Using spatial autocorrelation to quantify the effects of sea ice fragmentation on polar bear movement in Hudson Bay

by

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Abstract

Habitat fragmentation occurs when continuous habitat gets broken up as a result of ecosystem change. While commonly studied in terrestrial ecosystems, Arctic sea ice ecosystems also experience fragmentation, but are rarely studied in this context. Most fragmentation analyses are conducted using patch-based metrics, which are potentially less suitable for sea ice that has gradual changes between sea ice cover values, rather than distinct patches. Thus, using an integrated step selection analysis, I compared the predictive power of a patch-based metric to a more novel metric, the variation in local spatial autocorrelation of sea ice cover over time. I used satellite telemetry data from 39 adult female polar bears (*Ursus maritimus*) in Hudson Bay to examine the relationship between bear movement and their sea ice habitat using Advanced Microwave Scanning Radiometer 2 data during sea ice break-up in May through July from 2013-2018. Spatial autocorrelation resulted in better model fits across 64% of individuals, although both spatial autocorrelation and patch-based metrics were more effective in predicting movement patterns than habitat selection. After determining the effectiveness of spatial autocorrelation for quantifying fragmentation, I used this metric to explore individual variation in multiple aspects of polar bear migratory movement to land during break-up. In late break-up, bears that moved through habitat with higher variability in spatial autocorrelation of sea ice cover were correlated with increased path tortuosity. As well, individuals arrived on land significantly later as paths in late break-up moved through sea ice with increasing variation in spatial autocorrelation. Reproductive status of adult female polar bears had no effect on the variability of sea ice an individual travelled through. Variation in spatial autocorrelation of sea ice provides a means of summarizing a complex and dynamic habitat and can be used to understand individual variation in polar bear movement and ecology.

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Chapter 1

1 Introduction

Habitat fragmentation is the disruption of continuous habitat into patches, causing habitat loss or isolation (Wilcove et al., 1986, Fahrig, 2003). The major components of fragmented habitat are patches, matrix, and corridors (Wilcove et al., 1986, Fahrig, 2003, Debinski, 2006, Falcy and Estades, 2007). Patches are the remaining usable habitat for a species or group of species and are the focus of the majority of fragmentation analyses (Bender et al., 2003, Fahrig, 2003, Schtickzelle and Baguette, 2003). The size, shape, and distribution of habitat patches in a fragmented landscape affect how severely an organism experiences fragmentation, and species in the same habitat can react differently to fragmentation based on their preferred habitat and movement abilities (Hill et al., 1996, Bender et al., 2003, Godefroid and Koedam, 2003,). Matrix exists between patches, it is considered the main isolating factor in a fragmented habitat, and varies based on habitat type, the fragmentation cause, and the species (Henle et al., 2004, Schooley and Wiens, 2004, Debinski, 2006).

Corridors or stepping stones create connections between habitat patches, composed of habitat that is more easily traversed than the matrix but lesser in quality than patches. Corridors and stepping stones allow for animal movement between patches (Tigas et al., 2002, Haddad and Tewksbury, 2005, Falcy and Estades, 2007). The effectiveness of corridors is restricted in habitats with matrix that has higher resistance to movement (Baum et al., 2004) and enlarged patch sizes are more effective than the corridor connectivity in maintaining populations (Falcy and Estades, 2007). The extent of patch isolation can be the result of the hospitability of the matrix and the presence of corridors (Ricketts, 2001, Debinski, 2006). Insufficient connectivity between patches can lead to genetic isolation between populations (Templeton et al., 1990, Lino et al., 2018). In a non-fragmented landscape, gene flow occurs between populations (Slatkin, 1987), but when fragmentation occurs that gene flow is reduced or stopped which leads to genetic differentiation between populations (Keller and Largiader, 2003, Yamamoto et al., 2004). Further, this isolation can lead to depressed genetic diversity and increased inbreeding within these isolated populations which may affect fitness (Templeton et al., 1990, Andersen et al., 2004, Dixo et al., 2009).

Habitat fragmentation is not restricted to landscapes that have undergone a physical change to create patches and matrix. Islands are pre-existing habitat patches, where fragmentation is intrinsic to the structure of the habitat itself (MacArthur and Wilson, 1967, Quinn and Harrison, 1988, Jenkins et al., 2016). Island archipelagos, although different in many ways from landscape fragmentation, still exhibit isolation from other patches or islands, immigration, emigration, and can have some degree of connectivity (Quinn and Harrison, 1988, Jenkins et al., 2016). In climates where the open water between islands freezes on an annual basis the connectivity between those patches or islands is greatly impacted by temporal variability in sea ice presence (Geffen et al., 2007, Jenkins et al., 2016). Sea ice formation between islands provides a corridor whereby species can immigrate, emigrate, and increase gene flow between populations that might otherwise be isolated (Geffen et al., 2007, Norén et al., 2011, Jenkins et al., 2016). For example, Peary caribou (*Rangifer tarandus pearyi*) in northern Canada use sea ice corridors to move between islands, but with sea ice decline their population viability is threatened due to increased isolation (Jenkins et al., 2016).

Many species rely on sea ice as their primary habitat (Johannessen and Miles, 2011). Sea ice is highly dynamic, with much of it going through annual freeze-thaw cycles, and its distribution is affected by ocean currents, gyres, and wind currents (Markham, 1986). Annual sea ice cycles result in an ice-free season, and a sea ice season, punctuated by periods of freeze-up and break-up (Gagnon and Gough, 2005, Mahoney et al., 2014, Stern and Laidre, 2016). Thus, the species that live on sea ice experience habitat fragmentation, most notably during the break-up period as the ice melts, when fragmentation happens at an accelerated rate (Sahanatien and Derocher, 2012).

Many factors affect the structure and function of an ecosystem, including latitude, climate, evolutionary history, and connectivity to surrounding ecosystems. Compared to other ecosystems across the globe the Arctic exhibits lower diversity across multiple levels of the food web, primarily the result of extreme climate at high latitudes (Kaplan et al., 2003, Callaghan et al., 2004). Although they are most commonly characterized by low primary productivity (Summerhayes and Elton, 1923), Arctic ecosystems are highly interconnected (Wirta et al., 2015).

Arctic marine ecosystems are characterized by seasonal or perennial sea-ice cover, and a community of organisms that rely on the presence of sea ice to varying degrees (Schunemann and Werner, 2005, Freitas et al., 2008, Mallory et al., 2010, Regehr et al., 2010). Due to low temperatures, and seasonal variation in both photoperiod and primary production, many Arctic marine species are endemic to the region, exhibiting specialization to this habitat (Wassmann et al., 2011, Darnis et al., 2012). Pelagic phytoplankton create the foundation for Arctic marine food webs, as the source of primary production (Matishov et al., 2017). Primary productivity in Arctic ice-covered ecosystems is dominated by sympagic (ice-associated) carbon that support the food web all the way up to polar bears (*Ursus maritimus*), the top of the Arctic marine food web (Hobson and Welch, 1992, Brown et al., 2018). Ecological processes and life cycles for many Arctic marine organisms are closely tied to the presence, absence, and seasonality of sea ice

(Arndt and Swadling, 2006, Bluhm and Gradinger, 2008, Leu et al., 2011). Changes in sea ice area, thickness, or duration of cover have the potential to endanger the organisms that inhabit Arctic marine ecosystems (Flato and Brown, 1996).

Sea ice is complex and dynamic. Ice undergoes annual cycles corresponding to the seasons, which vary by location (Markham, 1986, Stern and Laidre, 2016). During the summer, sea ice declines, and in its most southern extent, all ice melts, whereas in regions closer to the pole the total extent of ice cover is reduced, but some ice remains year-round. The ice that remains and is then built upon as winter returns is multiyear ice. Multiyear ice is important for ecosystems for a variety of reasons, ranging from habitat for ice-associated microbes (Palmisano and Sullivan, 1983), to maternal denning areas for polar bears (Amstrup and Gardner, 1994). In areas without multiyear ice organisms will spend the ice free season in the water or on land, depending on the species (Freitas et al., 2008, Atwood et al., 2015, Pongracz and Derocher, 2017). Over the past 40 years the length of the sea ice season has declined across the Arctic, with the number of ice-free days increasing by 5 to 41 days per decade (Stern and Laidre, 2016).

Climate change not only affects sea ice characteristics but also the organisms that depend on it (Hunt et al., 2002, Serreze and Barry, 2011, Wassmann et al., 2011, Jenkins et al., 2016). The effects of sea ice loss include changing growth of sympagic phytoplankton, which can create a trophic mismatch for the organisms that rely on this primary production (Post et al., 2013). At a larger scale, sea ice loss also affects marine mammals (Burek et al., 2008, Laidre et al., 2008, Post et al., 2013, Jenkins et al., 2016). There are multiple marine mammals that use sea ice as primary habitat, and all which inhabit regions with an annual ice cycle experience a period of intense habitat fragmentation when the ice melts (Gagnon and Gough, 2005, Regehr et al., 2007). Marine mammals exhibit multiple uses for sea ice, including habitat for mating, giving birth, raising offspring, moulting, resting, and foraging on ice-associated prey (Laidre et al., 2008, Kovacs et al., 2011, Wassmann et al., 2011). Many species of seal rely on ice for pupping, raising offspring, and moulting; with earlier break-up related to climate warming the recruitment and survival of these species is being threatened (Ferguson et al., 2005, Kovacs et al., 2011). The location of sea ice is often important, as it allows many species to haul out over shallow water to remain close to high productivity regions for foraging (Bluhm and Gradinger, 2008, Kovacs et al., 2011, Wilson et al., 2016). Polar bears are highly ice-associated, not only sensitive to the presence of ice, but also to the structure of their sea ice habitat (Ferguson et al., 2000, McCall et al., 2016, Wilson et al., 2016).

Polar bears live, travel, mate, and access prey on sea ice so alterations to its presence or structure may reduce their habitat quality (Sahanatien and Derocher, 2012, McCall et al., 2016). They prey largely on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Smith, 1980, Thiemann et al., 2008), and gain access to prey via ice, therefore the seasonality of sea ice conditions results in fluctuations in availability, distribution, and abundance of seals, affecting hunting success (Stirling and Archibald, 1977, Kingsley et al., 1985, Galicia et al., 2016). Sea ice phenology also influences polar bear migration patterns with bears spending winters on ice and migrating onto land or moving northward to multiyear ice as it retreats in spring (Durner et al., 2009, Cherry et al., 2013). Reproduction is associated with migration as mated females migrate to land or pack-ice to create maternity dens after the mating season (Amstrup and Gardner, 1994, Stirling et al., 2016). As sea ice cycles change, the many aspects of polar bear survival connected to ice are being threatened, and as of yet, it is unknown if and how polar bears will adapt to these changes.

Polar bears are distributed in 19 populations across the circumpolar Arctic (IUCN/SSC PBSG 2010). Sea ice cover is declining across all 19 populations, with the most extreme loss occurring in the Barents Sea and Arctic Basin (Stern and Laidre, 2016). Those in Hudson Bay are the lesser impacted subpopulations (Stern and Laidre, 2016), but are still of particular interest as they extend furthest south and may be impacted by temperature fluctuations and changes in sea ice in the future (Macdonald and Kuzyk, 2011). Hudson Bay polar bears are also the best studied of all subpopulations (Vongraven et al., 2012). Under two separate Canadian climate models, Hudson Bay is predicted to experience reduced ice cover and an extended ice-free period over time (Gough and Wolfe, 2001). Polar bear sea ice habitat in Hudson Bay is predicted to deteriorate to such an extent that polar bears may struggle to persist there after 2050 (Castro de la Guardia et al., 2017). There are three polar bear subpopulations that utilize Hudson Bay, I focus on the Western Hudson Bay (WH) subpopulation from 2013-2018 in this thesis. WH polar bears spend the ice-free season on land along the south western coast of Hudson Bay.

