Space and habitat use of polar bears (*Ursus maritimus*) in Davis Strait in relation to sea ice conditions and harp seals (*Pagophilus groenlandicus*)

by

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Abstract

Patterns of space use and habitat selection by polar bears (*Ursus maritimus*) vary among subpopulations where they have been studied. The Davis Strait subpopulation is one of the least researched polar bear subpopulations and their spatial ecology is largely unknown. As an obligate carnivore, polar bears rely largely on seals as their primary prey, yet predator-prey spatial relationships are poorly studied. In order to assess the spatial relationship between polar bears in Davis Strait and harp seals, one of their primary prey, we first analyzed trends in sea ice dynamics to understand sea ice conditions that may affect each species' distribution. We found that the availability of sea ice for polar bears decreased over time, resulting in a significant lengthening of the ice-free season (10.9 d/decade). We used remotely sensed imagery of sea ice (1979 – 2021) in relation to the movements of both polar bears (n=27) and harp seals (n=29) as determined by satellite telemetry. We calculated annual home range sizes, seasonal movement rates, and seasonal directionality for the Davis Strait subpopulation of polar bears (1991 – 2001). The mean annual home range size of polar bears was 101,775 km^2 (range=699-280,539 km^2) but varied with the statistical method used. Bears travelled a mean speed of 0.53 km/h (range=0-2.19 km/h) with the fastest rates in winter and slowest in freeze-up. Bears showed significant southward orientation during break-up and northward orientation during freeze-up but had no significant orientation in winter. We used resource selection functions to analyze seasonal habitat selection for both polar bears (1991 – 2001) and harp seals (1993 – 2005). The only covariate important to bear resource selection was distance to land during break-up, with null models placing top for the other seasons. For harp seals, ocean depth, sea ice concentration, distance to land, distance to open water, and distance to open water ^{2} were selected but their importance varied by season. To investigate the seasonal overlap in habitat between these two species, we compared resource selection and mapped seasonal kernel density overlap. We found that sea ice season affected space use and habitat selection for both species. Polar bears and harp seals were more likely to overlap during break-up and freeze-up but did so to a greater extent during freeze-up, but this may be due to sampling methods. This study illustrates the need to collect more polar bear telemetry data, particularly for those in less-studied regions. With climate change altering available habitats for all polar bear subpopulations, there is an urgency to understand how they are being spatially affected by a changing environment and our study provides a starting point for future studies.

Preface

This thesis is the original work of Larissa Thelin. It is a national research collaboration led by Dr. Andrew Derocher at the University of Alberta. Polar bear movement data used in this study was obtained by satellite transmitted collars deployed by Government of Nunavut and Environment and Climate Change Canada staff. Harp seal movement data was obtained by satellite transmitted devices deployed by staff of Department of Fisheries and Oceans Canada. All animal handling protocols received research ethics approval from the University of Alberta Animal Care and Use Committee for Biosciences, under the project names "Polar Bears and Climate Change: Habitat Use and Trophic Interactions" (AUP00000033) and "Polar Bear Ecology" (AUP00003667).

I dedicate this work to my mother, Cindy.

In a lifetime of hardship, you continue to choose love.

Because of you, love is the thing that guides me.

"*Let your heart be governed by your head, and let your head be governed by your heart.*"

– Dr. Jane Goodall

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Introduction

Where a species exists in space and how it uses its environment is a foundational component of spatial ecology (Johnson 1980; Aarts et al. 2008). Investigating the former for a particular species leads to increased understanding of *where* it exists, while the latter tells us *why* it can be found there (Aarts et al. 2008). Species occur in geographic space at varying scales – where it can be found in general is considered first-order selection, the location of each individual's home range can be referred to as second-order selection, while third-order selection outlines the specific habitat components within a home range, and fourth-order refers to when the individual obtains resources within their selected habitat (Johnson 1980). Understanding species' spatial ecology at varying scales and determining why they use such spaces has implications for conservation management (Aarts et al. 2008).

Second-order selection, the species' home range scale, can be defined as the area where it performs all of its regular activities, such as searching for food or mates, or caring for its young, and normally excludes forays outside of the most-used area (Burt 1943; Johnson 1980). Further, the size of home ranges can vary by sex or reproductive status within a population (Burt 1943). Using location data for a species', home ranges can be estimated using minimum convex polygons (MCPs), which involves delineating a polygon around the individual's known locations (Anderson 1982; Harris et al. 1990; Burgman & Fox 2003; Laver & Kelly 2008). Alternatively, a utilization distribution approach can be used that estimates the probability of finding the animal in a given location (Anderson 1982; Worton 1989; Laver & Kelly 2008).

Third-order selection can be estimated using the concept of habitat selection, the selection of specific areas by an animal to meet necessary life history components, such as for food or shelter (Johnson 1980; Boyce & McDonald 1999; Hamilton 2019). The term "habitat" is species specific with selection for different areas varying by resource need and often between seasons (Boyce & McDonald 1999; Garshelis 2000b; Doligez & Boulinier 2008). We can define habitat based on patches within a larger area, where an individual performs activities or spends short periods, or as the larger area as a whole (Fretwell & Lucas 1969; Garshelis 2000a; Doligez & Boulinier 2008). Animals choose a specific location based on its knowledge of its surroundings (i.e., "habitat selection"), and when the larger area contains the resources it needs to survive, the area is considered suitable habitat (Fretwell & Lucas 1969; Garshelis 2000b; Johnson et al. 2004b; Doligez & Boulinier 2008). Resource selection functions (RSFs) have emerged as a prominent method to study habitat selection, through the use of statistical models, and they have also been used to predict species interactions (Hebblewhite et al. 2005; Boyce 2006). RSFs allow assessment of environmental variables that identify where a species may occur based on their presence or absence (Johnson et al. 2004b; Hirzel & Le Lay 2008; McCall et al. 2016). Once a species' suitable habitat is determined, it can then be extrapolated to larger areas (Johnson et al. 2004a; McCall et al. 2016).

Investigating the spatial and temporal overlap of space use and habitat selection between species can help to understand species interactions, such as predator-prey dynamics (Carroll et al. 2019). For vulnerable species, understanding their spatial ecology, as well as that of their prey, can aid their conservation as it allows us to identify their habitats (Boyce & McDonald 1999; Doligez & Boulinier 2008). With increasing anthropogenic pressure on ecosystems understanding and monitoring species' spatial ecology has emerged as a priority in wildlife management (Heller & Zavaleta 2009).

In the Arctic, a region warming faster than the global average, climate change has emerged as a significant threat to wildlife (Serreze & Francis 2006; Wassmann et al. 2011;

Cohen et al. 2014). Sea ice extent, concentration, thickness, phenology, drift, and age are changing across the Arctic (Serreze et al. 2007; Onarheim et al. 2018; Serreze & Meier 2019) and are affecting Arctic marine ecosystems (Arrigo et al. 2008; Bluhm & Gradinger 2008; Burek et al. 2008; Descamps et al. 2020) including ice-dependent marine mammals (Tynan & DeMaster 1997; Burek et al. 2008; Laidre et al. 2008). For polar bears (*Ursus maritimus*), the top predator in the Arctic marine food web, sea ice is necessary for travel, hunting, and reproduction (Stirling & Derocher 1993; Regehr et al. 2010). Due to the negative effects of climate change affecting their Arctic range, they are globally listed as vulnerable (Regehr et al. 2016). Altered sea ice patterns are associated with decreasing body condition, survival, and reproduction as well as changes in the accessibility of both habitats and prey for polar bears (e.g., Derocher et al. 2004; Molnár et al. 2010; Lunn et al. 2016; Obbard et al. 2016; Merkel & Aars 2022). Arctic seals, the primary prey of polar bears, also require sea ice for whelping and moulting (Lydersen & Kovacs 1999; Thiemann et al. 2008). Thus, as climate change continues to affect sea ice, both polar bears and their prey lose habitat.

The impacts of climate change on Arctic marine ecosystems vary across the range of polar bears (Hamilton & Derocher 2018). Higher sea ice loss is happening at the edges of their range (Regehr et al. 2016; Stern & Laidre 2016). Thus, the spatial ecology and habitat selection of polar bears vary across space, and climate change may uniquely influence each (e.g.; Durner et al. 2009; McCall et al. 2014; Wilson et al. 2016; Durner et al. 2017). For example, annual home range sizes (2nd order selection) vary from <1,000 km^2 to >500,000 km^2, depending on the subpopulation studied (e.g., Ferguson et al. 1999; Mauritzen et al. 2001; McCall et al. 2014; Auger-Méthé et al. 2016). Habitat selection (3rd order selection) also varies across the global population of polar bears. Broadly, polar bears select habitat with medium to high sea ice concentrations and avoid very high or low concentrations (e.g., Durner et al. 2009; Pilfold et al. 2014; McCall et al. 2016). They also tend to select sea ice over the continental shelf due to both higher biological productivity and prey density (e.g., Stirling & Derocher 1993; Frost et al. 2004; Wilson et al. 2016; Lone et al. 2018). The importance of other covariates, such as distances to denning areas, seasonal variability and distribution of open water, land, and land-fast ice, or floe size and ice thickness vary by subpopulation as well (e.g., Durner et al. 2009; McCall et al. 2016; Laidre et al. 2018b; Johnson & Derocher 2020). RSFs of polar bears have ranged from studies of the global population to a single subpopulation (e.g. Durner et al. 2009; e.g. McCall et al. 2016; Wilson et al. 2016; Laidre et al. 2018b; Lone et al. 2018). None, however, have examined the Davis Strait subpopulation (hereafter DS) in eastern Canada and southern Greenland, and few have investigated the overlap in space use or habitat selection between polar bears and their prey (Hamilton et al. 2014; Pilfold et al. 2014; Hamilton et al. 2017b; Hamilton et al. 2017a). These studies concluded that spatial overlap between polar bears and ringed seals (*Pusa hispida*) varies with the time of year and that climate change is affecting this relationship through its influence on sea ice (Pilfold et al. 2013; Hamilton et al. 2014; Hamilton et al. 2017b; 2017a).

