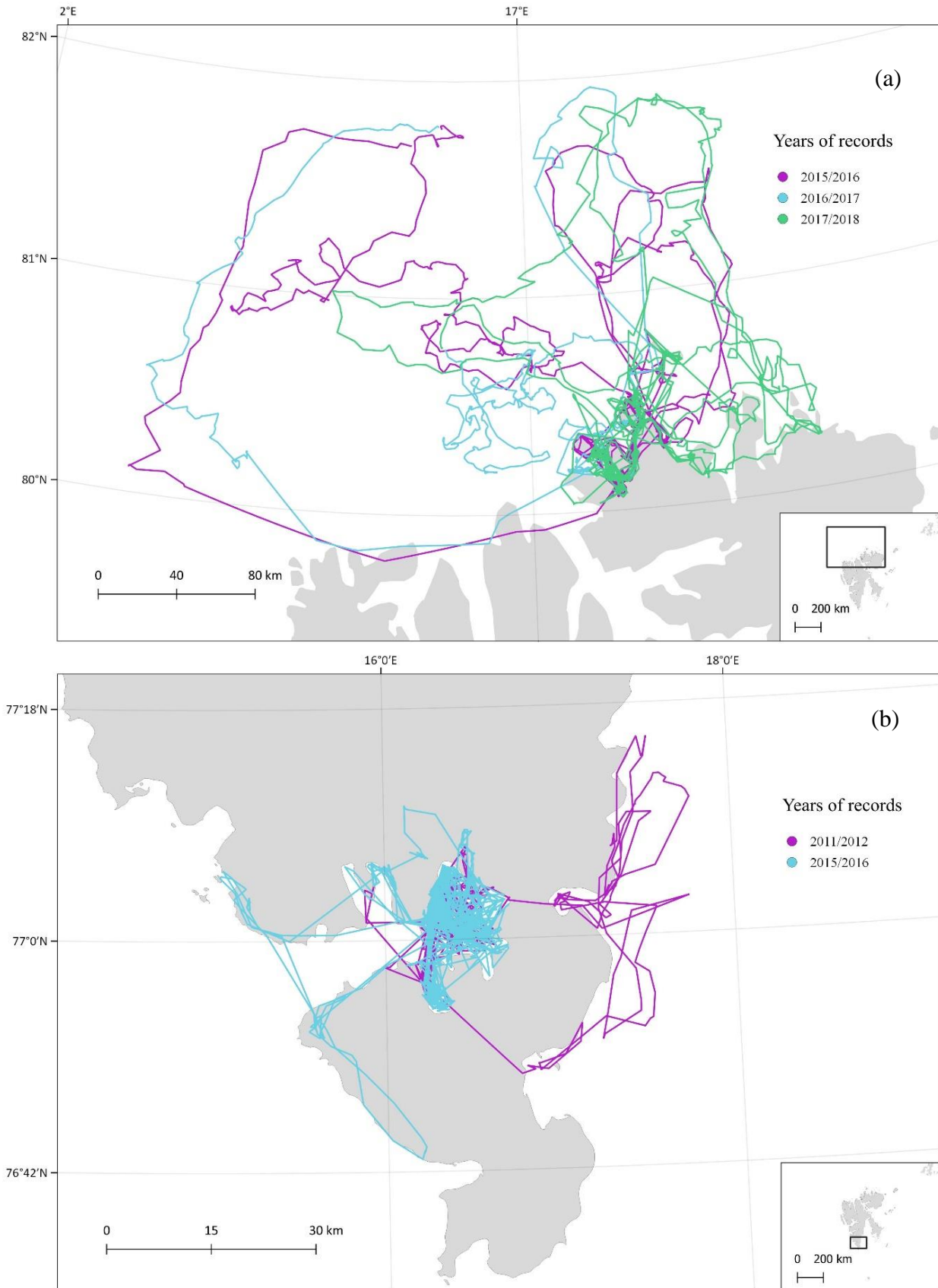


Figure 4. Examples of annual tracks of 2 Svalbard coastal female polar bears instrumented for (a) 3 years and (b) 2 years