Quantifying the effects of sea ice loss and fragmentation are important for understanding how polar bears, and other ice-associated species, will respond to a changing Arctic. The variability in sea ice adds a layer of complexity to this, as habitat cannot be classified in the same way that static landscapes are. Therefore, in Chapter 2 I compare a novel method of sea ice fragmentation quantification, using spatial autocorrelation, to common patch-based methods. The effectiveness of these two metrics will be measured using integrated step selection analyses to determine if they are effective predictors of polar bear habitat selection and movement patterns. In Chapter 3 I apply my spatial autocorrelation sea ice metric to further explore how this metric can be used to analyze individual variation in polar bear movement during migration to land. In Chapter 4 I discuss the broader scope for the use of a spatial autocorrelation sea ice metric, to increase both spatial and temporal applications, as well as the species considered. By exploring sea ice fragmentation, I aim to further develop the overall understanding of polar bear habitat use and how habitat variability affects their movement patterns.

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Chapter 2

2 Comparing sea ice habitat fragmentation metrics using integrated step selection analysis

2.1 Introduction

Habitat fragmentation is the separation of continuous habitat into smaller, isolated patches, which often occurs with habitat loss (Wilcove et al., 1986, Fahrig, 2003). As the amount of available habitat decreases, the distance between patches often increases resulting in greater fragmentation (Andren, 1994, Goodsell and Connell, 2002). The characteristics of the matrix between patches affect how fragmentation influences wildlife, based mainly on how organisms move among patches (Taylor et al., 1993, Boudjemadi et al., 1999, Sondgerath and Schroder, 2002).

For ice-associated species, variation in sea ice cover and open water can create a distinction between habitat and matrix, comparable to patches in fragmented terrestrial landscapes (Sahanatien and Derocher, 2012). Arctic sea ice is a dynamic habitat in both space and time, which is affected by ocean currents, winds, and temperature (Markham, 1986, Wang et al., 1994, Saucier et al., 2004, Stern and Laidre, 2016). Sea ice undergoes annual cycles, concurrent with the seasons, where ice thaws during break-up and southern Arctic regions become ice free in summer. Freeze-up occurs in the winter, and sea ice reaches its maximum extent in March (Stern and Laidre, 2016). Break-up reflects a period where sea ice declines rapidly and habitat continually changes until it is lost (Saucier et al., 2004, Stroeve and Notz, 2018). Although the timing follows a predictable annual pattern, the fast-paced change means the length, start, and end of break-up are variable (Gagnon and Gough, 2005). Sea ice change is variable across the Arctic, but over the last four decades, all regions have had an increased ice-free season and a decrease in cover when ice is present (Comiso, 2012, Parkinson, 2014, Stern and Laidre, 2016). Temporal variation in sea ice cover adds complexity to spatial variation, affecting the species that utilize this habitat.

Fragmentation analyses are often conducted using patch-based metrics, such as patch size, distance between patches, and patch shape (i.e. Bender et al., 2003, Sahanatien and Derocher, 2012, Liu et al., 2014, Petrasova-Sibikova et al., 2017). Patch-based metrics have been used in many different ecosystems and scales to classify landscape pattern and to evaluate how landscapes change over time (Haddad et al., 2015). In most ecosystems, annual or even decadal changes in fragmentation are often sufficient to understand how wildlife will react to fragmentation (Echeverría et al., 2006, Keleş et al., 2008, Reddy et al., 2013). However, in some ecosystems like Arctic sea ice, patch-based metrics may miss the crucial fine scale spatial variation and temporal dynamics of fragmentation that occur on daily time scales.

Despite the obvious parallels with fragmentation of terrestrial systems, use of patch-based metrics to understand wildlife behavior in Arctic systems is not common. This is in part, because gradual changes between sea ice cover and the temporal dynamics make the delineation of daily patches data intensive and thus, analytically challenging. Alternative approaches that have been used to quantify habitat fragmentation in dynamic urban landscapes where patch edges are not particularly discrete, are spatial autocorrelation metrics (Roberts et al., 2000, Pearson, 2002, Fan and Myint, 2014, Fan et al., 2015). There is potential for spatial autocorrelation metrics to address the spatially dynamic component of sea ice habitat because of their ability to quantify fragmentation without the creation of patches.

Spatial autocorrelation can be used to quantify habitat continuity at a local scale, which describes variability in habitat cover across an entire habitat. In terms of sea ice, positive spatial autocorrelation reveals regions of similar sea ice cover. Negative spatial autocorrelation reflects regions of discontinuous habitat, where sea ice cover is inconsistent. Sea ice is not only complex spatially, but also temporally, thus the spatial variation quantified by local spatial autocorrelation can include temporal variation by considering the variation in spatial autocorrelation over time.

Many species in Arctic marine ecosystems are partially or wholly ice-associated. The presence, absence and variability of sea ice impacts the space use of organisms that live in, on, and underneath the ice (Arndt and Swadling, 2006, Mallory et al., 2010, Wassmann et al., 2011, Post et al., 2013). Polar bears (*Ursus maritiumus*) are a species strongly associated with ice fragmentation as they are only able to stay in the marine environment when sea ice is present (Stirling et al., 1977, Stirling et al., 1993, Ferguson et al., 2001, Cherry et al., 2013). They live, travel, access prey, and mate on ice so alterations to its presence, structure, or fragmentation reduces their habitat quality (Sahanatien and Derocher, 2012, McCall et al., 2016). Polar bears prey largely on phocid seals (Smith, 1980, Thiemann et al., 2008), and gain access to prey via sea ice, therefore the seasonality of sea ice conditions results in fluctuations in availability, distribution, and abundance of seals, affecting a bear's hunting success (Stirling and Archibald, 1977, Kingsley et al., 1985, Galicia et al., 2016).

Polar bear habitat use varies seasonally, where bears select for high ice cover when it is available and more open ice during seasons when closed ice is less available (Mauritzen et al., 2003, McCall et al., 2016, Wilson et al., 2016). Ice cover selected by polar bears for habitat varies regionally and with methodologies for quantifying selection, but ≥85% ice cover tends to be identified as ideal habitat that is most selected for when available. Cover ≥60% is a common delineation for encompassing both preferred and ideal habitat, which would be available to bears during periods of sea ice break-up and freeze-up (Mauritzen et al., 2003, Sahanatien and

Derocher, 2012, Cherry et al., 2013, Laidre et al., 2015, Cherry et al., 2016, Lone et al., 2018). Quantifying changes in fragmentation during break-up may be crucial for understanding hunting success, energetics, migration, and the initiation of on land fasting period (Watts and Hansen, 1987, Sahanatien and Derocher, 2012, Cherry et al., 2013).

The objective of this study is to compare whether spatial autocorrelation or patch-based metrics of habitat fragmentation better describe polar bear movement. Both spatial autocorrelation and patch-based metrics are used in integrated step selection analyses to analyze polar bear habitat selection and movement patterns. I hypothesize that the spatial autocorrelation metric will be the better descriptor of polar bear movement because of the detail in sea ice cover is retained by avoiding the creation of patches.

2.2 Methods

2.2.1 Study Area

Hudson Bay, Canada, (Figure 2.1) is a shallow (mean depth of 125 – 150 m) inland sea, covering 1 240 000 km^2 (Macdonald and Kuzyk, 2011). The Bay undergoes an annual cryogenic cycle with general trends of sea ice present from November to June followed by an ice-free period from July to October (Gough and Wolfe, 2001). Ice presence and absence are punctuated by periods of ice break-up in May – July and freeze-up in November – December (Castro de la Guardia et al., 2017). This study focuses on the habitat conditions of polar bears in the Western Hudson Bay (WH) population. In the past four decades this population has declined by ~30%, which has been correlated with a decline in the length of ice presence (Lunn et al., 2016).

2.2.2 Animal Data Collection

Adult (≥5 years old) female polar bears were immobilized from 2012 - 2017 via remote injection of Zoletil® (Virbac S.A., Carros, France) following standard protocols (Stirling et al., 1989) as part of ongoing, long-term research on the ecology of the WH population (e.g., Ramsay and Stirling, 1988, Derocher and Stirling, 1995, Stirling et al., 1999, Regehr et al., 2007, Lunn et al., 2016). Capture and handling protocols were reviewed and approved annually by the Environment and Climate Change Canada, Prairie and Northern Region Animal Care Committee and the University of Alberta Biological Sciences Animal Policy and Welfare Committee in accordance with the Canadian Council on Animal Care. Bears were fitted with Argos or Iridium satellite-linked geographic position system collars (Telonics, Mesa, AZ, USA), programmed to record locations at 4-hour intervals. Locations where movement would be biologically impossible were removed (i.e. >30 km/h). The study area was delineated by a 100% minimum convex polygon of telemetry locations, trimmed to the Hudson Bay coastline (Figure 2.1).

2.2.3 Quantifying Fragmentation

Monthly ice coverage data was obtained from the National Snow and Ice Data Center (Boulder, CO). The data were collected via the Advanced Microwave Scanning Radiometer 2 (AMSR-2) on the GCOM-W1 platform with a resolution of 6.25 km x 6.25 km grid cells from 2013 – 2018 (Spreen et al. 2008). This is the highest resolution sea ice cover data currently available in Hudson Bay. Each grid cell, or pixel, had a value from 0 – 200 defining ice cover, which was divided by 2 to give the percentage sea ice coverage. Within each pixel, ice cover <60% was considered suboptimal habitat and ≥60% was optimal habitat based on other studies where both preferred and ideal habitat were defined (Mauritzen et al., 2003, Sahanatien and Derocher, 2012, Cherry et al., 2013, Pilfold et al., 2014, Laidre et al., 2015, Cherry et al., 2016, Lone et al., 2018). I used ArcGIS version 10.5.1 (Environmental Systems Research Institute, Redlands, CA) to classify the daily ice cover as either optimal or suboptimal habitat. I computed global percentage of optimal habitat (PHAB: called PLAND in the software) using FRAGSTATS (McGarigal et al. 2012) to determine amount of habitat available daily from 2013 to 2018. In this context global refers to the entire study area. I examined the break-up period, defined by the first date in any year where PHAB dropped and remained below 95%, until the day before PHAB dropped and remained below 5%. I further separated the break-up period into early and late, defined by the date that PHAB reached 50% in each year.

To create my local habitat fragmentation metrics for comparison I used a moving window around each pixel to scale fragmentation to the local potential habitat an individual bear could experience in one day. Collared bears travelled a mean distance of 21 km/day (SD = 5.3 km/day, range: 11 - 31 km/day) during break-up. I used 21 km as a radius to define an area of potential daily use. This resulted in an area of 1385 km^2 which I translated into ~35 6.25 x 6.25 km pixels, which was rounded to a 25 pixel (5 pixel x 5 pixel) moving window, because local analyses required a central pixel (Figure 2.2).

To create a spatial autocorrelation metric to compare to patch-based metrics I used local Geary's *c*, a local indicator of spatial association (Haining, 1993, Anselin, 1995), to determine daily spatial autocorrelation of sea ice cover during break-up across all years. The statistic for each pixel was calculated using the 5 x 5 pixel moving window defined above. Pixels around the edge of study area that did not have sufficient surrounding pixels to fill the moving window were assigned null values. I used Geary's *c* because it focuses on dissimilarity, where greater values reflect negative spatial autocorrelation (Anselin, 1995, Anselin, 2018) and identify regions where sea ice cover is more variable and thus fragmented. Geary's *c* values can range from 0 to unspecified values > 1. Values close to 0 reflect positive spatial autocorrelation and large values reflect negative spatial autocorrelation which describes fragmented, discontinuous sea ice.