The DS polar bear subpopulation has about 2,150 individuals in three genetic groups (i.e., north, central, and south) that differ in survival and reproduction rates, with higher rates in the south, apparently because of greater access to harp seals (*Pagophilus groenlandicus*; Peacock et al. 2013). The subpopulation appears to be stable (PBSG 2019; Dyck et al. 2021), although previous declining body condition and low reproductive rates possibly associated with density-dependent effects or climate change impacts have been observed (Peacock et al. 2013). The ice-cover period in DS has declined by 17.1 days/decade over 1979 – 2014 (Stern & Laidre 2016), which may negatively influence DS polar bears.

The diet of polar bears in DS is more varied than many other subpopulations and includes, in order of diet contribution (i.e., most to least), harp seals, ringed seals, bearded seals (*Erignathus barbatus*), hooded seals (*Cystophora cristata*), walrus (*Odobenus rosmarus*), harbor seals (*Phoca vitulina*), beluga whales (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*; Thiemann et al. 2008; Galicia et al. 2021). Although polar bears in most subpopulations prey primarily on ringed seals and bearded seals, in Davis Strait 30-90% of polar bear diet may consist of harp seals (Iverson et al. 2006; Thiemann et al. 2008; Peacock et al. 2013; Smith & Stirling 2019). Few bear subpopulations have access to harp seals because harp seal range is restricted to the North Atlantic and adjoining areas (Lavigne & Kovacs 1988; Thiemann et al. 2008; Stenson et al. 2020). The harp seal population in the Northwest Atlantic (hereafter NWA) has two main herds that breed off the northeast coast of Newfoundland and Labrador (the 'Front' herd) and another further south near the Magdalen Islands (the 'Gulf' herd; Lavigne & Kovacs 1988; Johnston et al. 2005; Fisheries and Oceans Canada 2020). Since 1995, the NWA harp seal population has been relatively stable, but has recently increased following a major decline in 2010-2011 (Fisheries and Oceans Canada 2020). In 2019 there were an estimated 7.6 million seals, but they may have been near carrying capacity (Fisheries and Oceans Canada 2020).

Most NWA harp seals spend their summers feeding in Baffin Bay and adjacent water bodies before migrating south in autumn to winter near southern Labrador or the Gulf of St. Lawrence (Lavigne & Kovacs 1988; Fisheries and Oceans Canada 2020). Whelping, breeding, and moulting occur on pack ice from February-May when harp seals are most at risk of predation from polar bears (Lavigne & Kovacs 1988; Fisheries and Oceans Canada 2020). During the rest of the year, harp seals spend the majority of their time in open water (Lavigne & Kovacs 1988;

Smith & Stirling 2019). However, they sometimes aggregate when searching for concentrations of Arctic cod (*Boreogadus saida*) in drifting pack ice, where they are vulnerable to polar bear predation (Smith & Stirling 2019). Because of their need for access to stable sea for pupping, harp seals are vulnerable to changes in ice conditions both seasonally and between years (Sergeant 1991; Johnston et al. 2012; Hammill et al. 2021).

The main objective of this study is to examine the spatial ecology of DS polar bears relative to NA harp seals to understand the extent and biological importance of overlap between their space use and habitat selection. We also examine the historical trends in sea ice within DS and explore relationships with environmental variables using satellite imagery (1979 – 2021) to provide context for temporal trends in habitat. We use satellite telemetry data for both DS polar bears (1991 – 2001) and NA harp seals (1993 – 2005) to examine annual and seasonal home range sizes, as well as seasonal habitat selection and the extent of possible overlap between the two species. We also examine seasonal differences in movement patterns for DS polar bears.

Based on past trends in sea ice, we predicted an overall decline in suitable habitat associated with climate change with a decrease in sea ice extent and a lengthening of the ice-free period. We predicted that sea ice concentration, distance to open ocean, distance to land, and bathymetry would be important habitat covariates for both species, but their importance would vary seasonally. We predicted that bears would avoid very high and low sea ice concentrations in all seasons, because of possible negative influences on hunting opportunities, but would remain over the continental shelf due to high biological diversity, which may result in the use of less preferred sea ice concentration. We predicted that harp seals would stay over the continental shelf throughout the year. We also expected them to avoid areas of high sea ice concentration throughout most of the year except for the spring when ice is required for pupping and moulting.

We also predicted that we would find overlap in the habitat between polar bears and harp seals during all seasons except for the ice-free season when polar bears are on land.

Methods

Study area

The study area is in Davis Strait in northeastern Canada off of Newfoundland and Labrador, Québec, between Baffin Island (Nunavut, Canada), and Greenland (Figure 1). The DS management area includes Davis Strait, the Labrador Sea, and eastern Hudson Strait (Figure 1; Taylor et al. 2001). The continental shelf is approximately 300 m deep within the management area and extends farther offshore on the Canadian side than the Greenland side (Figure 1; Stern & Laidre 2016). Beyond the shelf, depths can exceed 3000 m (Curry et al. 2011). The northern extent of the subpopulation range is shallower than the southern portion. There are two major currents in Davis Strait: the Baffin Island Current, which flows southward on the western side, and the West Greenland Current that flows northward along Greenland's western coast (Curry et al. 2011; Wu et al. 2013). The Baffin Island Current continues south along Canada's eastern coast as the Labrador Current (Townsend et al. 2004). These currents, particular the warmer West Greenland Current, assist in keeping the Strait ice free in summer (Stern & Heide-Jørgensen 2003). This area is part of the Seasonal Ice Ecoregion, defined by sea ice that melts every summer (Amstrup et al. 2008; Rode et al. 2011; Sahanatien et al. 2015a). During the ice-free period, DS polar bears move on land (Rode et al. 2011), when they are largely food deprived.

Historical and current trends in Davis Strait sea ice

We used NASA Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data V001 (25 km x 25 km pixels) to obtain sea ice concentration maps of the Arctic from Jan 1, 1979 to Dec 31, 2021 (Cavalieri et al. 1996; National Aeronautics and Space Administration 2019). SSMR data was available every second day from Jan 1, 1979 to Aug 20, 1987, SSM/I were daily from Aug 21, 1987 to Dec 31, 2007, and SSMIS were daily from Jan 1, 2008 to Dec 31, 2021 (Cavalieri et al. 1996) for a total of 14,120 rasters. We analyzed sea ice within a 100% minimum convex polygon of all on-ice polar bear locations. We examined the relationship between the Arctic Oscillation (AO), the North Atlantic Oscillation, and sea ice concentration, area, and phenology (NAO; National Weather Service 2020b, a). NAO affects both sea ice and harp seal survival in eastern Canada and is correlated with the AO (Wang & Ikeda 2000; Ambaum et al. 2001; Stern & Heide-Jørgensen 2003; Johnston et al. 2005). We therefore predicted that NAO would have a more detectable effect on the sea ice in our analyses compared to the AO.

We created sea ice seasons using mean daily sea ice concentrations ranging from 0 (open water) to 1 (100% concentration). Where imagery was collected every two days, ice concentrations on intervening days were linearly interpolated using the *zoo* R package (Zeileis & Grothendieck 2005). These values were plotted, and the mean of all daily concentrations was calculated, resulting in the mean concentration/day (Figures 8-9 in Appendix A). To compare with other studies, we defined four sea ice seasons, freeze-up, winter, break-up, and ice-free (Durner et al. 2009; McCall et al. 2016), using a segmented regression model from the *segmented* R package (Muggeo 2008). The model was applied to the mean daily concentrations (where n(breaks)=4; Figure 9 in Appendix A). These seasons were used to separate telemetry data into in order to analyze seasonal variation in both species' habitat selection.

We quantified four ice metrics following Stern & Laidre (2016): annual dates of ice retreat and advance, ice-free period duration, and mean summer ice concentration. Dates of ice retreat and advance were determined using a kernel smoother for the daily ice area (area >15% concentration) within ±1 week of the central value for each year (Stern & Laidre 2016). The mean ice area for both the minimum and maximum months were calculated and the midway point between them ("threshold") was used for determining the dates of retreat and advance. Annual ice retreat date occurred when the smoothed ice area met the threshold to the summer minimum, and the ice advance date occurred at the same intersect to the winter maximum. The dates, and the difference between them (i.e., ice-free season), were analyzed for temporal trends. Mean summer concentration was calculated using mean daily ice concentration for the ice-free period, as defined using a segmented regression. We also calculated the rate of sea ice decay following Lunn et al. (2016), using the absolute values of slope for ice concentration during the break-up season each year, which were then analyzed similar to other metrics.

We linearly modelled each metric and conducted Durbin-Watson tests for autocorrelation of residuals (using the *car* R package; Fox & Weisberg 2019). Where autocorrelation was not detected (i.e., Durbin-Watson $p>0.05$), we analyzed the data using both linear models (using the base R *lm* function) and non-linear local regressions (using the *gam* function from the *gam* package, where the span=0.5; Hastie 2020). Where autocorrelation was detected (i.e., Durbin-Watson $p\leq0.05$), we used linear models fit with generalized least squares using the *nlme* package, with an autocorrelation of order 1 (i.e., correlation=corAR1; Pinheiro et al. 2020), as well as the same non-linear local regressions as above, but with an autocorrelation of order 1 (Hastie 2020). We analyzed the relationship between each metric with AO and NAO, using seasonal means created from the daily values. We determined the correlation of each seasonal

AO and NAO for the same season as each metric, as well as lag effects; twenty-five models were used in total (Table 1; see Appendix A for how lag effects were determined). Top models were determined using corrected Akaike information criterion (AIC_c) and in most models with AO or NAO incorporated, AIC_c values increased after a one-year lag. Thus, we analyzed lag effects up to one year and one season before the seasonal metric being analyzed, where the first season (i.e., no lag) was unique to each metric being analyzed (e.g., ice advance start dates fall within freeze-up and the rate of ice decay falls within the break-up). To calculate the change in each metric per decade, we determined the slope of linear regressions for each metric plotted by year and multiplied the slope by 10.