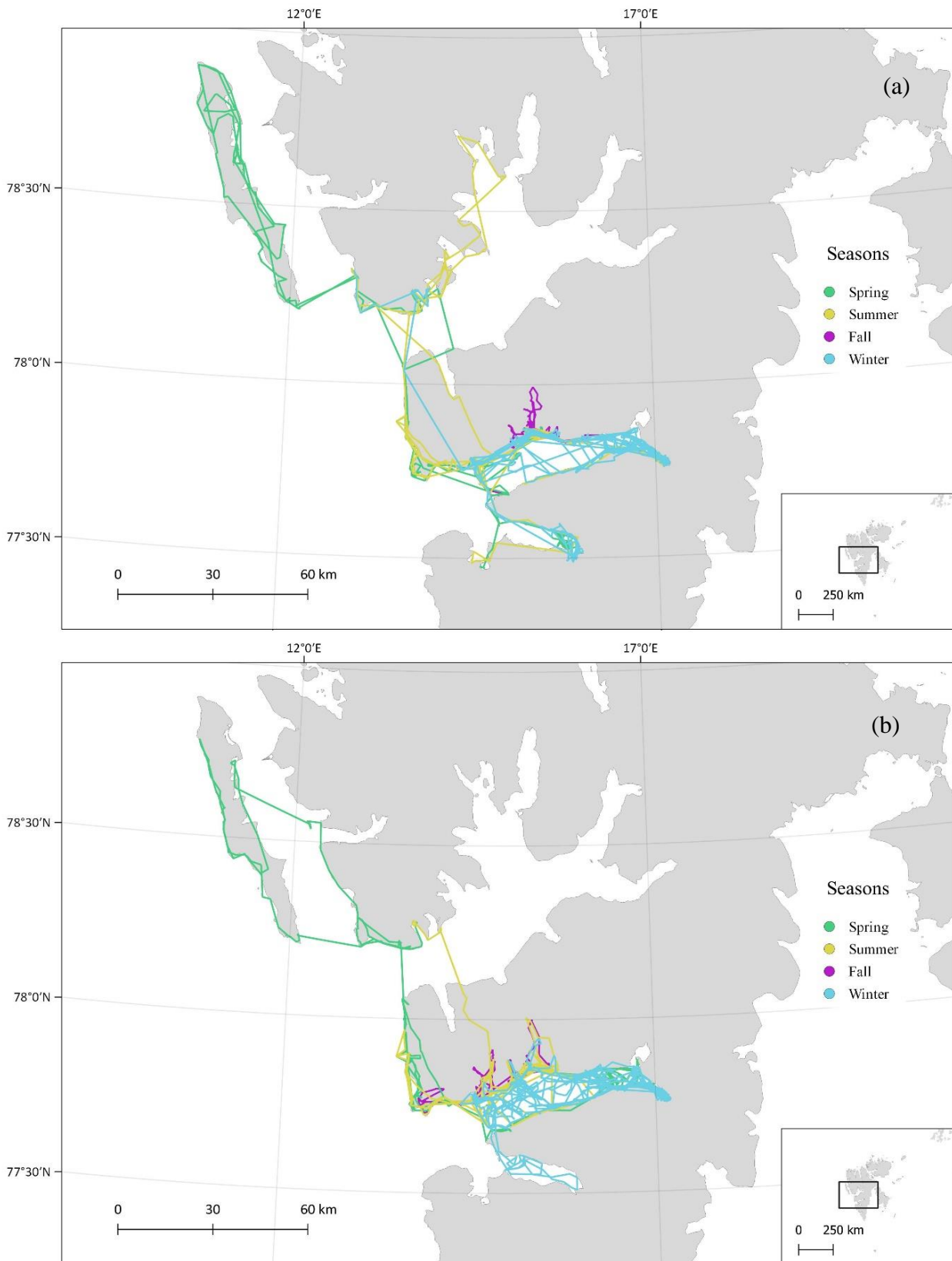


Figure 5. Examples of annual tracks of a Svalbard coastal female polar bear instrumented in (a) 2015-2016 and (b) 2017-2018. The tracks are colour-coded according to the seasons

The minimum distance between 2 annual HR centroids of the same bear was 2 km found for female H between 2015-2016 and 2018-2019 (Table 3). Her HR centroid positions were in the north of Edgeøya in the eastern part of the Svalbard archipelago (Fig. 2). The maximum distance between individual's HRs was 63 km found for female F between 2014-2015 and 2017-2018 (Fig. 2, Table 3). Her annual centroid positions were in the east part of Barentsøya (Fig. 2). All annual HRs belonging to the same bear were found to overlap with an average of 44.2% (SD=20.9, range=8.5-95.8) (Fig. 2, Table 3).

The differences in time gaps between annual HRs did not explain the variation in percentages of overlap: there was no significant correlation between the percentages of annual HR overlaps and the time gaps existing between the compared years (Spearman Rank Coefficient, $S = 2083.1$ $P > 0.66$).