To assess the temporal dynamics of fragmentation I used the variation in spatial autocorrelation at each pixel in space over time. In each year, the standard deviation of the Geary's *c* value, or spatial autocorrelation standard deviation (SASD), for each pixel in the study area across early break-up was calculated and the resulting values were plotted. SASD was calculated for late break-up, resulting in two SASD raster files per year. Pixels with high SASD reflect locations where sea ice cover is highly variable and fragmentation most dynamic.

The same 5 x 5 pixel moving window as defined above was used for analysis of two local patch-based metrics, total edge (TE) and percent habitat (PHAB), using FRAGSTATS metrics TE and PLAND via the *landscapemetrics* package in R (R Core Team 2018, *v1.1*, Hesselbarth et al., 2019). I chose TE and PHAB because melting causes sea ice patches to be spatially correlated during break-up which precludes the use of configuration metrics in FRAGSTATS (Sahanatien and Derocher, 2012). The two habitat patch types were defined as above, as optimal or suboptimal habitat, and optimal habitat was used as the patch type of interest in analyses which resulted in separate daily raster files for local TE and local PHAB. High TE values reflect regions with more edge and thus more fragmented habitat, and lower TE reflects regions of constant habitat or non-habitat. High PHAB values reflect regions where local percent optimal habitat is high.

2.2.4 Integrated Step Selection Analysis

An integrated step selection analysis (iSSA) furthers habitat selection analysis by incorporating movement parameters (Avgar et al., 2016). The environmental covariates in an iSSA quantify habitat selection, while the interaction terms between environmental covariates and movement parameters, turning angle and step length, quantify the effect the environment has on movement. I developed four separate iSSAs using the *amt* package in R (Signer et al., 2019) to determine if SASD or PHAB and TE were better as predictors of habitat selection and movement patterns by polar bears. Analyses were separated into early and late break-up, resulting in SASD early, SASD late, PHAB/TE early, and PHAB/TE late models. Polar bear locations were resampled by burst, consisting of consecutive bursts of ≥3 steps, to account for missing location points. Each resulting step was matched to 10 random steps, which were plotted following a gamma distribution for step length, and a von Mises distribution for turning angle (Avgar et al., 2016). To confirm that the resolution of habitat data was suitable for analyses I found that only 23% of steps start and end in the same environmental pixel which allowed sufficient variation in used and random steps to determine habitat selection.

For SASD models, candidate environmental covariates of daily sea ice cover (ice), and SASD for early and late break-up were extracted at the end of both used and random steps. I also included the square of daily ice cover to test for a non-linear relationship. I extracted the distance from each point to Cape Churchill on the west coast of Hudson Bay at the end of each step as a proxy for summer refuge (refuge) as a candidate covariate as well (Figure 2.1). I tested interaction terms: SASD with the natural log of step length, and SASD with the cosine of turning angle, where SASD was extracted at the start of each step. These interaction terms examine how individual movement is affected by changes in SASD. Analysis was conducted for each bear in early and late break-up separately.

Candidate environmental covariates for patch-based models included daily sea ice cover (ice), PHAB, and TE, and were extracted at the end of used and random steps. Similar to above, the distance to summer refuge (refuge) was also a candidate covariate extracted at the end of each step. I also included PHAB and TE interacting with the natural log of step length, as well as PHAB and TE interacting with the cosine of turning angle, using PHAB and TE extracted at the start of each step to analyze movement. I examined all daily covariates for collinearity and excluded any with Pearson correlation values >|0.6| from the same models. Colinear covariates were tested in separate models and the one with better fit was retained. Models were run for individuals in both early and late break-up. Individuals with all locations in regions of solely optimal or suboptimal habitat locally resulted in no variation in PHAB and were removed from further analysis.

In each of the four model groups, SASD early, SASD late, PHAB/TE early, and PHAB/TE late, all combinations of all corresponding candidate covariates and interactions outlined above were tested for each individual. Akaike Information Criteria (AIC) was used for each individual in each group to determine model of best fit, where the top-ranked model was > 2 AIC lower than the next ranked model. The most common top ranked SASD and PHAB/TE models across all individuals in early and late break-up were chosen to facilitate the comparison between SASD and PHAB/TE. For each individual, I compared the Cox & Snell pseudo R-squared values of the top SASD and PHAB/TE iSSA models to determine which fragmentation metric had better model fits (Cox and Snell, 1989). Results are presented as beta coefficients for each covariate in the top models and 95% confidence intervals.

2.3 Results

There were 39 collared polar bears in early break-up, and 29 of those maintained locations into late break-up. Maximum speed of bear movement was 15.5 km/h.

The global percent of optimal sea ice habitat (PHAB) was similar across all years, with a significant sigmoidal trend in mean global PHAB during break-up (logistic regression: horizontal asymptote = 90.8%, $p < 0.001$; x-value at half asymptote = June 24, $p < 0.001$; scale = -8.7, $p < 0.001$) (Figure 2.3). Mean break-up period lasted 63 days (SD = 15.7, n = 6) and ranged from 44 days in 2014 to 81 days in 2015. The mean date for start of break-up was May 12 (range May 2 – May 29, SD = 10.0, n = 6). The mean date for end of break-up was July 14 (range July 6 – July 23, SD = 7.2, n = 6). The break-up period based on global PHAB, was May 2 to July 23. The start of the second half of break-up and was June 24, June 23, June 23, June 30, June 17, and June 26, in 2013 – 2018, respectively.

Standard deviation of local Geary's *c* (SASD) of sea ice cover for early and late break-up is shown in Figure 2.4. Late break-up in 2017 had the highest SASD, with a maximum pixel value in the study area of 1556, the next highest was late break-up in 2013, with a maximum SASD of 393. The period with the lowest maximum SASD was late break-up in 2015, with a maximum SASD of 56. There were qualitative differences in sea ice cover (Figure 2.4). Low SASD occurred consistently across all years in early break-up, mostly notably in the south-east, as this is where sea ice remains the longest and is the most intact. Conversely, the least variable regions in late break-up are open water regions, where the sea ice is lost earliest. The most variable regions in late break-up reflect regions where ice persists the longest and occurred in the south, along the south-west coast, although the specific areas of variability were not consistent across years.

For spatial autocorrelation analysis, the top iSSA model for the majority of individuals included covariates ice, SASD, and refuge, as well as the interaction between SASD and the cosine of turning angle (Table 2.1). The AIC values for multiple individuals were indistinguishable across the top three models. For 23 of the 39 individuals in early break-up the top model had beta coefficients that significantly differed from zero in ≥1 covariate (Figure 2.5a). There were 11 individuals with a significantly negative interaction between SASD and the cosine of turning angle. The negative interaction term reflects increased SASD significantly related to increased changes in the direction of travel (i.e. more deflection from a straight path from step to step). In late break-up, 17 of 29 individuals had ≥1 significant covariate in the top model (Figure 2.5b). There were 13 individuals with a significantly negative interaction term, reflecting increased changes in the direction of travel with higher SASD.

For patch-based analyses the top iSSA model for the majority of individuals included local PHAB, refuge, and the interaction between PHAB and the cosine of turning angle (Table 2.1). The AIC values for the top two models were indistinguishable for a number of individuals. Daily sea ice, TE, and PHAB could not be included in any of the same models because of collinearity. Models including PHAB had the lowest AIC of the three variables, and thus was included in the final model. Three individuals in early break-up and one in late break-up were removed as all used steps and random steps had no variation in PHAB. The top model had beta coefficients that significantly differed from zero for ≥1 of the covariates in 16 of 36 individuals during early break-up (Figure 2.5c). Nine individuals had a significant interaction between PHAB and the cosine of turning angle, reflecting increased changes in the direction of travel with increased PHAB. In late break-up, 8 of 28 individuals had significant models (Figure 2.5d). All eight of those individuals had a significant interaction reflecting increased changes in the direction of travel with higher PHAB.

In early break-up, the Cox & Snell pseudo R-squared value was higher for the SASD iSSA model in 61.1% of individuals, compared to 27.8% of individuals for the PHAB iSSA.

Similarly, in late break-up the pseudo R-squared value was higher for the SASD iSSA in 67.9% of individuals, PHAB iSSA had higher pseudo R-squared in 25% of individuals. All remaining individuals had the same pseudo R-squared values in both analyses (Table A2.1).

2.4 Discussion

Using polar bears as an ice-associated model species, I used multiple iSSAs to compare two methods of quantifying habitat fragmentation. I found that SASD resulted in better model fits than patch-based metrics when comparing different fragmentation metrics to describe polar bear habitat selection and movement patterns. Results from SASD and PHAB iSSAs explained the interaction between sea ice fragmentation and movement more effectively than they explained habitat selection.

Using variation in spatial autocorrelation over time to analyze sea ice fragmentation allows for a synthetic, yet complex spatial and temporal visualization of sea ice. SASD allowed for the summarization of habitat over time that would otherwise have to be considered on a daily scale, while still being an effective movement predictor. Break-up is often defined as a single time span (i.e. Parks et al., 2006, McCall et al., 2016), or even a single date (i.e. Stirling et al., 2004, Regehr et al., 2007, Sahanatien and Derocher, 2012). These definitions over simplify sea ice break-up, which is an important time for polar bears because it is the end of their ability to hunt seals (Stirling and McEwan, 1975, Watts and Hansen, 1987), the onset of migration (Cherry et al., 2013), and a period where their habitat becomes increasingly difficult to traverse. SASD of sea ice cover over time provides a detailed description of sea ice habitat, not just for polar bears, but for any ice-associated species, as the method can be altered to fit the spatial scale of an organism by altering the size of the moving window. The method can be further altered by using a temporal moving window to explore the effect of SASD at various time periods.

This is the first time an iSSA has been used for analyses of sea ice habitat or for polar bears. This methodology increased my ability to analyze the interactions between an ice-associated species and their temporally and spatially complex habitat. An iSSA was chosen because of its capacity to not only consider habitat selection, but also for the ability to explore how movement is affected by habitat characteristics (Avgar et al., 2016), an analytical possibility not available in an RSF or step selection function. Step length and turning angle are commonly interacted with environmental covariates to understand how movement changes with the habitat an individual is exposed to (Prokopenko et al., 2017, DeMars and Boutin, 2018). Although aspects of habitat selection by polar bears throughout the year are understood (Mauritzen et al., 2003, McCall et al., 2016, Pilfold et al., 2017), an iSSA enables the exploration of movement alongside habitat selection.

Habitat fragmentation is an important aspect of dynamic sea ice habitat, but it has not been included in previous habitat modelling for sea ice-associated marine mammals. Sea ice habitat fragmentation has been considered in a polar bear context for temporal trends (Sahanatien and Derocher, 2012), but has not been applied to habitat selection. Due to its dynamic nature, exploring the fragmented nature of sea ice habitat is complex and adding it into a habitat selection model is computationally intensive. To derive a local patch-based metric used, habitat patches first need to be created from sea ice data, then analyzed using FRAGSTATS to attain the metric outputs; for dynamic habitat such as sea ice this process must be repeated for each day. As the study area or period increases, working with data of this nature becomes increasingly analytically challenging. The creation of the SASD metric allowed me to synthesize daily sea ice fragmentation into a metric that was concise and easier to analyze, while still effectively describing the habitat and predicting the behaviour of the animals in the habitat. Spatial autocorrelation has been used in complex habitats where patches would not accurately describe the landscape (Roberts et al., 2000, Pearson, 2002, Fan and Myint, 2014), but is a novel approach for wildlife. I used spatial autocorrelation to include the intricacies of sea ice, as patches tend to create separations where realistically, they do not exist. The goal then was to expand the use of spatial autocorrelation from a metric that only describes fragmentation, to a metric that describes the temporal variability of fragmentation by focusing on the standard deviation over time. In a habitat as dynamic as sea ice, the temporal aspect is inherently important to those species that use it.