Table 1: Models used to analyze each sea ice metric (dates of advance and retreat, ice-free period duration, mean summer concentration, and rate of decay) within Davis Strait* (1979-2020), where superscripts denote the lag used for incorporating the Arctic (AO) or North Atlantic (NAO) oscillations: 0 = no lag; #s = number of seasons; #y = number of years. Models 2-13 are duplicates except for the oscillation used – one uses NAO, the other AO.

Model #	Predictor variables used in each model	K
1	year	1
2	$(N)AO^{0}$	1
3	$(N)AO^{1s}$	1
4	$(N)AO^{2s}$	1
5	$(N)AO^{3s}$	1
6	$(N)AO^{1y}$	1
7	$(N)AO^{1y+1s}$	1
8	$(N)AO^{0}$ + year	2
9	$(N)AO^{1s}$ + year	2
10	$(N)AO^{2s}$ + year	2
11	$(N)AO^{3s}$ + year	2
12	$(N)AO^{1y}$ + year	2
13	$(N)AO^{1y+1s}$ + year	2

*For additional information regarding how seasonal NAO means were incorporated into the sea ice analyses, see Table 12 in the Appendix.

Capture and handling

Between 1991 and 2001, adult (≥ 5 years old) female polar bears were located by helicopter, immobilized following Stirling et al. (1989), and equipped with Argos satellite PTT transmitters (Telonics, Mesa, AZ) programmed to provide one location/week with a spatial accuracy of ~2 km (Fancy et al. 1988). Reproductive status was recorded at capture. At the time of capture, there were 11 single adult females, 5 with cubs of the year, and 7 with yearlings (n=23). Six adult males were also ear tagged. Procedures were approved by the Environment and Climate Change Canada Prairie and Northern Region Animal Care Committee. We removed males, spurious locations, those with speeds >5 km/h (n=4), as polar bears rarely travel >4 km/h (Andersen et al. 2008), and duplicates (i.e., same individual and date), using the first recorded location per day. All on-land locations were also removed.

Most harp seals were captured and released in 1995, 1996, and 2004 during the moult season on the sea ice off Newfoundland using a throw net (Stenson & Sjare 1997; G. Stenson, personal communication, July 15, 2021). Seals were transported by ship to the Ocean Sciences Centre, Memorial University, St. John's NF, where they stayed until their moult was complete (Stenson & Sjare 1997). Following completion of the moult, seals were immobilized and Argos satellite PTT transmitters were attached to the new hair at the back of their necks using epoxy resin (Stenson & Sjare 1997), then were released near St. John's between May and June. In 1993, one seal was captured in a seal net near Nain, NF where it was immobilized, tagged, and released. The transmitters were programmed to provide up to 200-500 locations/day, although these were filtered so only the best location per day was retained (Stenson & Sjare 1997). Transmitters fell off by the following years' moult. Capture procedures were approved by Department of Fisheries and Oceans' Animal Care Committee. We removed spurious locations and spatial duplicates. We also filtered for speed, removing those with >32 km/h between locations; while this is conservative compared to other studies (Nordøy et al. 2008), it has been estimated that seals can travel at ~32 km/h (Sergeant 1991).

Annual home range sizes

We estimated individual annual home range sizes for both polar bears and harp seals using both 95% minimum convex polygons (MCPs) and 95% kernel density estimates (KDEs). MCPs were created using the *adehabitat* R package (Calenge 2006). No bear years in our dataset had 100 locations (mean n fixes/yr=27; max=62), the suggested sample size for MCPs (Bekoff & Mech 1984), so we used bears and seals with ≥50 locations. We also used a plug-in kernel density estimate (KDE) method (Tétreault & Franke 2017; Fletcher & Fortin 2018) for individuals using the *ks* R package (Chacón & Duong, 2018) and the asymptotic mean squared error (or *amse*) pilot (Tétreault & Franke 2017). For polar bears, we also used two other KDE Methods: 1) a least squares cross validation KDE, and 2) a first-generation smoothing reference KDE. The former did not work with our dataset, however, and the second over-estimated home range sizes, the results of which can be found in Appendix B (Figures 12-13). Home ranges were mapped in QGIS (QGIS Development Team 2019). To assess home range sizes for polar bears over time, we modelled the yearly means of each metric using linear regressions (and using the base R *lm* function).

Seasonal movement rates and directionality

Polar bear movement rates (km/h) were quantified using the *argosfilter* R package (Freitas 2012). To address pseudoreplication, we limited the data to one year per bear, and used the year with the most locations. Movement data were not normally distributed, even when $\log_{10}$ transformed (Kolmogorov-Smirnov test in base R, $p<0.05$) so we compared sea ice season and movement rates using a Kruskal-Wallis test (from the *rstatix* R package; Kassambara 2021). We then used a pairwise Wilcox test (using the base R *pairwise.wilcox.test* function) to test differences between seasons.

Using the same data noted above, we assessed seasonal directionality of polar bear movement using the R *argosfilter* package (Freitas 2012) to account for temporal autocorrelation. We used a Rayleigh test in the *circular* R package (Lund et al. 2017) to determine if there were significant differences between seasons in directionality. We then used Watson's two-sample test of homogeneity (using the *circular* R package; Lund et al. 2017) to determine seasonal differences.

Seasonal habitat selection

To analyze habitat selection, we used daily mean sea ice concentration using the *raster* R package (Hijmans et al. 2020), distance to open water for each location (i.e., to centre of the closest open water pixel for each date) using the *RANN* R package (Arya et al. 2019), bathymetry (General Bathymetric Chart of the Oceans n.d.), and distance to land using shoreline shapefiles (Table 2; Natural Earth 2021). Mapping data were re-projected to polar stereographic to match the sea ice rasters. Analyses were conducted in either R, (R Core Team 2019) through the RStudio interface (RStudio Team 2015), or in QGIS (QGIS Development Team 2019).

To analyze habitat selection, we generated random points within a circular buffer around each on-ice used location (Arthur et al. 1996; Boyce et al. 2002). The radius of the buffers was calculated by multiplying the mean daily movement rate by the mean number of days between fixes. Movement rates were calculated using the *argosfilter* R package (Freitas et al. 2008). We removed land and generated 50 random points within each buffer using the *spatialEco* R package (Evans 2020), which were the available habitat. Used and available sea ice data were matched to the same day (Arthur et al. 1996). Covariates were tested for correlation in each season using a Pearson correlation matrix (Durner et al. 2009); covariates with a correlation coefficient of $r = |0.6|$ were not included in the same models together.

Table 2: Habitat covariates, with their abbreviations and format types, used to create seasonal resource selection functions for the analysis of polar bear and harp seal habitat selection in Davis Strait

Covariate	Abbreviation	Format type
Individual identification	ID	Discrete
Sea ice concentration	ICE	Continuous
Bathymetry	BATH	Continuous
Distance to open water	LAND	Continuous
Distance to land	WATER	Continuous

We created seasonal RSFs for both species with individual fixes pooled by season. To determine seasonal overlap between polar bears and harp seals, we mapped 100% minimum species-specific convex polygons in each sea ice season. We created RSFs for seals only during the season when they overlapped with bears. We used mixed effect logistic regressions where environmental covariates were fixed effects, and random effects were the intercept of individuals to account for individual variation in resource selection (Muff et al. 2020). We scaled and centered all covariate values (where mean=0 and SD=1) and only used individuals that had ≥20 locations for each RSF and ensured that we had ≥5 individuals per RSF for mixed effects models (Gelman & Hill 2006). For polar bears, we created two sets of RSF models: one where all used and available points were used, and another where all points with sea ice that was ≤15% in concentration were removed, as this is often a threshold used to determine the presence of sea ice, which was the focus of this study (e.g., Parkinson 2014; Atwood et al. 2016; Stern & Laidre 2016). Because harp seals often require less ice or open water for swimming (Lavigne & Kovacs 1988; Smith & Stirling 2019) we did not feel these additional models were meaningful for this species. Top models were chosen using both corrected Akaike Information Criterion (AICc) scores, which account for small sample sizes, and AIC weights (Burnham & Anderson 2002).

Polar bear and harp seal habitat overlap

We used two methods to analyze seasonal overlap in space and habitat use between DS polar bears and harp seals. We first created maps of the seasonal RSF predictions for each species, separating the predicted values into 5 equal area bins, where higher values were considered higher quality habitat than lower values. We then mapped the two species' RSF predictions by season and determined the areas where they overlapped. Because the sea ice data can change daily or significantly within seasons, we chose one random day per season to illustrate the maps: freeze-up = Dec 2, 2005 and break-up = Jun 16, 1990. The second method involved creating both 50% and 95% KDEs for each species and pooled data for each species by season. The maps of each were overlain to determine the area of overlap. The final maps for both methods were created in QGIS (QGIS Development Team 2019).

Results

Historical and current trends in Davis Strait sea ice

The 100% minimum convex polygon we used to analyze sea ice trends covered 1,141,625 km^2 (Figure 1). Examining the effect of NAO and AO, we found that the majority (75%) of the top models included NAO rather than AO (Table 13 in Appendix A). Although the non-linear models illustrated some cyclicity in the data, they occur on a longer timescale than the location datasets used in our study, and thus do not affect them (Figure 11 in Appendix A). The linear trends illustrate broad patterns, which were sufficient for our understanding of the general sea ice conditions within Davis Strait. Thus, we focus only on NAO and linear models (see AO and non-linear analyses in Appendix A).