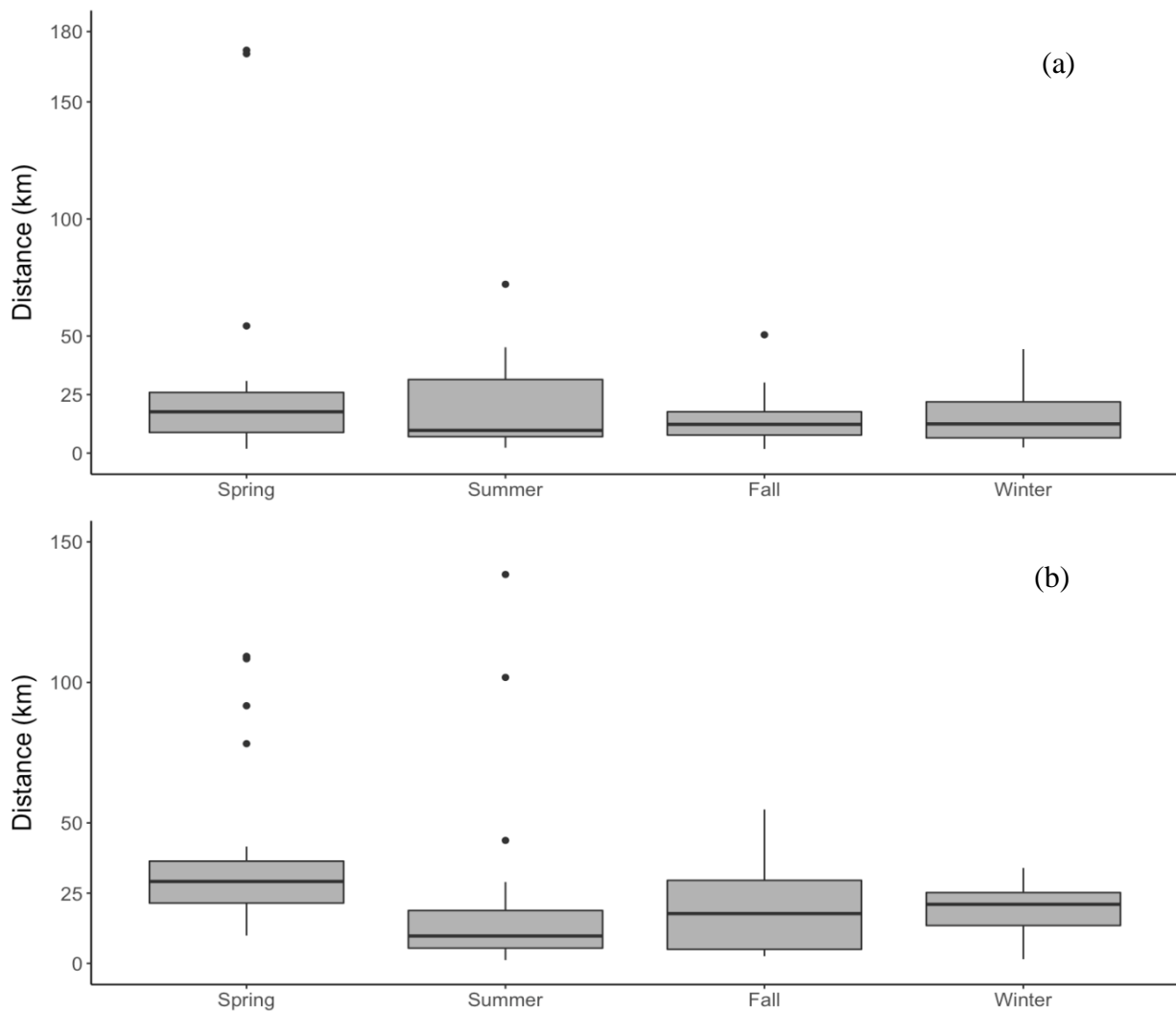


Figure 6. (a) Distances between seasonal home range (HR) centroid positions belonging to the same coastal female polar bear (n=13). (b) Distances between seasonal HR centroid positions between related coastal female polar bears (n=11)

3.1.2 Seasonal variability

Individual HR sizes varied between seasons (Kruskal-Wallis chi-squared=35.161, df=3, $P < 1.127 \times 10^{-6}$). Larger HR sizes were found in spring compared to the other seasons with an average of 2 915 km² (SD=4 809) (Table 3). Averages for the 3 other seasons were 792 (SD=1 728), 268 (SD=278.9) and 1 284 km² (SD=1 488.5) in summer, fall and winter respectively (Table 3). Distances between season-specific individual HR centroid positions were on average below 30 km for the 4 seasons with a highest mean of 29.7 km (SD=45.1, range=1.9-172.0 km) in spring and a lowest of 14 km (SD=11, range=1.8-50.5 km) in fall (Fig. 6a, Table 3). These differences were not statistically significant (Kruskal-Wallis test; chi-squared=1.6702, df=3, $P = 0.6436$) (Fig. 6a). GPS tracks of individual Da illustrate the fidelity in seasonal movement patterns (Fig. 5). She utilized the area of Van Mijen fjord in winter and migrated to Prins Karls Forland in spring during the 2 non-consecutive years of her records (2015-2016 and 2017-2018). The minimum distance between 2 seasonal HR centroids of the same bear was 1.9 km found for the female Ea during the fall season (Table 3). The maximum distance between 2 HR centroids of the same bear was 172 km found for the female F during the spring season (Table 3). Twenty-three out of the 24 pairs of HRs overlapped in spring, 22/24 in summer, 16/24 in fall and 21/24 in winter.