Neither SASD nor PHAB show a quantifiable effect on habitat selection, but they revealed a connection to movement. Including sea ice habitat fragmentation in an iSSA was ineffective for predicting habitat selection with either of the fragmentation metrics even though ice-associated species are affected by the temporal and spatial dynamics of sea ice. Extreme changes to sea ice habitat during break-up have an effect on behaviour and habitat use, including alterations to migration an feeding behaviour (Nilssen, 1995, Pilfold et al., 2017), but the impact of fragmentation within a habitat selection context remain unclear. McCall et al. (2016) quantified polar bear habitat selection during break-up in Hudson Bay using multiple environmental covariates including water depth and distance to various concentrations of ice. This level of habitat selection was not reflected in my analyses as I opted to keep my iSSA simple, focusing on the fragmentation metrics instead of including numerous environmental covariates. Fragmentation covariates predicted significant habitat selection in few of the individuals, but the benefit of using an iSSA is that I could consider the relationship between my fragmentation metrics and movement. Turning angle is affected by fragmentation, most prominently when fragmentation was quantified using the SASD metric.

Although SASD and PHAB were comparable, iSSAs using SASD had a better model fits for the majority of individuals. In the context of describing movement, SASD is promising because of its ability to describe the relationship between fragmentation and direction of travel. The tendency for SASD to explain movement, rather than habitat selection could relate to break-up occurring so quickly that bears are not necessarily selecting for habitat, but rather their ability to move is being affected by the variability of the habitat they encounter while break-up occurs (Cherry et al., 2013, Pilfold et al., 2017). The multiple individuals which showed more changes in directionality in regions of greater SASD could reflect forced changes in direction brought on by rapidly changing habitat. Similarly, models using PHAB, a patch-based metric, describe movement more effectively than they describe habitat selection during break-up. While this is less intuitive than the relationship between movement and SASD, greater changes in directionality in regions of higher PHAB could be a result of individuals using specific types of ice within the defined optimal habitat for hunting. This could explain why a selection signal for PHAB as a whole was not evident. My defined optimal habitat patches included sea ice cover from 60-100% so active ice is included in optimal habitat but does not make up the entirety of it. Active ice has greater movement and variation in cover, exhibits more cracks and open water than consolidated ice, and is often related to seal availability (Ferguson et al. 2001). The use of active ice could explain changes in direction of travel resulting from both hunting strategy and the dynamic nature of the ice. The grouping of sea ice into patch types could have resulted in the loss of ice variability details which were retained in SASD, thus restricting my ability to interpret PHAB results.

The response of movement and not habitat selection to habitat fragmentation could contribute to further relationships between polar bears and sea ice habitat. If fragmentation is one of the primary drivers of variation in movement, then it is possible the location and severity of fragmented ice could affect selection of other habitat covariates that have been included in other polar bear habitat selection models (i.e. Mauritzen et al., 2003, McCall et al., 2016, Wilson et al., 2016). Including habitat fragmentation in subsequent selection models allows the consideration of ecological trade-offs between movement constrained by fragmentation and accessing ideal habitat or resources. Variation in spatial autocorrelation of sea ice has the potential to quantify an aspect of sea ice habitat that has previously been ignored as an inhibitor of selection.

While not the focus of my models, the inclusion of distance to refuge in all top models, and daily sea ice cover in SASD models shows their importance to polar bear movement. Although selection for distance to refuge was not evident in most individuals, break-up is a migratory period for WH polar bears where they generally head toward land (Cherry et al., 2013, McCall et al., 2016). Aspects of local habitat and hunting activity likely affect directed movement toward refuge, resulting in a lack of selection signal. Sea ice cover is also important for polar bear movement because much of their locomotion relies on the presence of ice (McCall et al., 2016, Laidre et al., 2018). The reason for a lack of selection signal for sea ice cover is unclear but could be the result of bears using a range sea ice cover.

Perhaps most compelling in the comparison of the two fragmentation metrics is the simplicity SASD brings to a complicated system. SASD combines the variation across all days in the study into one metric while still being an effective predictor of movement. For sea ice habitat that changes daily, this approach reduced the amount of data needed in the model, but still allows changes in habitat to be considered in detail. Such an approach may prove useful in identifying important marine habitats for ice-dependent species or considering broad scale habitat change. Multiple studies have examined how a changing sea ice season is predicted to affect polar bears (i.e. Cherry et al., 2009, Kovacs et al., 2011, Sahanatien and Derocher, 2012, Castro de la Guardia et al., 2017, Laidre et al., 2018), but fine scale detail on the effects of sea ice dynamics on individual bears is lacking. Individual fitness is contingent upon the habitat they are exposed to, and success can be variable within a population due to habitat variation (Pettorelli et al., 2001, Nilsen et al., 2004). Polar bears experience different habitats at an individual level due to the dynamic nature of sea ice. Finding the variation in local scale spatial autocorrelation over break-up describes temporal and spatial sea ice patterns which can be applied at an individual scale. Patch-based metrics at a local scale can also provide local descriptions of habitat but lack the temporal concision of the SASD metric.

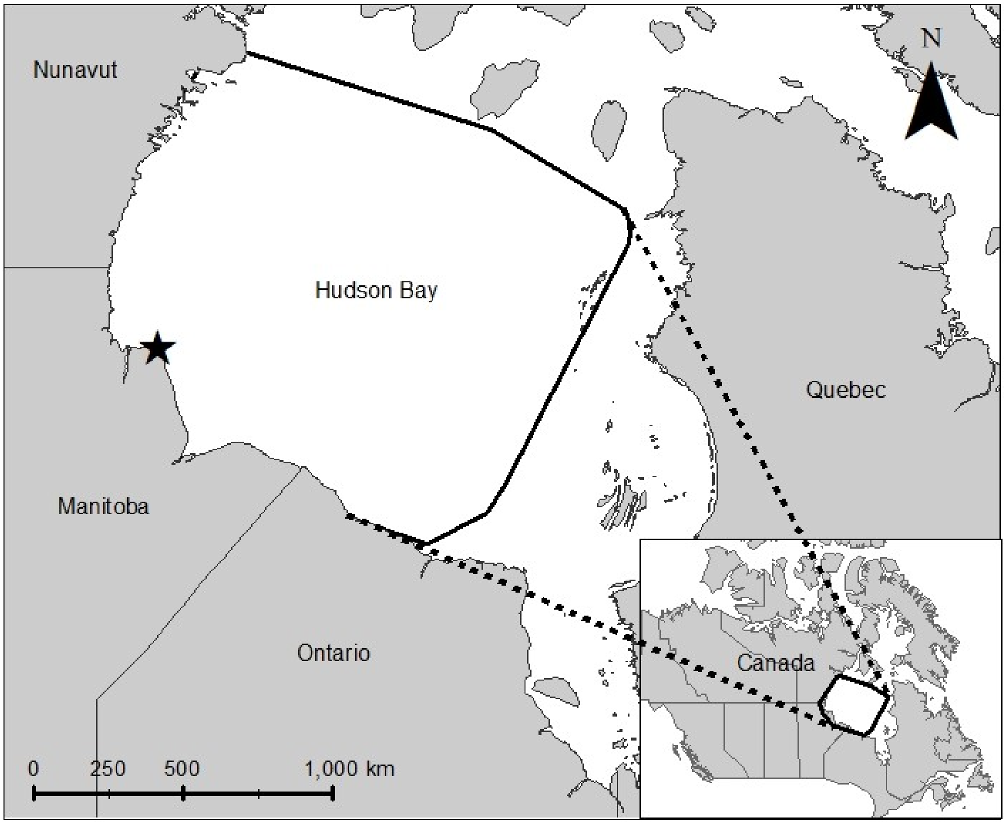


Figure 2.1 Map of Canada showing the study area in Hudson Bay outlined in black, determined with a 100% minimum convex polygon using locations of geographic position system collared adult female polar bears in the Western Hudson Bay subpopulation from 2012-2018, trimmed to Hudson Bay coastline. Cape Churchill, a proxy for polar bear summer refuge, is denoted with a star.

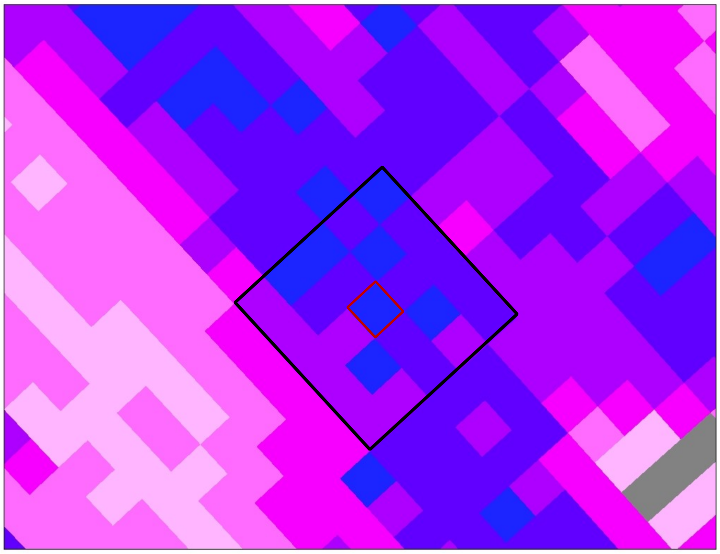


Figure 2.2 Example of moving window size (black) used to determine the local sea ice fragmentation metric value for the central pixel (red) on 6.25 x 6.25 km resolution sea ice cover data. This was repeated for each pixel in the study area.