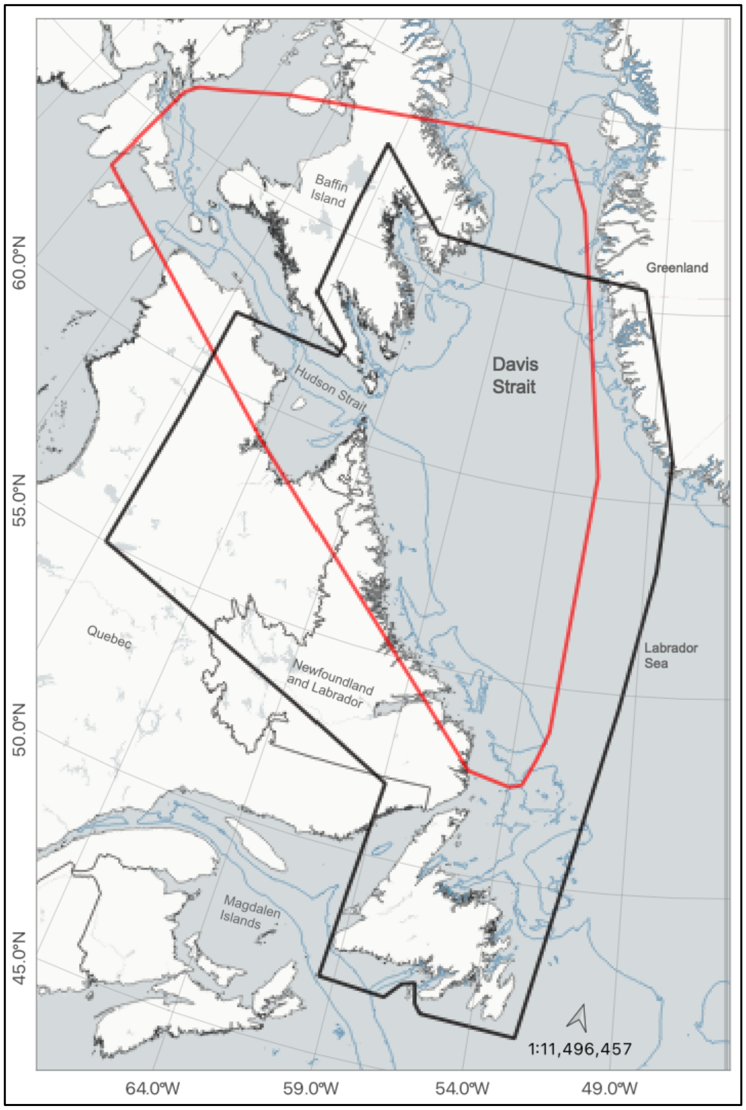

Figure 1: The Davis Strait subpopulation of polar bears. The management area is delineated in black, a 100% minimum convex polygon of all polar bear locations is outlined in red, and the 300 m contour for ocean depth is outlined in blue. Bathymetry data was obtained from the General Bathymetric Chart of the Oceans (General Bathymetric Chart of the Oceans n.d.), DS management area was digitized from a map of polar bear subpopulations (Environment and Climate Change Canada 2018).

The mean ice area between March and September (the maximum and minimum months, respectively) made up the threshold (381,533 km^2) used to determine the dates of ice retreat and advance (Figure 10 in the Appendix A). Ice advance dates were not temporally correlated (Durbin-Watson $p=0.17$), but dates of retreat were (Durbin-Watson $p=0.04$). Ice advance dates were significantly later over time (linear regression $p<0.001$). There was no significant difference between the two top models for dates of retreat ($\Delta AIC_c < 2.0$; Table 3), but both illustrated that the dates occurred earlier over time (linear regressions $p<0.001$). The ice-free period lengthened over time (Figure 2; linear regression $p=0.01$); this metric was temporally correlated (Durbin-Watson $p=0.008$). The dates of retreat occurred 5.4 d/decade (SE=1.3) earlier, while the dates of advance occurred 5.3 d/decade (SE=1.1) later resulting in the ice-free period lengthening 10.7 d/decade (SE=2.1; Table 4). NAO affected these three metrics differently. For the ice-free period duration, no NAO lag was detected, but dates of sea ice advance had a one-year lag and dates of retreat had a lag of two to three seasons (Table 3).

Mean summer ice concentration values were not temporally correlated (Durbin-Watson $p=0.48$), so linear models were used. The top model indicated that mean summer sea ice concentration significantly decreased over time (linear regression $p<0.001$; Figure 2), and that NAO had a lag effect of two seasons (Table 3). Mean summer concentration decreased by 0.4 percent/decade (SE=0.1; Table 4). Rate of decay was not temporally correlated by year (Durbin-Watson $p=0.62$). There was no significant difference between the three top models for rate of decay ($\Delta AIC_c < 2.0$), and each illustrated no significant linear trend (all linear regressions $p>0.05$).

Table 3: Top three models for each sea ice metric* (dates of advance and retreat, ice-free period duration, mean summer concentration, and rate of decay) analyzed in Davis Strait (1979-2021). Linear regressions are listed in order of AIC_c ranking and top models are bolded.

Model #	Variables^a	AIC_c	ΔAIC_c	Adjusted R^2	RSE
Dates of advance					
12	**NAO^{1y} + year**	**302.73**	**0.00**	**0.4699**	**9.023**
9	NAO^{1s} + year	306.32	3.59	0.3534	9.427
13	NAO^{1y+1s} + year	314.91	12.18	0.2865	10.470
Dates of retreat					
10	**NAO^{2s} + year**	**303.59**	**0.00**	**--**	**10.095**
11	NAO^{3s} + year	304.59	1.00	--	10.536
4	NAO^{2s}	305.90	2.31	--	12.350
Ice-free period duration					
8	**NAO^{0} + year**	**334.77**	**0.00**	**--**	**16.353**
2	NAO^{0}	336.97	2.20	--	19.731
11	NAO^{3s} + year	342.51	7.74	--	16.881
Mean summer concentration					
10	**NAO^{2s} + year**	**-310.65**	**0.00**	**0.4392**	**0.006**
1	year	-306.96	3.69	0.3691	0.006
9	NAO^{1s} + year	-305.58	5.07	0.369	0.007
Rate of decay					
2	**NAO^{0}**	**-486.70**	**0.00**	**0.023**	**0.001**
8	NAO^{0} + year	-486.67	0.03	0.053	0.001
3	NAO^{1s}	-486.61	0.09	0.021	0.001

*See Table 1 for superscript definitions

Table 4: Trends in dates of sea ice advance (days/decade), retreat (days/decade), ice-free period duration (days/decade), mean summer concentration (percent/decade), and the number of ice-covered days (days/decade) for Davis Strait from 1979-2021.

	Advance dates	Retreat dates	Ice-free period duration	Mean summer concentration
Trend	+5.3	-5.4	+10.7	-0.4
P	<0.001	<0.001	<0.001	<0.001

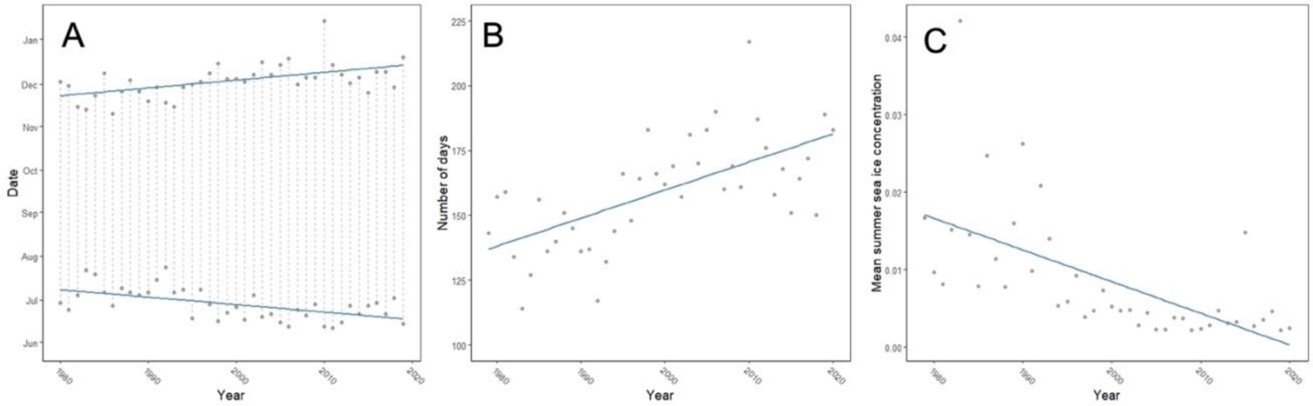

Figure 2: Sea ice analysis of Davis Strait from 1979-2021, including: A) dates of sea ice retreat and advance, B) ice-free season duration, and C) mean summer sea ice concentration. Linear regressions are illustrated in blue, and all are significant (p<0.001).

Annual home range sizes

Polar bear telemetry data provided 1,903 locations for 29 bears and we retained 1,351 locations for 22 bears (71% of original dataset), with a mean of 61 locations/bear (SE=5.3, range 23–119) between 1991 and 2001 excluding 1996 due to lack of data. Seven bear years were included in the MCP analysis, and the mean annual home range was 137,336 km^2 (SE=73,985 km^2, range 49,362–280,539 km^2; Table 5; Figures 3-4). Thirty-one bear years were used for annual 95% KDEs which averaged 66,215 km^2 (SE=59,688 km^2, range 699–233,927 km^2; Table 5; Figures 3-4). Mean home range sizes did not change over time for both home range estimators (i.e., linear regressions p >0.05).

Harp seals tags provided 5,859 locations and we retained 5,686 locations with a mean of 139 locations/seal (SE=25, range 4–624) from 1993 to 1995 and 2004 to 2005. Twenty-nine seal years were included in the MCP analysis and the mean annual home range 495,150 km^2 (SE=56,179 km^2, range 29,687–965,800 km^2; Figure 4). For annual 95% KDEs, 37 seal years were included with a mean of 256,016 km^2 (SE=31,566 km^2, range 16,156–612,715 km^2; Figure 4).

Table 5: Mean annual 95% home range sizes using minimum convex polygons and kernel density estimates for Davis Strait polar bears (1991-1999).