3.2 Kinship

3.2.1 Annual variability

HR sizes varied between coastal female polar bears of the different matriline and ranged from 96 to 22 545 km² (Fig. 7a, Table 3). Within the matriline B, mother B and her 2 daughters Ba and Bb had very similar HR sizes with 864, 844 and 829 km², respectively. The smallest HR sizes were found for the 2 sisters of the matriline E with 254 km² for Ea and 100 km² for Eb. These females were both utilizing the most southern part of Spitsbergen Island exclusively; they spent a significant amount of time in Hornsund fjord (Fig. 7a). Matrilines A and D had HR sizes ranging from 1 644 to 3 954 km². The related bears of the matriline C had the largest difference: the annual HR size for mother C was 21 958 km² while the one for her daughter Ca was 1 459 km² (Fig. 7).

Related bears utilized similar regions of the archipelago (Fig. 7a). Annual HR centroid positions of related individuals were much closer together than those of non-related

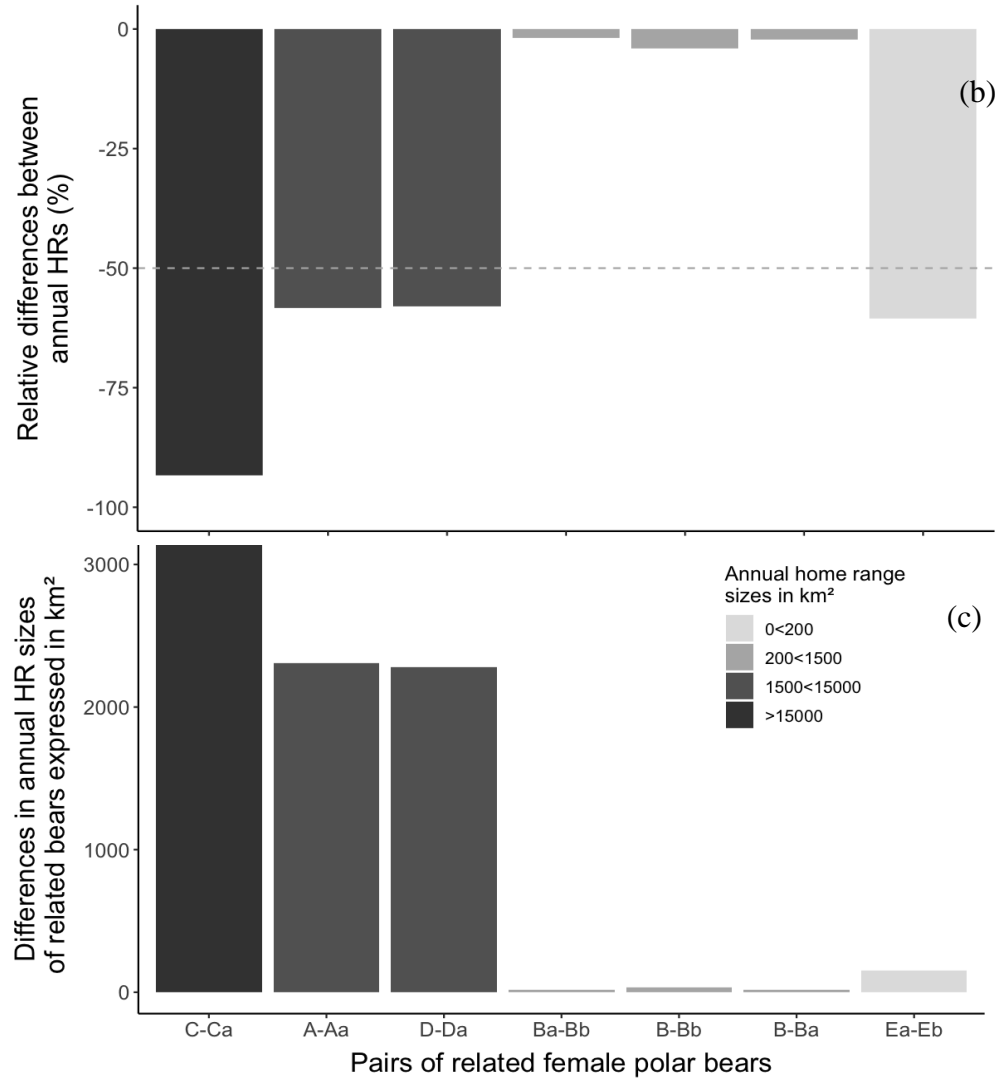
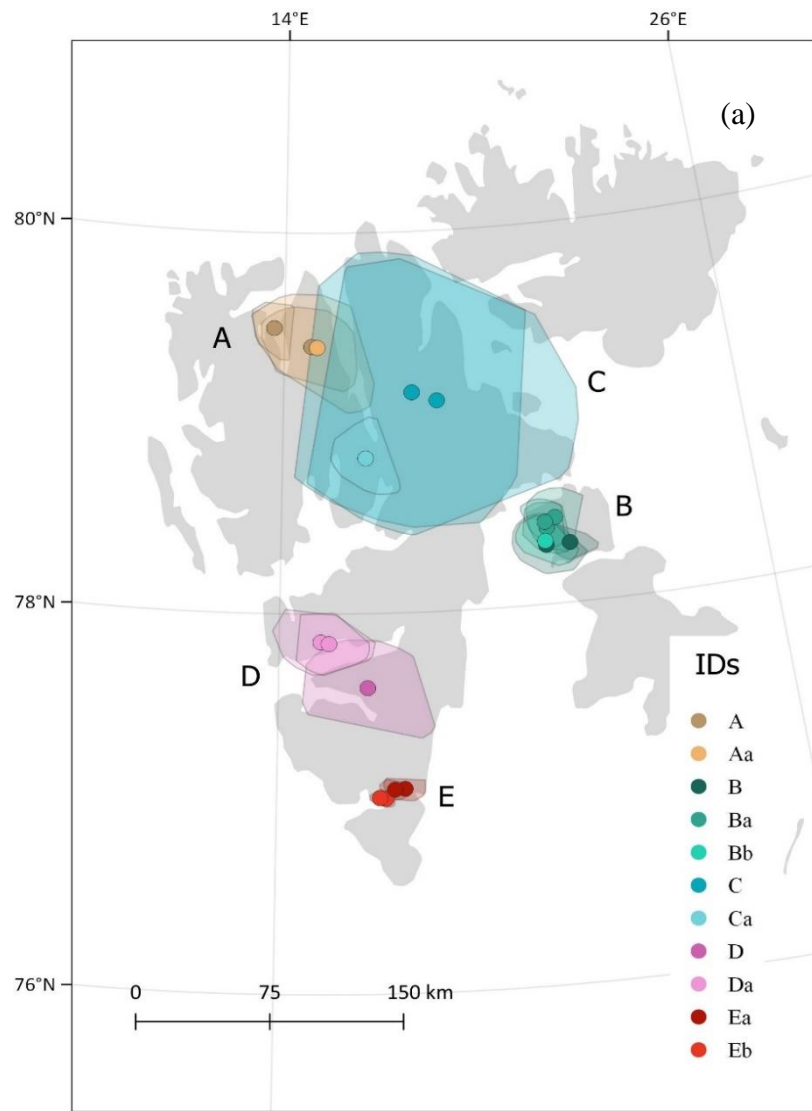