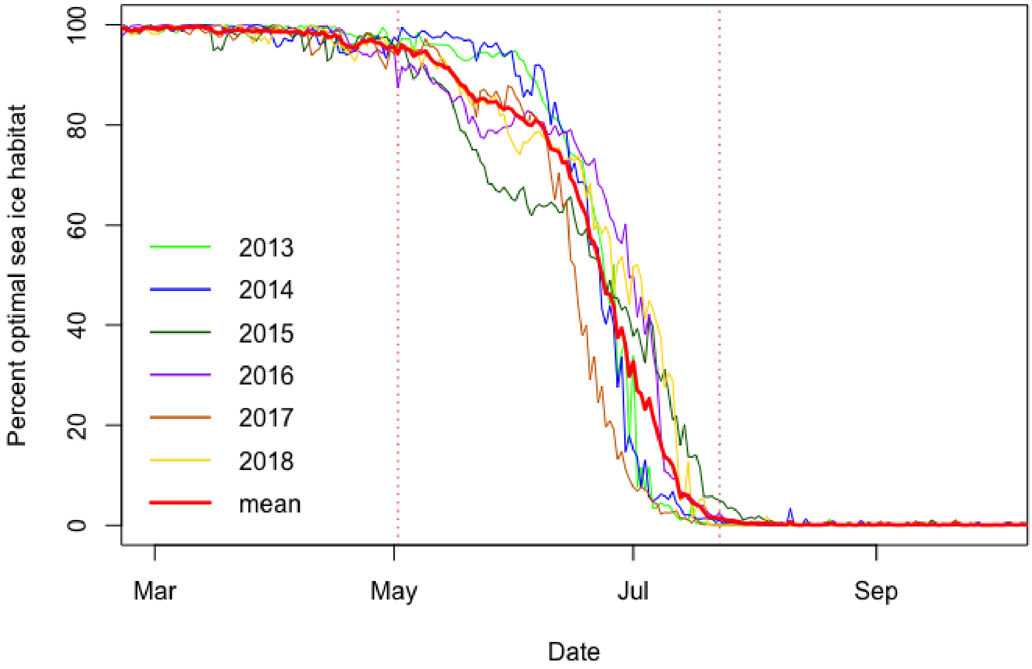
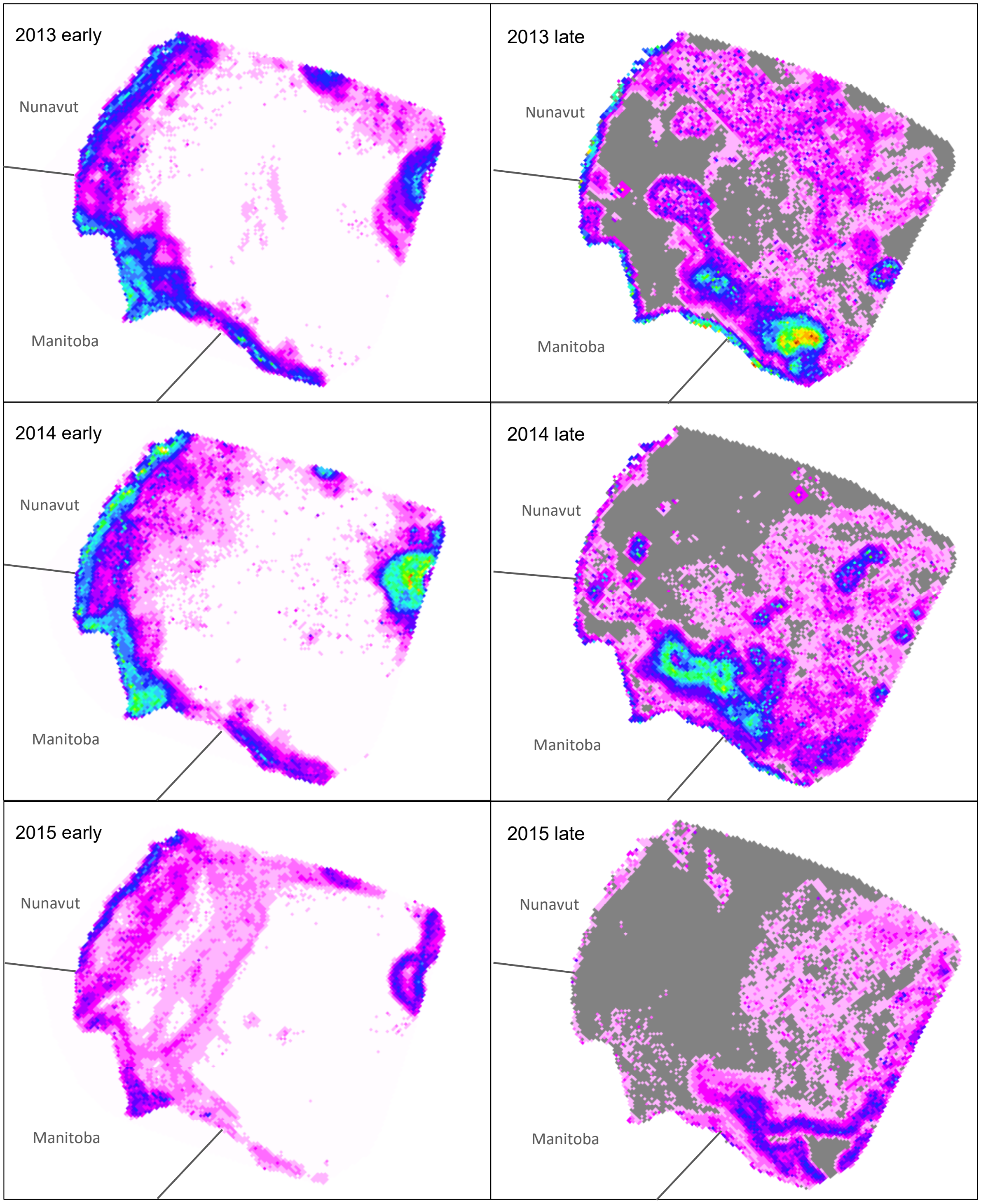


Figure 2.3 Percent of optimal sea ice habitat (ice cover ≥ 60%) available to WH polar bears in relation to year for 2013 – 2018. Vertical red dotted lines outline the start and end dates of the defined break-up period defined by earliest start of break-up (percent habitat ≤ 95%) and latest end of break-up (percent habitat ≤ 5%) in all years.


2013 early
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Manitoba
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Nunavut
Manitoba

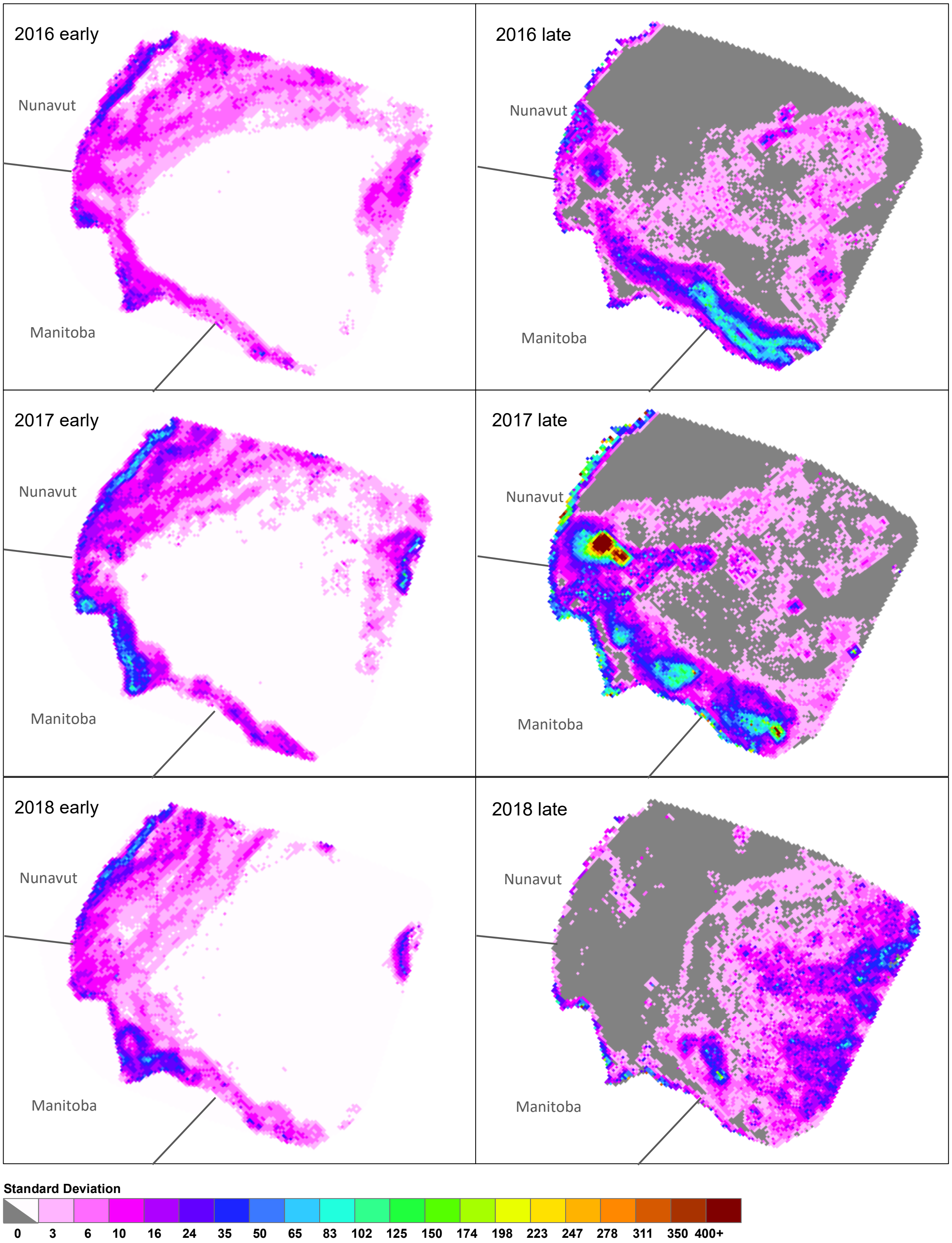
2016 early
Nunavut
Manitoba
2016 late
Nunavut
Manitoba
2017 early
Nunavut
Manitoba
2017 late
Nunavut
Manitoba
2018 early
Nunavut
Manitoba
2018 late
Nunavut
Manitoba
Standard Deviation
0
3
6
10
16
24
35
50
65
83
102
125
150
174
198
223
247
278
311
350
400+

Figure 2.4 Standard deviation of local Geary's *c* (quantified using a 5 x 5 pixel moving window) of sea ice cover in each pixel across early break-up, from May 2 to 50% optimal habitat in each year, and late break-up, from 50% optimal habitat in each year to July 23, in the Hudson Bay study area from 2013 – 2018. White zero values represent constant sea ice; grey zero values represent constant open water.

Table 2.1 Tally of the number of individuals with the lowest AIC (by Δ2 or greater) for the top three spatial autocorrelation models and the top 2 patch-based models. Highest total determined the top model.

SPATIAL AUTOCORRELATION TOP MODELS	EARLY BREAK-UP	LATE BREAK-UP	TOTAL
SASD + ice + refuge + SASD:cos(turning angle)	8	3	11
SASD + ice + refuge + SASD:cos(turning angle) + SASD:ln(step length)	8	1	9
SASD + ice + SASD:cos(turning angle)	6	2	8
No difference	17	23	40

PATCH-BASED TOP MODELS	EARLY BREAK-UP	LATE BREAK-UP	TOTAL
PHAB + refuge + PHAB:cos(turning angle)	13	5	18
PHAB + refuge + PHAB:cos(turning angle) + PHAB:ln(step length)	3	4	7
No difference	23	20	43