Year	Minimum convex polygon		Kernel density estimate	
	# Individuals	Mean area	# Individuals	Mean area (km^2)
1991	1	177,325	1	59,762
1992	--	--	2	103,044
1993	1	103,162	7	69,888
1994	4	137,011	9	79,400
1995	1	132,818	5	53,517
1998	--	--	3	61,384
1999	--	--	4	32,801

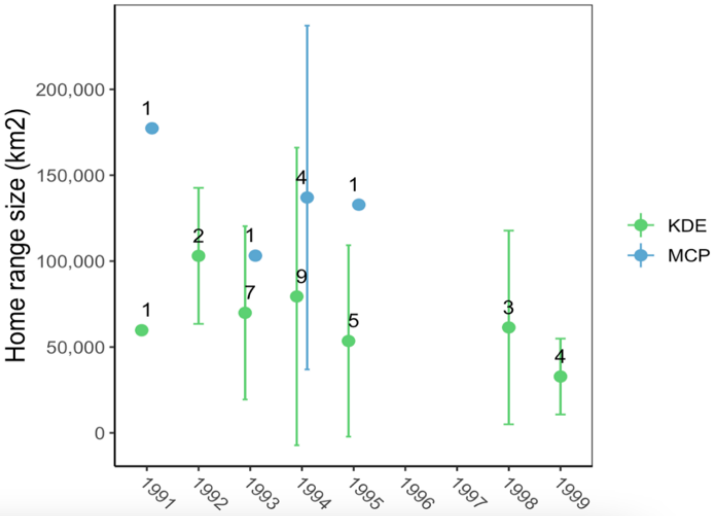

Figure 3: Mean home range sizes (95%), with standard deviations, for female polar bears in Davis Strait from 1991-2001 tracked by satellite radio collars. Two metrics were used: MCP = minimum convex polygon; KDE = kernel density estimates.

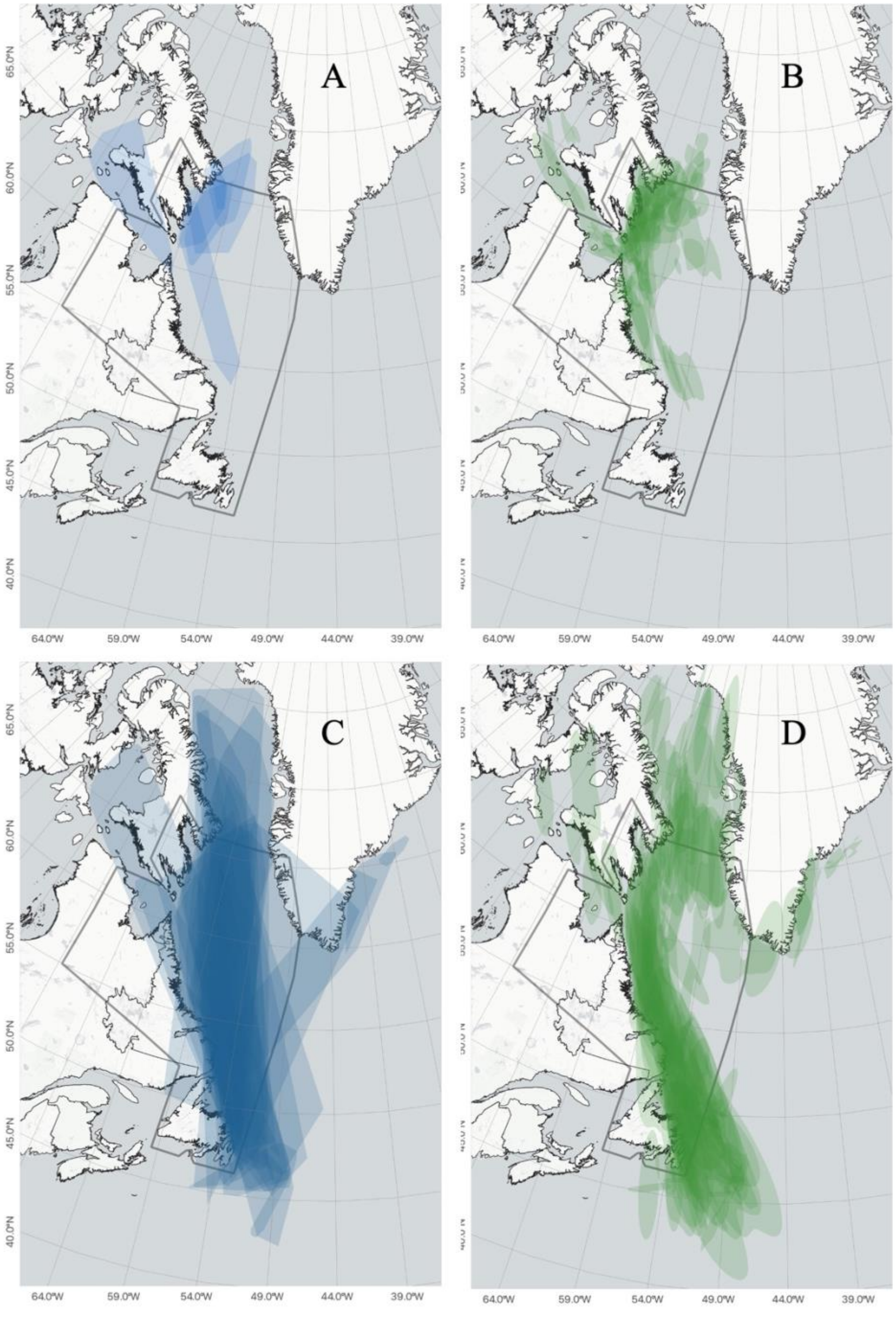

Figure 4: Annual 95% home ranges for female polar bears in Davis Strait (1991-2001) and Northwest Atlantic harp seals (1993-2005) tracked by satellite radio collars where minimum convex polygons (MCPs) are in blue and kernel density estimates (KDEs) are in green: A) MCPs for polar bears (n= 7), B) KDEs for polar bears (KDE, n=31), C) MCPs for harp seals (n=29), and D) KDEs for harp seals (n=37). The Davis Strait management area was digitized from a map of polar bear subpopulations (Environment and Climate Change Canada 2018).

Seasonal movement rates and directionality

The start dates for each season were: winter – Feb 20, break-up – Apr 26, ice-free – Jul 31, and freeze-up – Nov 2. The pairwise Wilcox test found significant differences in polar bear (n=27) movement rates between winter and both break-up and freeze-up (Table 6; Figure 5). Break-up and freeze-up were not significantly different from one another (Table 6; Figure 5). The overall mean speed of bears was 0.53 km/h pooled across seasons with a mean of 0.39 km/h in freeze-up (range: 0.00-0.83; SE: 0.07), 0.58 km/h in winter (range: 0.05-2.19; SE: 0.08), and 0.46 km/h in break-up (range: 0.05-1.37; SE: 0.05).

Table 6: Pairwise Wilcox test results for comparing movement rates between sea ice seasons for Davis Strait polar bears. Significant differences are bolded.

Seasons	Break-up	Freeze-up
Freeze-up	0.11	-
Winter	**0.04**	**0.002**

Bears showed significant orientation during break-up and freeze-up (Rayleigh test $p<0.05$; Figure 5). Polar bears moved northward in freeze-up and southward in break-up but had no significant orientation in the winter. The Watson's two-sample test of homogeneity found significant differences in seasonal directionality of movement. Freeze-up was significantly different than each of the other seasons, which were not different from one another (Table 7; Figure 5).

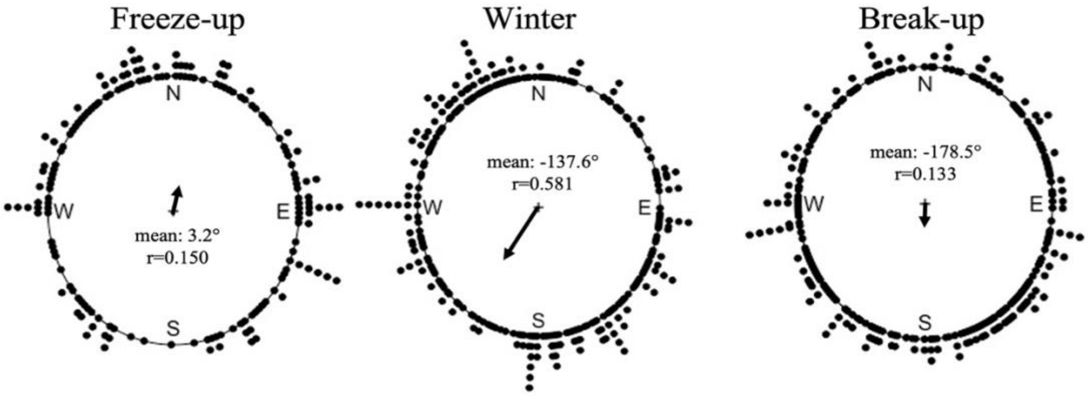

Figure 5: Mean direction of movement (degrees) between consecutive locations for Davis Strait polar bears by season (1991-2001), collected by telemetry data. All individual polar bear directions are illustrated with points outside the circle, with the mean of each season highlighted with an arrow and text. Rayleigh test results are also illustrated (r values), with the length of the arrow illustrating the strength of the relationship (where the edge of the circle = 1.0).

Table 7: Watson's two-sample test results for comparing movement directionality between sea ice seasons for Davis Strait polar bears. Significant differences are bolded.

Seasons	Break-up	Freeze-up
Freeze-up	**<0.001**	-
Winter	0.10	**<0.001**

Seasonal habitat selection

For polar bears, a 94 km radius was used to delineate available habitat and was based on a 9-d movement rate (the mean time between fixes was 8.6 d) and a mean daily movement rate of 10.4 km/d. For harp seals, we used a radius of 78 km, based on a mean time between fixes of 1.8 d and a mean movement rate of 44 km/d. For both polar bears and harp seals, fourteen candidate models were created for each RSF, with variations that include quadratic terms for both ice concentration and distance to open water (Table 8). Where covariates were correlated seasonally, models with correlated covariates were not included for that season.

Table 8: Candidate resource selection function models used to analyze seasonal Davis Strait polar bear (1991-2001) and harp seal (1993-2005) resource selection from telemetry data and environmental variables: ocean depth (DEPTH), sea ice concentration (ICE), quadratic sea ice concentration (ICE^2), distance to land (LAND), distance to water (WATER), and quadratic distance to water ($WATER^2$). The variations (e.g., a or b) for models 2, 4-5, and 7-14 include the quadratic terms for sea ice concentration and/or distance to water.