Figure 7. (a) Annual home ranges (HR) defined as 50% minimum convex polygons for 11 related coastal female polar bears belonging to 5 different matriline instrumented in the Archipelago of Svalbard between 2011 and 2019. Related animals were coded with similar colours and follow each other in the legend. Mothers are named under a unique capital letter and daughters/sisters under two letters. The points represent the centroids for each polygon. (b) Relative variation between the largest and the smallest annual HR areas between pairs of related females. The shades of grey represent the size of the largest HR within pairs of females. (c) Variation in km² between the largest and the smallest annual HR areas within pairs of related females. The shades of grey are identical than for (b). Value for C-Ca is not shown due to difference is size; the value is 20 499 km²

individuals: an average of 160.5 km (SD=54.7, range=59-283 km) separated locations of HR centroid positions of individuals belonging to different matriline while only 18.4 km (SD=13.5, range=2-52 km) separated locations of HR centroids of individuals belonging to the same matriline (Fig. 7a, Table 3). The minimum distance between HR centroid positions of 2 related animals was 2.4 km found between mother B in year 2017-2018 and her daughter Bb in year 2018-2019. The maximum distance was 52.4 km between the mother C in year 2015-2016 and her daughter Ca in year 2018-2019 (Table. 3). Twenty out of the 21 pairs of annual HRs belonging to female polar bears of the same matriline overlapped (Fig. 7a). On average, pairs of annual HRs of related bears overlapped by 23.8% (SD=19, range=0-66) (Table. 3). The only pair of HRs not overlapping was between the female Ea in year 2015-2016 and her sister Eb in year 2017-2018. They were still in very close proximity as the centroids of their respective annual HRs were separated by only 15 km (Fig. 7a).

3.2.2 Seasonal variability

Related bears were in very close proximity in all seasons (Fig. 6b, Table 3). On average, distances between HR centroid positions of related individuals were below 40 km for the 4 seasons with a highest mean of 38 km (SD=30.8) in spring and a lowest of 19.6 km (SD=13.7) in fall (Fig. 6b, Table 3). The distances separating seasonal HR centroids of related females differed significantly between seasons (Kruskal-Wallis chi-squared=12.45, df=3, P<0.006). Wilcoxon signed-rank tests revealed that only spring distances were significantly greater than for other seasons (Fig. 6b). The minimum distance between 2 seasonal HRs of related bears was 1.2 km for the sisters Ba and Bb in summer (Table. 3). The maximum distance between 2 seasonal HRs of related bears was 138.4 km for the mother C and the daughter Ca in summer. Fifteen out of the 21 pairs of HRs overlapped in spring, 15/21 in summer, 9/21 in fall and 15/21 in winter.