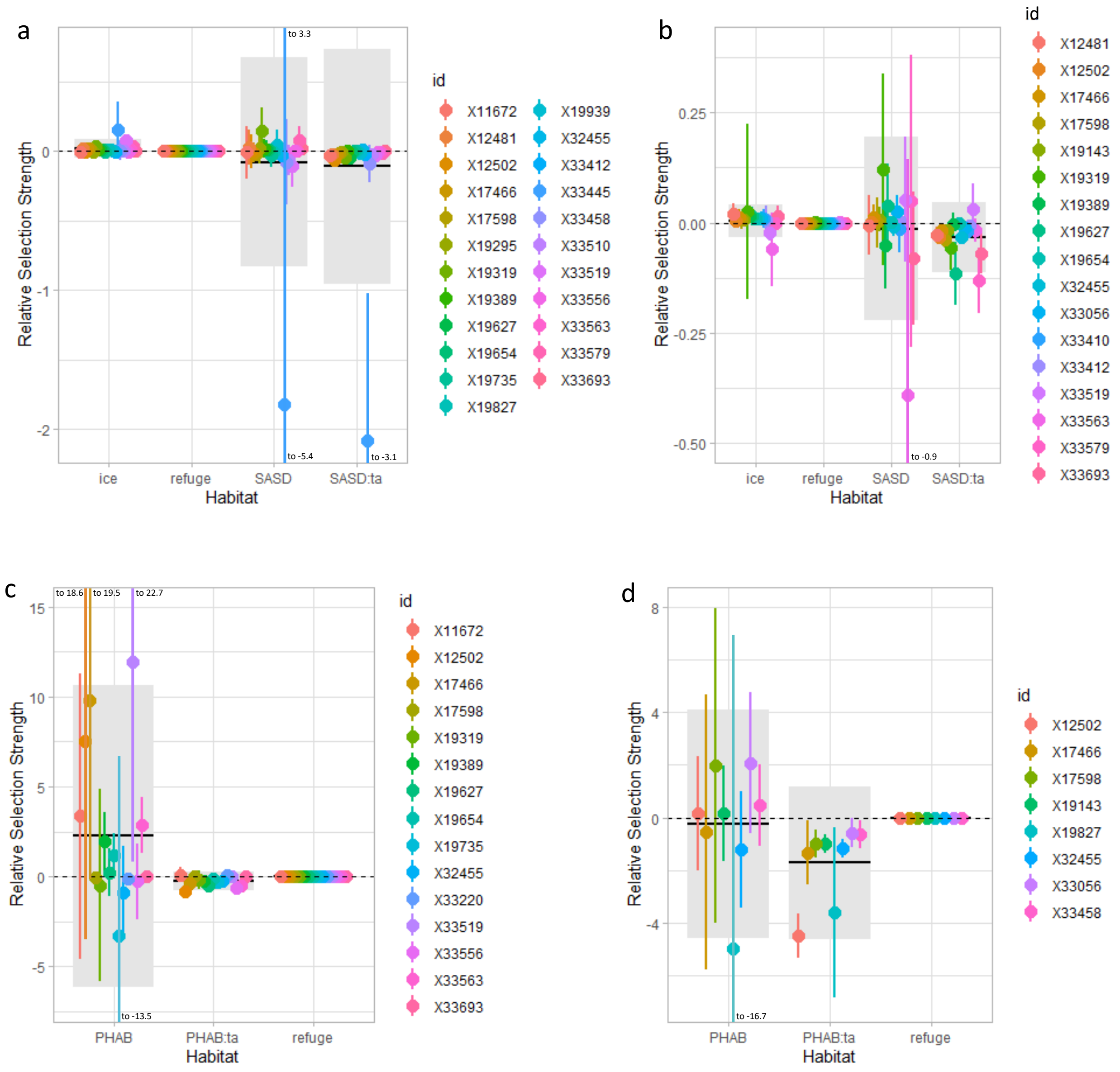

Figure 2.5 Integrated step selection analysis beta coefficients and 95% confidence intervals for individual adult female polar bears in Western Hudson Bay with ≥1 significant covariate in the top model for each model group: a) SASD early, b) SASD late, c) PHAB early, and d) PHAB late. Black bars show population mean beta coefficients for each covariate and grey boxes show 95% confidence intervals.

2.5 References

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2.6 Appendix

Table A2.1 Cox & Snell pseudo R-squared values from integrated step selection analyses comparing two methods of quantifying habitat fragmentation: standard deviation of Geary's *c* (SASD) and local percentage of optimal habitat (PHAB) using locations from adult female polar bears in Hudson Bay from 2013-2018. Maximum possible pseudo R-squared value for all models was 0.353. Individuals removed from analyses denoted as n/a.

Early Break-up			Late Break-up		
Individual Bear	**SASD pseudo R-squared**	**PHAB pseudo R-squared**	**Individual Bear**	**SASD pseudo R-squared**	**PHAB pseudo R-squared**
1	0.012	0.011	1	0.353	0.353
2	0.007	0.005	2	0.067	0.045
3	0.003	0.001	3	0.015	0.007
4	0.01	0.029	4	0.151	0.153
5	0.008	0.005	5	0.075	0.02
6	0.067	0.003	6	0.021	0.02
7	0.027	n/a	7	0.01	0.005
8	0.001	0.001	8	0.029	0.023
9	0.003	0.001	9	0.075	n/a
10	0.003	0.009	10	0.009	0.004
11	0.014	0.009	11	0.032	0.008
12	0.023	0.002	12	0.015	0.017
13	0.025	0.013	13	0.01	0.01
14	0.002	0.004	14	0.01	0.012
15	0.071	0.049	15	0.108	0.002
16	0.009	0.01	16	0.014	0.004
17	0.008	0.011	17	0.018	0.003
18	0.006	0.015	18	0.01	0.005
19	0.007	0.004	19	0.084	0.038
20	0.003	0.002	20	0.031	0.01
21	0.001	0.001	21	0.015	0.003
22	0.005	0.002	22	0.022	0.021
23	0.003	0.004	23	0.014	0.015
24	0.005	0.002	24	0.002	0.001
25	0.002	0.002	25	0.006	0.052
26	0.037	n/a	26	0.007	0.012
27	0.016	0.006	27	0.014	0.011
28	0.007	0.005	28	0.038	0.018

29	0.009	0.008	29	0.004	0.005
30	0.005	0.013			
31	0.006	0.004			
32	0.004	0.006			
33	0.001	0.001			
34	0.003	0.002			
35	0.005	0.001			
36	0.003	0.001			
37	0.001	0.004			
38	0.005	0			
39	0.004	n/a			

Chapter 3

3 Effects of sea ice fragmentation on individual variation in polar bear movement in Hudson Bay

3.1 Introduction

The ability for an organism to move through a habitat is dependent on habitat structure, where heterogeneity and resource distribution affect how, when, and where an individual can move (Schooley and Wiens, 2004, Schtickzelle et al., 2007). Movement patterns vary based on activity, whereby many organisms show distinct differences in movement patterns when foraging, searching for mates, or migrating (i.e. Andrews et al., 2018, Foley et al., 2018, Hetherington et al., 2018). Organisms that inhabit seasonal ecosystems often show movement behaviour that reflects temporal changes in habitat, such as migration or altered foraging (Kutilek, 1979, Borghesio and Laiolo, 2004, Cherry et al., 2013). The period of change between seasons is generally associated with high movement for migratory species as they relocate due to changes in resource or habitat availability (Levey and Stiles, 1992, Chapman et al., 2014).

Habitat fragmentation is the separation of habitat into isolated patches (Wilcove et al., 1986, Fahrig, 2003) and can impede both migratory and local animal movement (Diffendorfer et al., 1995, Bender et al., 2003). Organisms become more isolated as patches become smaller and the distance between patches increases (Wilcove et al., 1986). The ability to move between patches is affected by characteristics of the matrix, the degree of patch aggregation, and the presence of corridors (Ricketts, 2001, Tigas et al., 2002, Schtickzelle and Baguette, 2003). Highly fragmented landscapes are often associated with more costly movement, as the matrix is usually less preferable habitat that an animal must expend more energy, time, or risk to traverse (Hinsley, 2000, Bonte et al., 2012). Increased path tortuosity often increases movement costs and is linked to increased fragmentation (Benhamou, 2004, Fahrig, 2007, Mitrovich et al., 2009). Increased energetic costs can be challenging for animals moving shorter distances through habitats for foraging and mate searching, as well as long distances for migration (Mahan and Yahner, 1999, Collingham and Huntley, 2000, Dale, 2001, Bartlam-Brooks et al., 2011).

Polar bears (*Ursus maritimus*) are migratory and move annually to hunt, reproduce, or find refuge due to changes in habitat availability (Stirling and Archibald, 1977, Parks et al., 2006, Cherry et al., 2013, 2016). Sea ice, identified as primary polar bear habitat (Stirling et al., 1993, Ferguson et al., 2000, McCall et al., 2016), is dynamic, and changes with wind, ocean currents, melting, and freezing with changing seasons (Markham, 1986, Saucier et al., 2004, Parkinson, 2014). Polar bears use sea ice when it is present, but during spring and summer, temperatures increase, ice melts, and bears are forced onto land or further north onto multiyear ice over the Arctic Basin (Durner et al., 2009, Pongracz and Derocher, 2017). During break-up sea ice undergoes fragmentation (Sahanatien and Derocher, 2012), and as ice floe habitat patches break up and shrink, bears are forced to swim through open water matrix more often (Pilfold et al., 2017). Although patch-based metrics are commonly used to quantify fragmentation, spatial autocorrelation is potentially more effective for describing fragmentation in habitats that do not have distinct patches that last for extended periods, like sea ice. Spatial autocorrelation has previously been used in geographic studies to describe heterogeneity of complex landscapes (Roberts et al., 2000, Pearson, 2002, Fan and Myint, 2014). Local spatial autocorrelation metrics may be more effective at describing patterns of habitat fragmentation because sea ice does not have to be grouped into arbitrary patch types, which allows gradients in ice cover to be described. The details that spatial autocorrelation maintains concerning the variation of ice cover could be important for understanding sea ice ecosystems.

Sea ice is dynamic both spatially and temporally. Using spatial autocorrelation aids in the analysis of spatial complexity, but it does not account for temporal complexity. Similar to patch-based metrics, spatial autocorrelation describes habitat at a singular point in time. The majority of habitat fragmentation analyses focus on terrestrial habitat, which often undergo changes relatively slowly so quantifying fragmentation periodically is effective (i.e. Keleş et al., 2008, Korfanta et al., 2012, Reddy et al., 2013). Sea ice changes much more rapidly (Saucier et al., 2004), so including a temporal aspect in spatial analysis is important to get a nuanced understanding of what ice-associated species experience. Considering the standard deviation in spatial autocorrelation (SASD) over time adds a layer onto fragmentation analyses to consider both the structure of the habitat and the variability of that structure. SASD was more effective than commonly used patch-based metrics for predicting the effect of habitat fragmentation on polar bear movement (refer to Ch. 2).

Over the past four decades the ice-free period has lengthened by 5 – 41 days/decade depending on the region (Parkinson, 2014, Stern and Laidre, 2016, Stroeve and Notz, 2018). For polar bears, ice loss may increase the energetic costs of searching for prey (Durner et al., 2011, Sahanatien and Derocher, 2012), reflected in the tendency for individuals to swim longer distances more often in regions of increased open water (Pilfold et al., 2017). Migration patterns are linked to sea ice conditions, thus earlier break-up and later freeze-up, mean less time on ice and longer on shore fasting periods (Cherry et al., 2013).

Individual variance in migration timing is evident in polar bears, and is predicted, in part, by exposure to low sea ice cover for extended periods (Cherry et al., 2016). Polar bears are primarily solitary so individual variation in movements through fragmented sea ice can likely be explained further by variation in their experience with nearby sea ice.

The objective of this study is to examine interactions between sea ice fragmentation during break-up measured using the standard deviation in spatial autocorrelation (SASD) and characteristics of polar bear movement to determine if SASD can explain individual variation in polar bear migration patterns. I used telemetry location data from geographic position system (GPS) collared adult female polar bears in Western Hudson Bay (WH) from 2013 – 2018. I had 3 main goals: 1) explore the relationship between sea ice SASD and individual path tortuosity, 2) explore the relationship between sea ice SASD and the date an individual arrives on land, and 3) assess if female polar bears of different reproductive status show differences in the SASD of sea ice they move through. I hypothesize sea ice variability will have greater effects on movement later in break-up as fragmentation progresses.

3.2 Material and Methods

3.2.1 Study Area

The study area in Hudson Bay (Figure 3.1) is a shallow inland sea with an area of 1 240 000 km^2 (Macdonald and Kuzyk, 2011). Sea ice in Hudson Bay undergoes an annual cycle with ice present from November to July (Gough and Wolfe, 2001). Freeze-up starts in autumn, while break-up typically starts in spring (Derocher and Stirling, 1990, Saucier et al., 2004). My analysis examines the WH population, one of the southernmost polar bear populations, from spring 2013 to summer 2018.