Model #		Covariates used in each model
Null		ID
1		ID + DEPTH
2	a	ID + ICE
	b	ID + ICE + ICE^2
3		ID + LAND
4	a	ID + WATER
	b	ID + WATER + $WATER^2$
5	a	ID + DEPTH + ICE
	b	ID + DEPTH + ICE + ICE^2
6		ID + DEPTH + LAND
7	a	ID + DEPTH + WATER
	b	ID + DEPTH + WATER + $WATER^2$
8	a	ID + ICE + LAND
	b	ID + ICE + ICE^2 + LAND
9	a	ID + ICE + WATER
	b	ID + ICE + ICE^2 + WATER
	c	ID + ICE + WATER + $WATER^2$
	d	ID + ICE + ICE^2 + WATER + $WATER^2$
10	a	ID + LAND + WATER
	b	ID + LAND + WATER + $WATER^2$
11	a	ID + ICE + DEPTH + LAND
	b	ID + ICE + ICE^2 + DEPTH + LAND
12	a	ID + ICE + DEPTH + WATER
	b	ID + ICE + ICE^2 + DEPTH + WATER
	c	ID + ICE + DEPTH + WATER + $WATER^2$
	d	ID + ICE + ICE^2 + DEPTH + WATER + $WATER^2$
13	a	ID + DEPTH + LAND + WATER
	b	ID + DEPTH + LAND + WATER + $WATER^2$
14	a	ID + DEPTH + ICE + LAND + WATER
	b	ID + DEPTH + ICE + ICE^2 + LAND + WATER + $WATER^2$

For polar bears, in both freeze-up and winter, ocean depth and distance to land were correlated, so models 6, 11, 13, and 14 were not analyzed for those seasons (Table 14 in Appendix C). No covariates were correlated in break-up, so all 14 models were used (Table 14 in Appendix C). Where all points were used, the freeze-up RSF for polar bears had 165 used (n=5 bears; mean # points=33/individual; range=31-41/individual) and 8,250 available points. The top model included ocean depth, sea ice concentration, and sea ice concentration^2 (Table 9; Table 15 & Figures 14, 17-19 in Appendix C). When points associated with ≤15% ice concentration were removed (n=5 bears; mean # points=31/individual; range=25-34/individual; 145 used points [88% of dataset] and 7,747 available), the top model was the null model (Table 9; Table 15 & Figure 14 in Appendix C). The winter seasonal RSFs with all points had 232 used (n=9 bears; mean # points=21/individual; range=21-47/individual) and 11,600 available points. The top model was the same as freeze-up (Table 9; Table 15 & Figure 14 in Appendix C). When points associated with ≤15% ice concentration were removed, 4 bears were dropped due to data loss (n=5 bears; mean # points=28.4/individual; range=21-46/individual; 201 used points [87% of dataset] and 11,162 available). The top model for this was also the null (Table 9; Table 15 in Appendix C). The break-up RSF with all points had 317 used (n=10 bears; mean # points=74/individual; range=20-180/individual) and 15,850 available points. The top model was different from the other two seasons and included distance to land, sea ice concentration, and sea ice concentration^2 (Table 9; Table 15 and Figure 20 in Appendix C). When low-ice points were removed, 1 bear was removed due to data loss (n=9 bears; mean # points=28.7/individual; range=24-42/individual; 297 used points [94% of dataset] and 15,725 available). The top model included only distance to land (Table 9; Table 15 in Appendix C). When all points were used, selection for all covariates varied among seasons. In freeze-up and winter, bears selected for shallow water and low sea ice concentrations (Figure 15 in Appendix C). In break-up they also selected for low sea ice concentrations, but ocean depth was not a significant covariate and instead they selected to be closer to shore (Figure 15 in Appendix C).

Polar bears and harp seals overlapped in freeze-up and break-up but not in winter (Figure 6), possibly because harp seals are primarily pelagic (Smith & Stirling 2019) and may spend most of their time in open water during winter. Therefore, we only analyzed seasonal habitat selection for harp seals during freeze-up and break-up. The freeze-up RSFs for harp seals had 1,122 used (mean=86/individual; range=32-241/individual) and 56,100 available with the top model including ocean depth, sea ice concentration, distance to open water, and distance to open water^2 (Table 10; Table 16 in Appendix C). The break-up RSFs had 1,773 used (mean=74/individual; range=20-180/individual) and 88,650 available points and the top model included ocean depth, distance to land, distance to open water, and distance to open water^2 (Table 10; Table 16 in Appendix C). In both seasons harp seals selected for shallow water. In freeze-up, however, they selected to be farther from open water than in break-up. They also selected for lower sea ice concentrations during freeze-up and to be closer to shore during break-up (Figures 16, 21-22 in Appendix C).

Table 9: Top 3 model results for each seasonal resource selection function (freeze-up, winter, and break-up) used to analyze Davis Strait polar bear resource selection (1991-2001) on sea ice concentration above 15%. Models are listed in order of AICc ranking and weight. See Table 8 for the predictor variables used in each model.

Model #	Covariates	K	Deviance	Log likelihood	AICc	ΔAIC	AICw
Freeze-up (all points)							
5b	ID + DEPTH + ICE + ICE ^{2}	4	1589.7	-794.9	1599.71	0.0	0.45
5a	ID + DEPTH + ICE	3	1592.0	-796.0	1600.01	0.3	0.38
12b	ID + ICE + ICE^2 + DEPTH + WATER	5	1643.8	-794.8	1601.58	1.9	0.17
Freeze-up (without low ice)							
Null	ID	1	1446.4	-723.2	1450.41	0.0	0.50
4b	ID + WATER + WATER^2	3	1443.4	-721.7	1451.45	1.04	0.30
1	ID + DEPTH	2	1446.2	-723.1	1452.16	1.75	0.21
Winter (all points)							
5b	ID + DEPTH + ICE + ICE ^{2}	4	2199.1	-1099.5	2209.09	0.0	0.63
12b	ID + DEPTH + ICE + ICE^2 + WATER	5	2198.8	-1099.4	2210.83	1.74	0.26
12d	ID + DEPTH + ICE + ICE^2 + WATER + WATER^2	6	2198.5	-1099.2	2212.51	3.42	0.11
Winter (without low ice)							
Null	ID	1	1398.2	-699.1	1402.15	0.0	0.37
1	ID + DEPTH	2	1396.3	-698.2	1402.34	0.19	0.34
3	ID + LAND	2	1396.6	-698.3	1402.65	0.5	0.29
Break-up (all points)							
8b	ID + ICE + ICE^2 + LAND	4	3064.8	-1532.4	3074.82	0.0	0.66
11b	ID + ICE + ICE^2 + DEPTH + LAND	5	3064.8	-1532.4	3076.77	2.0	0.24
14b	ID + DEPTH + ICE + ICE ^{2} + LAND + WATER	6	3064.7	-1532.4	3078.73	3.9	0.09
Break-up (without low ice)							
3	ID + LAND	2	2833.5	-1416.8	2839.54	0.0	0.44
8a	ID + ICE + LAND	3	2831.9	-1415.9	2839.88	0.34	0.37
6	ID + DEPTH + LAND	3	2833.2	-1416.6	2841.22	1.68	0.19

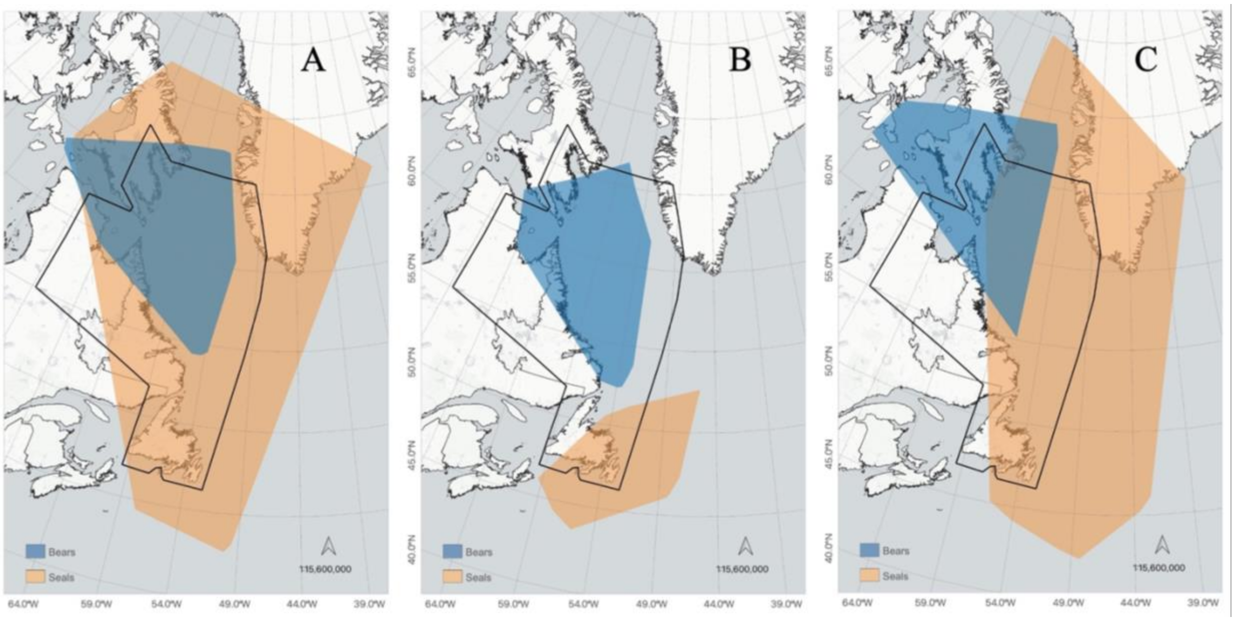

Figure 6: 100% minimum convex polygons for polar bears (1991-2001; blue) and harp seals (1993-2005; orange) collected using satellite telemetry in Davis Strait by sea ice season, where A) freeze-up; B) winter; C) break-up.

Table 10: Top 3 model results for each seasonal resource selection function (freeze-up, winter, and break-up) used to analyze Davis Strait harp seal resource selection (1993-2005). Models are listed in order of AIC ranking and weight (AICw).