4 Discussion

Coastal female polar bears of the Svalbard archipelago exhibit a very high degree of philopatry in both consecutive and non-consecutive years. The results of this study are consistent with prior research on the polar bear site fidelity in the Barents Sea region (Wiig 1995, Mauritzen et al. 2001, Lone et al. 2013) where the species seems to exhibit a higher degree of philopatry than known from other parts of its range (Born et al. 1997, Taylor et al. 2001). Over the study period, home range (HR) centroid positions of individual bears were

separated by less than 20 km. This finding further confirms that long-term site fidelity is used as a spatial strategy.

Despite living in a highly dynamic environment and having great dispersal potential, individual coastal female polar bears typically remain within the same area of the Svalbard archipelago year-round. By displaying long-term site fidelity, individuals may gain important knowledge of their HR's foraging sites, geography, and routes. Animals avoid the costs of dispersal such as the need to familiarize with a new site or the energy spent to get to a new territory (Switzer 1993). Switzer (1993) argued that in unpredictable environments, philopatry is related to the quality of HRs: animals should remain within a particular territory when surrounding territories are of equal quality. According to this assumption, many areas in the Svalbard archipelago are providing suitable habitats in which coastal female polar bears can remain highly philopatric. Due to the mating system of the species, only female individuals are likely to display this behaviour. Polar bears are polygamous. Females do not have to disperse to access unrelated males for reproduction as males roam over large areas during the breeding season in the effort to maximize encounters with receptive females (Greenwood 1980, Clutton-Brock & Lukas 2012, Laidre et al. 2013). In addition, the strong philopatry exhibiting by female individuals might favour male dispersal.

The Svalbard female polar bears of the coastal ecotype exhibit a great habitat fidelity. This constancy was revealed by the estimated intra-individual variance, which only accounted for 24.7% of the total variance in annual HR size. Coastal bears, in contrast to offshore bears, have the particularity of remaining close to the Svalbard archipelago year-round (Mauritzen et al. 2001, Aars et al. 2017). Coastal bears utilize land-fast ice as a platform to move and spend a significant time foraging close to glacier fronts in spring and early summer (Freitas et al. 2012, Hamilton et al. 2017a). However, some bears also utilize the marginal ice zone in spring and summer moving away from coastal areas. Foraging strategies appear to be individually specific. These individual strategies seem to be stable over time and differ considerably between females. Individuals targeting fjords and glacier fronts as main foraging habitats likely encounter a higher abundance of prey than the ones utilizing mostly the pack ice habitat where seals are sparsely distributed. This could explain large inter-individual variations in HR size. Annual HR sizes of coastal females vary from 96 to 22 545 km². These sizes are very small compared to averages found in other parts of the species range. For example, Ferguson et al. (1999) documented an average HR size of 125 100 km² in females of the Canadian Arctic. In the Beaufort Sea region, the average was

149 000 km² (Amstrup et al. 2000) and in North East Greenland, 72 263 km² (Born et al. 1997). In Svalbard, polar bears of the coastal ecotype seem to have some of the smallest HRs yet described for the species with several females using less than 1 000 km² annually. This could be partly explained by the rather predictable ice in fjord systems and by the great amount of coastline habitat enhancing local productivity (Ferguson et al. 1999).

Intra-individual differences in annual HR size were observed for all individuals with female F having the largest variation: her HR in year 2017-2018 was 91.8% smaller than for the year 2014-2015. These intra-individual differences in movement patterns are possibly linked to external factors such as changes in environmental conditions like the local sea ice distribution (Garner et al. 1990). Additionally, internal factors such as the reproductive status of individuals could affect their movement pattern. For example, presence of cubs is linked to a decrease in range size in the female brown bear and is thought to be partly due to avoidance behaviour from males' infanticide (Dahle & Swenson 2003). Female polar bears are likely to exhibit similar behavioural patterns since adult males were reported killing and eating dependent cubs (Derocher & Wiig 1999, Amstrup 2003, Stone & Derocher 2007). The small sample size did not allow this correlation to be tested in this study.

Coastal female polar bears exhibit a strong site fidelity in all seasons. In spring, the increase in polar bear mobility is associated with a peak of prey availability as seals give birth to their pups on sea ice (Messier et al. 1992, Lydersen 1998). This increase in foraging activity was indicated by larger HR sizes in comparison to the other seasons. Distances between individual's spring HR centroids were less than 30 km on average, indicating faithfulness to foraging areas. The degree of site fidelity was even higher during the summer, fall and winter seasons, resulting in smaller HRs and shorter distances between intra-individual HR centroids than in spring. These results show that site fidelity is not restricted to the breeding period in spring and to the denning areas in winter but can be observed in every season by the female polar bears of the coastal ecotype. The smaller HR sizes found in summer, fall and winter, compared to spring, reflect a lower activity level, presumably due to limited food availability combined with more severe seasonal environmental conditions. (Messier et al. 1992).