3.2.2 Animal Capture and Handling

Adult (≥5 years old) female polar bears were immobilized via remote injection of Zoletil® (Virbac S.A., Carros, France) from a helicopter following Stirling et al. (1989). Bears were fitted with satellite-linked collars (Telonics, Mesa, AZ, USA), programmed to collect a GPS location every 4 hours. I used all locations in a 100% minimum convex polygon trimmed to remove terrestrial areas to delineate the study area (Figure 3.1). Capture and handling protocols were approved by the Environment and Climate Change Canada, Prairie and Northern Region Animal Care Committee and the University of Alberta Biological Sciences Animal Policy and Welfare Committee, in accordance with the Canadian Council on Animal Care guidelines.

3.2.3 Sea Ice Data

Sea ice cover was collected with the Advanced Microwave Scanning Radiometer 2 (AMSR-2) on the GCOM-W1 platform with a resolution of 6.25 x 6.25 km obtained from the National Snow and Ice Data Center (Boulder, CO). The cover value in each pixel ranged from 0 – 200, which was halved to reflect percentage of sea ice cover. I defined the break-up period using percentage of habitat (PHAB: called PLAND in the software) using FRAGSTATS (McGarigal et al. 2012). Sea ice cover values ≥60% per pixel were defined as optimal habitat and cover <60% per pixel was suboptimal habitat (Mauritzen et al., 2003, Sahanatien and Derocher, 2012, Cherry et al., 2013, Pilfold et al., 2014, Laidre et al., 2015, Cherry et al., 2016, Lone et al., 2018). I reclassified raster layers of daily sea ice cover in ArcGIS version 10.5.1 (Environmental Systems Research Institute, Redlands, CA) into optimal and suboptimal habitat and daily PHAB of optimal habitat was calculated. Start of break-up was defined as the first day across all years when PHAB dropped and remained < 95%, and the end of break-up was the last day before PHAB dropped and remained < 5%. Based on polar bear habitat use studies (Stirling et al., 1999, Cherry et al., 2016) I used the date in each year when PHAB dropped below 50% to separate break-up into early and late.

3.2.4 Habitat Fragmentation

To quantify habitat fragmentation, I used the standard deviation of local Geary's *c,* a spatial autocorrelation metric (SASD), this is a synthetic method that focuses on temporal variability in sea ice cover. Geary's *c* quantifies spatial autocorrelation based on dissimilarity, which ranges from 0, reflecting positive spatial autocorrelation which describes areas of similar habitat, to undefined values >1, reflecting negative spatial autocorrelation which describes a region of dissimilar habitat (Anselin, 1995, 2018). To get local SASD I used a moving window scaled to the mean distance bears travelled per day during break-up. Daily mean distance was 21 km (range: 11 – 31 km/day), which was used as a radius to calculate an area of 1385 km^2, which was translated into ~35 6.25 km x 6.25 km pixels. This was translated to a 5 x 5 pixel moving window because a central pixel was required for spatial autocorrelation analysis. Pixels were assigned null values if they were near the edge of study area and did not have sufficient surrounding pixels to fill the moving window. Geary's *c* was calculated daily using the moving window for each pixel, and the standard deviation of Geary's *c* was calculated for each pixel in early and late break-up to create the spatial autocorrelation standard deviation (SASD) metric. Pixels around the edge of study area were assigned null values as they did not have enough surrounding pixels to fill the moving window.

3.2.5 Movement Analyses

All locations from polar bears were included in analyses except those that were biologically impossible (i.e. >30 km/h). Locations from individuals were analyzed separately for early and late break-up. SASD was extracted at each location and I calculated mean SASD for each individual's path. Path tortuosity was calculated for each individual using a straightness index, where 1 reflects a straight path, and tortuosity increases towards 0 (Batschelet, 1981). The ordinal date on land was determined using ArcGIS to identify an individual's first location on the coast which marks the end of an individual's sea ice season. Presence and age of accompanying offspring was only included for females in years that they were collared with offspring or observed in the field with offspring, as reproductive status was uncertain beyond the year of handling. Collar failure resulted in missing data that affected sample size for some individuals. Paths with <1 location per day on average were removed from straightness index analyses to avoid underestimating tortuosity.

Normality of all variables included in analyses were tested using Kolmogorov-Smirnov tests. Mean SASD and straightness index were transformed using natural log (ln) to improve normality. A paired t-test was used to compare ln mean SASD of each individual in early and late break-up to determine if they should be pooled. Linear regressions were used to analyze the relationship between ln mean SASD and ln straightness index, and between ln mean SASD and date on land. I used a Kruskal-Wallis test to compare mean SASD for individuals with cubs of the year, yearlings, 2-year-olds, or without offspring.

3.3 Results

The break-up period for all years was May 2 – July 23, and late break-up started on June 24, June 23, June 23, June 30, June 17, and June 26, in 2013 – 2018, respectively. The variability in sea ice cover was quantified by SASD using Geary's *c* in each pixel, across early and late break-up. Most often, SASD was lowest in regions of consistent ice cover in early break-up, whereas in late break-up low SASD reflected regions of consistent open water. High SASD in late break-up reflected regions where sea ice patches remained the longest. Bear movement had a maximum speed of 15.5 km/h.

Mean SASD with ln transformation was normally distributed (Kolmogorov-Smirnov test; early: $D = 0.12$, $p = 0.26$; late: $D = 0.10$, $p = 0.69$) and ln transformation of straightness index was also normal (Kolmogorov-Smirnov test; early: $D = 0.10$, $p = 0.59$; late: $D = 0.12$, $p = 0.58$). Mean SASD of each individual's path was significantly different in early and late break-up (paired t-test: $t_{44} = 4.02$, $p < 0.001$), thus I kept early and late separate for all analyses. In early break-up there was no significant relationship between ln mean SASD and ln straightness index of a path (linear regression: $p = 0.47$, $R^2 = 0.009$, $df = 55$) (Figure 3.2a), or between ln mean SASD and ordinal date on land (linear regression: $p = 0.43$, $R^2 = 0.01$, $df = 51$) (Figure 3.2b). In contrast, during late break-up there was a significant relationship between ln mean SASD and ln straightness index (linear regression: $\beta = -0.36$, $p = 0.001$, $R^2 = 0.24$, $df = 40$), where a 10% increase in mean SASD resulted in a ~4% more tortuous path (Figure 3.2c). There was also a significant relationship between ln mean SASD in late break-up and ordinal date on land (linear regression: $\beta = 6.03$, $p < 0.001$, $R^2 = 0.27$, $df = 40$), where a 10% increase in mean SASD resulted in an individual arriving on land 0.6 days later (Figure 3.2d). There was no significant difference in mean SASD based on the presence or age of accompanying cubs in early (Kruskal-Wallis test: $\chi^2 = 0.70$, $p = 0.87$, $df = 3$) or late break-up (Kruskal-Wallis test: $\chi^2 = 3.00$, $p = 0.39$, $df = 3$).

3.4 Discussion

Understanding movement ecology in a complex habitat is important for predicting how habitat changes might affect organismal movement. I found that individual migratory variation is, to some extent, due to regional and temporal variation in sea ice during break-up. Fragmentation variability most notably affects polar bear movement in the latter half of break-up. Both the path travelled and the timing of migration were affected by the SASD of sea ice an individual bear encountered. Until now habitat fragmentation has not been explored for its effect on polar bear migration. Cherry et al. (2016) found migration was affected by the length of time an individual bear was exposed to deteriorating ice before it headed toward land, but the variability in the ice itself is a novel addition to this understanding.

In regions of low SASD, bears have the opportunity for direct movement trajectories, in regions of higher SASD bears may change direction to avoid swimming. Polar bears travel via sea ice and avoid swimming when possible to conserve energy (Monnett and Gleason, 2006, Durner et al., 2011, Pilfold et al., 2017, Griffen, 2018). Late break-up paths were more tortuous for individuals that moved through higher SASD, suggesting that bears were turning more in regions with more fragmentation. Some of this increased tortuosity may result from sea ice drift. Bears experience passive movement from ice drift that could cause their paths to seem more tortuous than their actual movements (Hakkinen et al., 2008, Spreen et al., 2011, Durner et al., 2017). Greater correlation in the relationship between SASD and tortuosity in late break-up was likely because although fragmentation occurs in early break-up, PHAB is still >50%. A greater amount of habitat allows bears to maintain straighter paths. As habitat declines during break-up movement becomes more directional (Ramsay and Andriashek, 1986, Parks et al., 2006). I found that high SASD of fragmented ice increases path tortuosity which potentially reduces the efficiency of directional movement.

The timing of directed movement to land is reliant on sea ice cover and individuals can be forced to swim long distances to the coast once sea ice connection to land is lost (Pilfold et al., 2017). In late break-up, individuals that moved through higher SASD sea ice came onto land later. The regions of highest SASD reflect regions where sea ice persists the longest in late break-up. The bears that spent more time in high SASD may delay coming onto land to utilize remaining sea ice patches for hunting, as longer time on ice is linked to better body condition (Stirling et al., 1999, Obbard et al., 2006, Galicia et al., 2019). Although the benefit of increased hunting may be outweighed by the cost of energy expenditure via swimming as ice retreats away from summer habitat (Cherry et al., 2013). Habitat wide environmental variables that affect the date polar bears come onto land have been considered for entire populations (Cherry et al., 2013). By using SASD, I found that variation in sea ice cover is useful in explaining individual variation in migration. Describing sea ice in terms of SASD I was able to show the importance of sea ice fluctuations to polar bears during migration. Previously, fluctuations in ice conditions were found to have no effect on the timing of migration (Cherry et al., 2016). In solitary animals such as polar bears, variation in the habitat experienced by an individual plays an important role in understanding body condition, which affects survival and reproduction. Due to its effect on migration timing, SASD has the potential to be extrapolated onto aspects of individual fitness.

I could not detect an effect of reproductive status on mean SASD of a female’s path. Similarly, reproductive status of female polar bears had no effect on home range size or activity levels during break-up (Messier et al., 1992, Parks et al., 2006). The lack of effect on movement metrics suggests that during break-up, fragmentation affects female movement similarly, regardless of the presence or age of offspring. However, the lack of certainty in reproductive status for female polar bears makes this finding tenuous.

There is spatial and temporal variability in sea ice cover which interact with each other to create dynamic habitat for ice-associated species. Polar bear migration is the result of an extreme period of habitat change, and SASD of sea ice cover explains individual variation in both path tortuosity and timing of migration. SASD is a useful approach for complex and dynamic ecosystems to uncover relationships between spatial and temporal variability in habitat fragmentation and the movement of organisms in those habitats.