Model #	Covariates	K	Deviance	Log likelihood	AIC	ΔAIC	AIC_w
Freeze-up							
12c	ID + DEPTH + ICE + WATER + $WATER^2$	5	10970.1	-5485.1	10982.14	0.0	0.42
7b	ID + DEPTH + WATER + $WATER^2$	4	10972.4	-5486.2	10982.43	0.3	0.36
13b	ID + DEPTH + LAND + WATER + $WATER^2$	5	10971.4	-5485.7	10983.45	1.3	0.22
Break-up							
13b	ID + DEPTH + LAND + WATER + $WATER^2$	5	17251.1	-8625.5	17263.10	0.0	0.50
7b	ID + DEPTH + WATER + $WATER^2$	4	17253.9	-8626.9	17263.87	0.77	0.34
14d	ID + DEPTH + ICE + ICE^2 + LAND + WATER + $WATER^2$	5	17249.4	-8624.7	17265.40	2.3	0.16

Polar bear and harp seal habitat overlap

After removing the polar bear points associated with sea ice concentration ≤15%, the only season with a top model that was not the null was the break-up season. We believe that one seasonal RSF map does not adequately explain the spatial relationship between these two species, so we focus on the overlap in utilization distributions for the remainder of this study instead.

When comparing utilization distributions between species, polar bears did not overlap with the 50% KDE (or “high-use habitat”) for seals in all seasons (Figure 7). However, the 95% (or “low-use habitat”) for seals did overlap with bears’ high-use habitat (50%). In freeze-up, the area of overlap between both species’ low-use habitat (95%) was 171,060 km^2, which makes up 33.9% of bears’ low-use habitat (Table 11). The area of overlap between the seal low-use and bear high-use habitat was 28,413 km^2, making up 30.3% of bear high-use habitat (Table 11). In break-up, the low-use habitat overlap made up 46,712 km^2, which is 13.2% of bear low-use habitat (Table 11). The overlap between seal low-use and bear high-use habitat, however, made up 6,213 km^2, equivalent to 10.3% of bear high-quality habitat (Table 11).

Table 11: Total areas (km^2) of polar bear (1991-2001) and harp seal (1993-2005) seasonal kernel density estimates (both 50% and 95%) collected using satellite telemetry in Davis Strait.

Season	Bears		Seals		Overlap	
	95%	50%	95%	50%	95%	50% bears & 95% seals
Freeze-up	505,214.18	93,813.66	1,465,177.65	294,196.27	171,059.89	28,413.38
Break-up	353,968.96	60,071.88	1,059,787.45	217,451.96	46,712.32	6,213.48

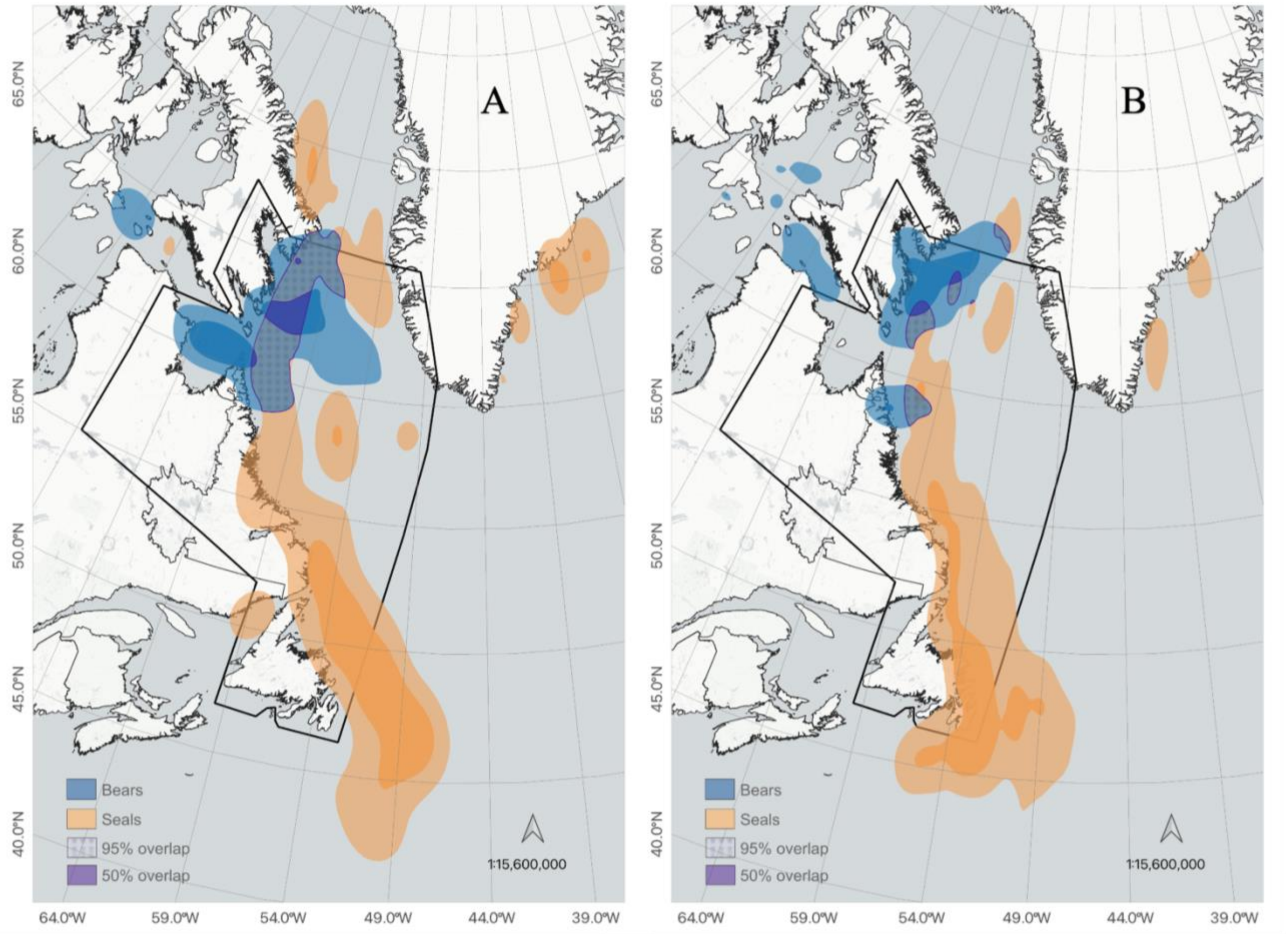

Figure 7: Kernel density estimates (DEs) for polar bears (1991-2001; blue) and harp seals (1993-2003; orange) collected using satellite telemetry in Davis Strait, where A) freeze-up and B) break-up. Both 95% (low-quality habitat; lighter shade) and 50% (high-quality habitat; darker shade) KDEs are included for each species. The overlap between the 95% seal KDE and the 95% bear KDE (light purple) as well as the overlap between the 95% seal KDE and the 50% bear KDE (dark purple) are included.

Discussion

Both polar bear and harp seal space use and habitat selection are influenced by sea ice seasons in Davis Strait. Yet, sea ice conditions within the Davis Strait region changed over the satellite record. Most significant to polar bears is the lengthening of the ice-free season; our results using a longer time series support earlier findings (Stern and Laidre 2016) that break-up is advancing and freeze-up is delaying over time. Other studies have illustrated the negative impacts of a longer fasting period on polar bear body condition, survival, and reproductive rates (Stirling et al. 1999; Regehr et al. 2007; Rode et al. 2010; Johnson et al. 2020). Stern & Laidre (2016) found that the ice-free season was lengthening by 16.6 d/decade, but their study was focused on the management area in its entirety. Our study examined the area used by our tracked polar bears and we documented a lengthening of the ice-free period by 10.7 d/decade. This slower rate, in comparison to Stern & Laidre (2016), may be due to the incorporation of sea ice data from slightly north of the management area, which may be persisting due to its northward extent. Regardless, the ice-free season in Davis Strait is lengthening the fourth fastest of nineteen subpopulations with only the Arctic Basin, Barents Sea, and Southern Beaufort subpopulations showing a more rapid increase (Stern & Laidre 2016). The possible effects of a longer ice-free period on DS polar bear space use and habitat selection are unknown. In terms of their health, Galicia et al. (2019) found that Davis Strait polar bear body conditions decreased in the fall during years with an earlier break-up. Further, the NAO, which causes differences in temperature and precipitation in various regions in the northern hemisphere (Walker 1928; Johnston et al. 2005), has a strong influence on sea ice dynamics in Davis Strait (Johnston et al. 2005; Friedlaender et al. 2010), yet the effects are often lagged. While the link between NAO and sea ice loss has been well-established, it only partially explains the decreasing Arctic sea ice conditions (Johnston et al. 2005; Serreze et al. 2007). Johnston et al. (2005) speculated that positive NAO values might be buffering the effects of climate change on Arctic sea ice, while Ding, et al. (2014) suggest that the NAO may be partially the cause of the DS region warming faster than other parts of the Arctic. Regardless, with ongoing warming and the expected continued melting of Arctic sea ice (Stroeve et al. 2012), Arctic ecosystems may become increasingly vulnerable to changes in NAO cycles in the future (Johnston et al. 2005).

DS polar bears had seasonal differences in movement rates, moving fastest in winter (0.58 km/h) and slowest during freeze-up (0.39 km/h). This is similar to polar bears in Foxe Basin, also within the Seasonal Ice Ecoregion, that moved fastest in winter and break-up but slowest during freeze-up because of differences in resource availability (Sahanatien et al. 2015b). In Hudson Bay, however, bears moved fastest during freeze-up or break-up, likely due to high ice drift rates, and slowest during the ice-free season because they are not as active while on land (Parks et al. 2006). Overall, polar bears move differently in each season depending on where they occur across the Arctic (e.g., Amstrup et al. 2000; Parks et al. 2006; Sahanatien et al. 2015b; Hamilton et al. 2017b). Other studies found that movement rates were influenced by sea ice season, but different seasons affected each subpopulation differently; rates were also influenced by year, geography, reproductive status, or changing sea ice conditions (Amstrup et al. 2000; Parks et al. 2006; Sahanatien et al. 2015b; Durner et al. 2017; Hamilton et al. 2017a).