As predicted, a strong relationship between spatial proximity and genetic relatedness exists in Svalbard coastal female polar bears. Relatives were found in very close proximity in the Svalbard archipelago year-round. This observation extends the findings of Zeyl et al.

(2009b), who documented a social structure based on female kin in the Barents Sea sub-population during the mating season in spring. All annual HRs belonging to related bears were found to overlap with the only exception of one comparison between the two sisters Ea and Eb in year 2017-2018 and 2015-2016 respectively. Their annual HRs were not overlapping but were only 15 km apart (centroids distance). On average, only 19.5 km (range=2-52 km) separated annual HR centroids of mothers-daughters and sisters-sisters. This negative correlation between distance and relatedness was weaker in spring relatively to the other seasons. This is perhaps due to an increase in HR size during this crucial hunting period when individuals widened their core areas in search of food resulting in larger distances between individuals. Female kinship structures exist in other species of ursids: in the brown bear, the social organization is based on a strong female kinship structure where relatedness determines proximity and HR overlap among females (Støen et al. 2005, Moyer et al. 2006, Zedrosser et al. 2007). Støen et al. (2005) have found an average dispersal distance of 15.7 km between closely related female brown bears and showed a correlation between relatedness and HR overlap in the species. Despite living in very different environments, the brown bear and the polar bear are sister species exhibiting similar patterns of female kin (Yu et al. 2004, Støen et al. 2005). The close proximity among related animals could be linked to the nature of their surroundings. Natal philopatry might be favoured when familiarity to foraging areas is crucial for survival (Waser et al. 1983, Lawson Handley & Perrin 2007). In the black bear, Hopkins (2013) showed, using genetic data, that mother-offspring social learning is a mechanism partly responsible for the choice of foraging sites at adulthood. Adult female polar bears may benefit from remaining within or near their mother's HR. They might use some of their knowledge of the terrain and important foraging sites gained alongside their mother before weaning resulting in a potential increase of fitness.

Additionally, tolerance and cooperation through kin can favour natal philopatry (Waser et al. 1983, Silk 2007, Clutton-Brock & Lukas 2012, Odden et al. 2014, Smith 2014). Such mechanisms have been found mostly in gregarious species compare to solitary ones (Silk 2007, Dobson et al. 2012). In the brown bear, Zedrosser et al. (2007) hypothesized that the increase in tolerance among related females decreases the probability of natal dispersal. The percentage of HR's overlap and the proximity among related female polar bears suggest that individuals manifest a certain degree of tolerance towards each other. Although polar bears lack territoriality, individuals may fight as a result of intra-specific competition for killed preys or carcasses (Stirling 1974). This antagonistic behaviour could potentially be

reduced or absent among related bears through kin recognition. The mechanisms behind kin recognition are unknown for the polar bear but are documented in some other species of mammals. Mateo (2002) showed that in Belding's ground squirrels (*Spermophilus beldingi*), individuals produce odours that correlate with relatedness. In the European polecat (*Mustela putorius*), a solitary mustelid species, Lodé (2008) suggested that recognition might be based on familiarization rather than on specialized kin recognition systems. In this case, familiarization influences behaviour and may reduce antagonistic encounters (Tang-Martinez 2001, Lodé 2008). In coastal female polar bears, mother-daughter and sister-sister pairs may maintain familiarity by overlapping their range. Whether the close proximity between related coastal female polar bears increases individual fitness through cooperation or tolerance remains unknown.

The findings of this study are restricted to the movement patterns of female polar bears of the coastal ecotype. Individuals of the offshore ecotype also exhibit site fidelity: a repeatability in movement patterns of offshore bears has been documented by Mauritzen et al. (2001). They suggested that this long-term fidelity was likely imposed to the animals by the sea ice advance and retreat. This does raise the question: do polar bears of the Barents Sea region belonging to the offshore ecotype exhibit a similar female kin structure than the one of the coastal females? To answer this question, one will face some great challenges: the elusive nature of offshore bears, which are not resident to the archipelago, results in a very low likelihood of recapture of related females.