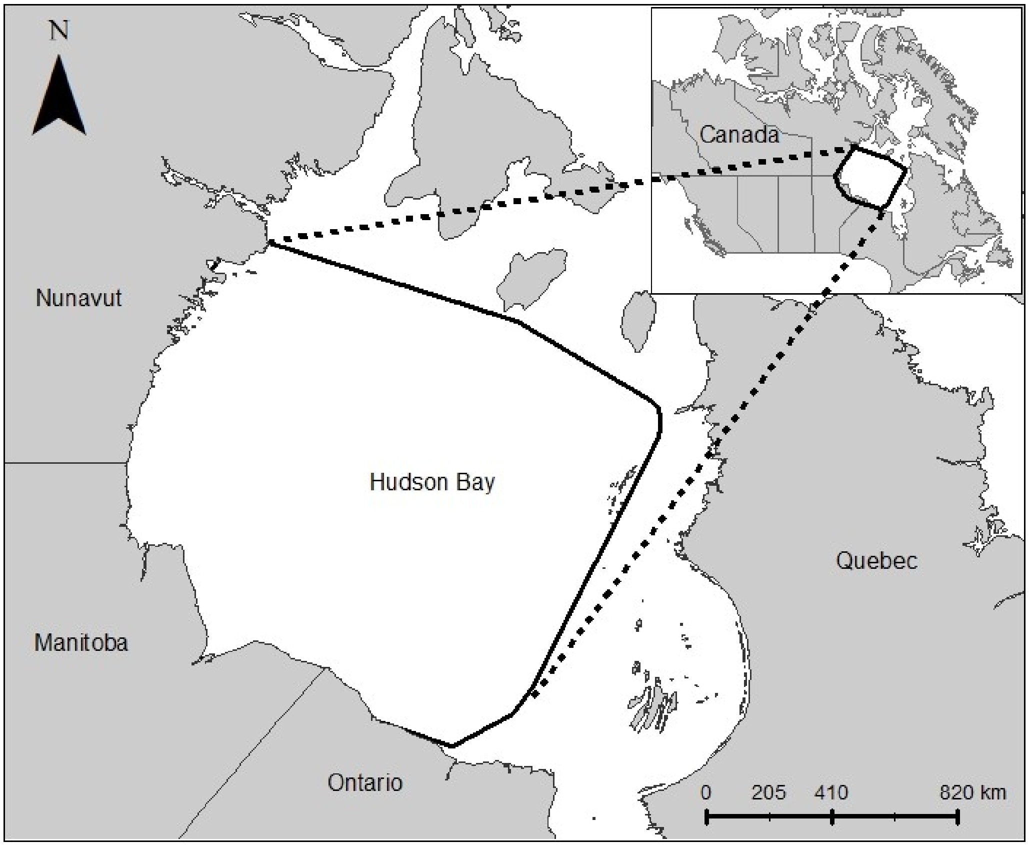

Figure 3.1 Map showing the study area in Hudson Bay, Canada outlined in black, determined with a 100% minimum convex polygon trimmed to marine areas using locations of GPS collared adult female polar bears in the Western Hudson Bay population from 2012-2018.

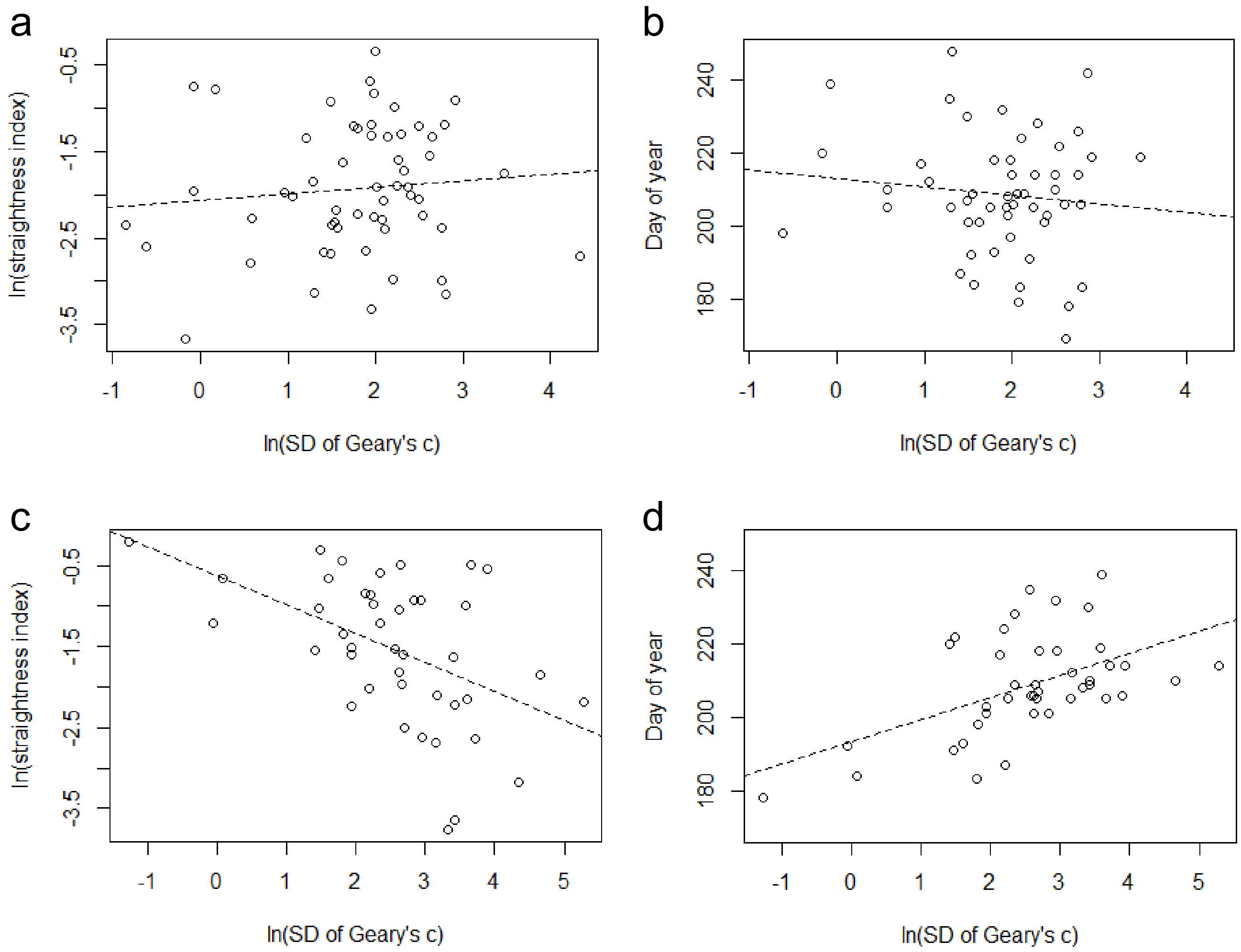

Figure 3.2 a) Natural log of straightness index as a function of the natural log of mean SASD of an individual's path in early break-up, b) date of arrival on land as a function of the natural log of mean SASD of a path in early break-up, c) natural log of straightness index as a function of the natural log of mean SASD of an individual's path in late break-up, and d) date of arrival on land as a function of the natural log of mean SASD of a path in late break-up. Linear regression line shown as a dashed line on each plot. All paths are from GPS locations of adult female polar bears in Hudson Bay during the sea ice break-up period from 2013-2018. Early break-up dates are May 2 to 50% PHAB in each year, and late break-up dates are from 50% PHAB in each year to July 23.

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Chapter 4

4 Conclusion

Fragmentation is an important aspect for understanding habitat change and is commonly studied in terrestrial habitats using patch-based metrics. However, sea ice fragmentation differs from terrestrial fragmentation as sea ice does not exhibit distinct patches, and thus I chose to explore an alternate method of quantification. I demonstrated that the standard deviation in spatial autocorrelation (SASD) over time can be effectively used to describe how sea ice fragmentation affects polar bear (*Ursus maritimus*) movement and migration patterns. Moving forward, SASD has the potential to be used to quantify sea ice cover across the Arctic. Using SASD to compare regions where ice remains in the summer and regions like Hudson Bay where ice is lost could reveal differences in ice variation based on annual cycles. SASD could also be used as a tool to explore changes in sea ice over the long term. There is potential for SASD to work alongside what we already know about sea ice loss (i.e. Sahanatien and Derocher, 2012, Parkinson, 2014, Stern and Laidre, 2016) to further our understanding of how ice is changing. The next step from exploring the ice itself, is to explore more species that utilize this habitat. The approach is applicable to many Arctic marine mammals including ringed seals (*Pusa hispida*), bearded seals (*Erignathus barbatus*), walrus (*Odobenus rosmarus*), narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*) among others. Exploring how variation in sea ice affects different species will develop our understanding of the interconnectedness of Arctic marine ecosystems and the species that utilize ice.

For many animals both the presence and location of sea ice are important aspects of habitat structure. Many seals and walrus require sea ice to be present for raising offspring, but they also use ice for hauling out and its presence over shallow waters increases their foraging distribution (Kovacs et al., 2011, Harwood et al., 2012). For cetaceans with Arctic or subarctic distributions, sea ice influences the availability and distribution of their prey, and most of these species spend the majority of the year in close proximity to ice (Moore et al., 2000, Kovacs et al., 2011). Seabirds are also affected by the presence of ice, often making use of leads and polynyas for foraging opportunities (Mallory et al., 2010). Variability in sea ice fragmentation affects species that use ice and understanding these dynamics may help uncover important regions for conservation and provide insight on how ice use may change across seasons and years. Species that avoid sea ice cover are also affected by variability in ice fragmentation. Killer whales (*Orcinus orca*) are constrained by sea ice presence but have expanded their range to the north as a result of sea ice loss (Higdon and Ferguson, 2009). Understanding sea ice variability could aid in predicting the future invasion of killer whales as a top predator in Arctic marine ecosystems. Using SASD to build on our knowledge of habitat use in ice-associated and ice-avoidant species will increase our understanding of the role of sea ice variation in individual movement and aspects of fitness.

Body condition is often used as a proxy for fitness. Exploring the relationships between body condition and SASD of sea ice could uncover how SASD affects fitness. Polar bear body condition data is difficult to work with as a fitness proxy due to high variation across season and rapid changes with consumption of prey (Atkinson et al., 1996, Obbard et al., 2006). Thus, body condition analysis could not be effectively explored using polar bears. With the goal of expanding SASD of sea ice analysis to other ice-associated marine mammals, there is potential to include fitness analyses using variation in individual body condition. Fitness could also be explored using the effect of SASD of sea ice on individual recruitment success. Considering the impacts of sea ice variability on species that birth and raise young on ice could aid in describing individual variation in reproductive success. Exploring measures of fitness in conjunction with SASD of sea ice could improve the effectiveness of my SASD metric by examining the relationships between sea ice variability and multiple Arctic species.

SASD has the potential to be used as a monitoring parameter. Based on my work, SASD is effective in describing sea ice habitat and some aspects of polar bear movement. Using SASD long term in conjunction with sea ice loss analyses creates potential to discover relationships between multiple species and SASD. Long term applications of SASD may first allow for further explanation of how different populations have changed over time, and those patterns can be built upon to determine how quantifiable changes in SASD might affect population demographics. Understanding more about sea ice in a context that can be directly applied to organismal movement shows rich opportunities to improve management. SASD could reveal recurring annual patterns in the sea ice, which may be connected to important regions for various species, helping to direct conservation and management efforts. Yurkowski et al. (2019) defined a number of biodiversity hotspots across the Arctic and applying SASD to our knowledge of pre-existing hotspots could reveal if variability in sea ice cover plays a role in species aggregation. If a connection exists between SASD and the location of hotspots, changes in species aggregation over time could be predicted using patterns in SASD over time. Further, SASD could benefit oil spill mitigation in the Arctic by defining regions where sea ice cover is more variable, which often reflects regions of high ice movement, which will help determine oil trajectory, and increase the effectiveness of oil spill response (Beegle-Krause et al., 2017). With sustained use SASD will potentially give a quantitative, long-term perspective on sea ice fragmentation while synthesizing temporal and spatial change in an efficient format and reducing the amount of data needed for sea ice analyses.

My work on sea ice fragmentation uncovered a method of quantification using SASD that was better than commonly used patch-based metrics at explaining the directionality of polar bear movement. Those results allowed me to explore further and determine that SASD has an effect on individual variation in polar bear migration. Sea ice extent is declining with climate change (Maslanik et al., 2007, Parkinson, 2014), and an improved understanding of sea ice dynamics will help us understand how these changes are affecting Arctic marine ecosystems.

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