In Svalbard, profound changes in sea ice conditions are affecting the Arctic marine mammals (Kovacs et al. 2011). By remaining highly philopatric, coastal female polar bears are particularly vulnerable to climate change as they ultimately depend on local environmental conditions. Sea ice decline affects predator-prey dynamics, one example being a decrease in the degree of spatial overlap between ringed seals and polar bears (Hamilton et al. 2017a). Coastal fast-ice areas, particularly the ones found close to glacier fronts, represent an essential foraging habitat for polar bears in Svalbard (Freitas et al. 2012). Hamilton et al. (2017a) showed that polar bears spent significantly less time at glacier fronts during summer and fall after the major loss of sea ice that occurred in 2006. The bears increased their proximity to nesting-ground bird colonies, demonstrating a shift in their foraging food sources (Prop et al. 2015, Hamilton et al. 2017a). The increase in land use in late summer and fall, when the sea ice cover is at its minimum, affects body condition, recruitment and survival (Rode et al. 2014, Prop et al. 2015, Atwood et al. 2016, Hamilton et al. 2017b). With

increasing loss of sea ice, the bears may be forced to modify their space-use strategy by exhibiting a lower degree of philopatry. Consequently, future alteration of the sea ice habitat around Svalbard will continue to have profound impacts on female polar bears of the coastal ecotype, particularly on the individuals that restrict their space use to a very small region of the archipelago.

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6 Appendix

Figure 8

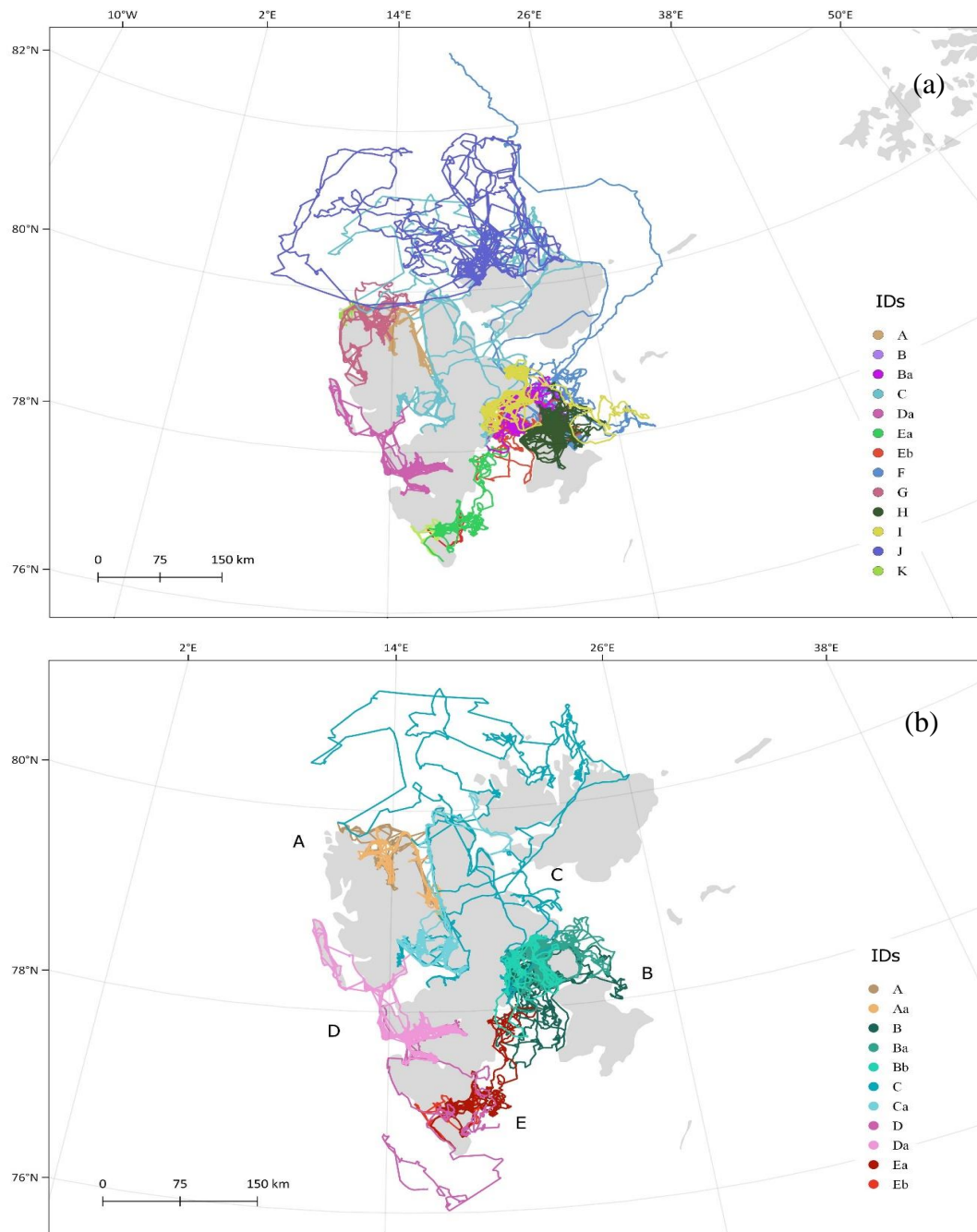


Figure 8. All tracks used in the present study of the coastal female polar bears instrumented in the archipelago of Svalbard between 2011 and 2019. (a) Tracks of the females used for the intra-individual analysis (n=13). (b) Tracks of the related females forming 5 matrilineal groups used for the kinship analysis (n=11)