DS polar bears also had seasonal differences in orientation, moving northward during freeze-up and southward during break-up. In Western Hudson Bay, within the Seasonal Ice Ecoregion, polar bears moved northeast during freeze-up but had no significant directionality in break-up (Parks et al. 2006; Klappstein et al. 2020). DS polar bears were likely heading north along stable nearshore ice while it was forming, and the opposite during the time of year when the ice melted. Other studies have illustrated that directionality of polar bears in other subpopulations may be influenced by ice conditions, particularly during freeze-up and break-up, or ice drift (Amstrup et al. 2000; Durner et al. 2017). Our movement rates and directionality were not corrected for sea ice drift, which is corrected in some studies (Durner et al. 2017; Klappstein et al. 2020) but not others (Amstrup et al. 2000; Parks et al. 2006). Additionally, polar bear movement rates and directionality in some parts of the Arctic are changing over time due to changes in sea ice dynamics (Parks et al. 2006; Durner et al. 2017).

DS polar bear home ranges varied from approximately 700 to 280,000 km^2, which is similar to Ferguson et al. (1999) that estimated a home range area of approximately 230,000 km^2 in DS (Ferguson et al. 1999) and falls within the range of polar bear home range sizes in other parts of the Arctic (Ferguson et al. 1999; Mauritzen et al. 2001; McCall et al. 2014; Auger-Méthé et al. 2016). Polar bears in areas within the Seasonal Ice Ecoregion had larger home ranges than other subpopulations likely due to the use of terrestrial environments (Ferguson et al. 1999). Other studies found that polar bear home range sizes may be influenced by subpopulation, year, ocean depth, time on land, seasonal variation in ice cover, ice drift, ice break-up date, and reproductive status (e.g., Ferguson et al. 1999; Mauritzen et al. 2001; McCall et al. 2014; Auger-Méthé et al. 2016). Further, individual polar bear home range sizes can contract in response to reduced sea ice extent and may result in latitudinal shifts (Laidre et al. 2018a). How home range size in DS is being affected by less available sea ice in recent years cannot be assessed with existing data and new data would allow improved understanding of the effects of climate change on space use. Harp seals covered a larger area than polar bears, with individual home range sizes ranging from approximately 30,000 to 965,000 km^2, but there are no other harp seal home range studies for comparison.

Polar bear and harp seal habitat selection was also influenced by sea ice season. When polar bear points associated with <15% ice concentration were removed, the only season with a top model that was not the null was break-up. During break-up, distance to land was the only important covariate, with bears selecting to be closer to shore. This finding contrasts with Laidre, et al. (2018b), but aligns with other studies that suggest that polar bears remain on sea ice for as long as possible during break-up since feeding during late spring and early summer is vital to maintaining healthy body conditions through their fast and into the fall (Galicia et al. 2019). They may also remain close to land to reduce the chances of having to swim ashore once the ice has melted completely (McCall et al. 2016). For NA harp seal habitat selection, distance to open water and ocean depth were important in both freeze-up and break-up, but sea ice concentration was important only during freeze-up, while distance to land was during break-up. Seals selected for shallower water in both seasons, likely because shallower water over the shelves is more biologically productive (Sakshaug 2004). They selected to be farther from open water during freeze-up, but also selected lower sea ice concentrations, which does not align with being farther from open water. Harp seals are ice-edge species (Smith & Stirling 2019; Stenson et al. 2020) and the ice edge is typically closer to open water, yet our analysis illustrates that they are selecting to be farther from open water. From our analysis, it is unclear why this is the case. NA harp seals also selected to be close to land during break-up, likely because closer to shore was where the last of the ice remained and possibly because it is more biologically productive.

The utilization distributions illustrate seasonal differences in the overlap between both species' space use. More of their habitat overlapped in freeze-up versus break-up, regardless of low- or high-use habitat. We would have expected otherwise, as February-May is when harp seals are most likely to be on ice (Lavigne & Kovacs 1988), and Derocher, et al. (2002) found that harp seals were only predated on in June, both of which corresponds with the break-up season, the most important time of the year for polar bears to feed on seals (Stirling & Derocher 1993; Stirling et al. 1999; Durner et al. 2009). This is especially true for polar bears in the Seasonal Ice Ecoregion who must fast shortly after (Stirling & Derocher 1993; Stirling et al. 1999; Durner et al. 2009). We speculated that DS polar bears are feeding on other seal species during break-up and choose to feed on harp seals during freeze-up, but Thiemann, et al. (2008) found that DS polar bear consumption of harp seals was higher during break-up than freeze-up. Thiemann et al. (2008) also found that the diets of Davis Strait polar bears were affected by age but not by sex, so the different timing of prey overlap we found in our study may be associated with not including juveniles in our analysis. Because our study uses data from a small sample of adult female polar bears only, we could not investigate the space use of juveniles or males. The bears collared for our study do not overlap with harp seal pupping areas during the pupping season at all, which may also suggest that this subset of the DS subpopulation is not heavily feeding on harp seals during this time of year. Further, the sampling methods used to determine which individuals were tagged for both species may affect our results since polar bear space use can be influenced by the individual itself (Mauritzen et al. 2001).

While other studies have investigated space or habitat overlap between polar bears and other seal species (e.g., ringed seals), none has specifically investigated the overlap between polar bears and harp seals. Yet understanding predator-prey relationships is necessary to fully grasp a species' spatial ecology. Predators choose habitats based on where and when their primary prey occur in their greatest abundance or accessibility (Holt 2008; Scoboda et al. 2019). For polar bears this is especially true – with just one primary prey type, their survival is grounded in their ability to find seals (Stirling & Derocher 1993; Durner et al. 2009; Regehr et al. 2010). Investigating where these species occur together in a changing sea ice environment is useful for understanding how and why polar bear demographics change over time.

In 2005-2007 the DS subpopulation of bears had a high density of individuals and low reproduction rates compared to other subpopulations (Peacock et al. 2013). In 2021, a study concluded that the DS subpopulation is likely stable, with a small potential decline of <100 bears due to increased harvest rates in parts of their range (Dyck et al. 2021). Other than females with offspring, DS polar bears had better body condition than the earlier study, but the authors note that this could have been indirectly affected by increased harvest rates reducing density (Dyck et al. 2021). The authors also noted that the rate of sea ice decay was negatively correlated with adult and subadult survival and that the lack of data in the region limited insight into the population dynamics of DS polar bears (Dyck et al. 2021). Due to a lack of data, we could not assess differences between sexes, ages, or reproductive statuses for either species, which is necessary to extrapolate this study to the whole subpopulation. We also could not examine temporal trends in their space use and habitat selection. Investigating how species' movements and habitats are changing over time is critical to understanding how they respond to a changing environment. Sea ice model projections suggest that the whole Arctic Ocean may eventually become seasonally ice-free (Serreze et al. 2007; Dufresne et al. 2013), which will affect polar bears across the Arctic. Yet without recent data we are unable to understand how climate change may be affecting this subpopulation. The benefits of collecting polar bear satellite telemetry data are well understood, as are the consequences of not collecting it (Laidre et al. 2022). This study illustrates the need to acquire more telemetry and body condition data for the polar bears of Davis Strait as well as for their primary prey. With sea ice conditions projecting to decline in the future, the urgency of understanding how climate change may impact these bears is clear, but we need the data to effectively do so.

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Appendix A

Davis Strait sea ice analysis

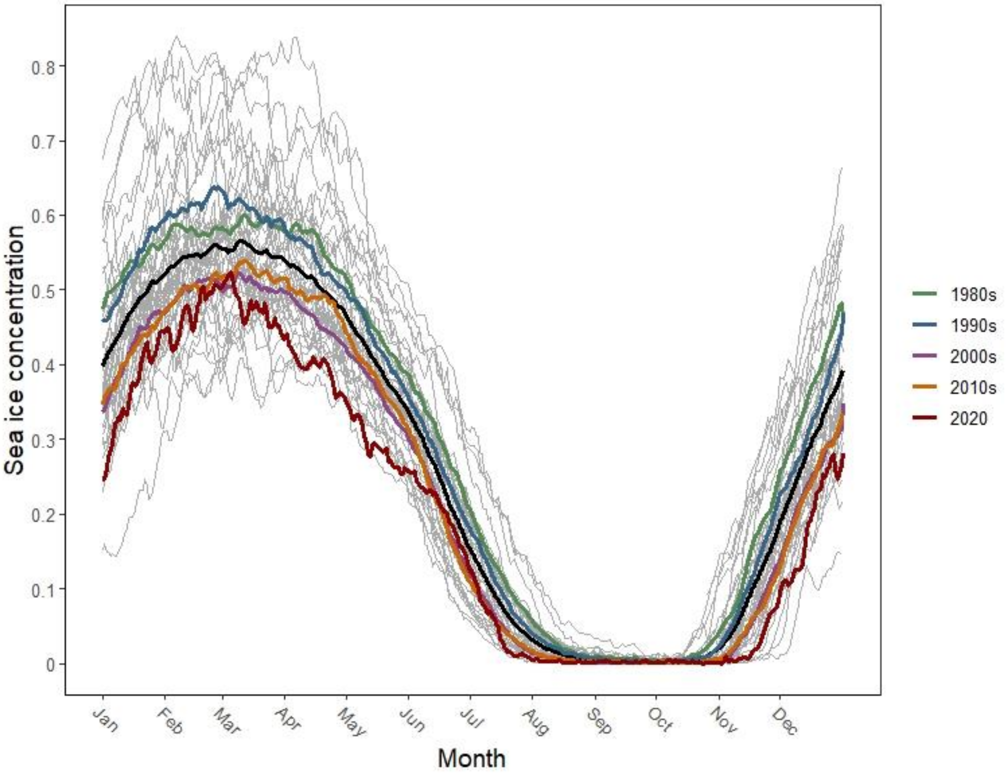

Figure 8: Daily sea ice concentration per year in Davis Strait from 1979-2021 with decadal means highlighted in varying colours and the overall mean in black.

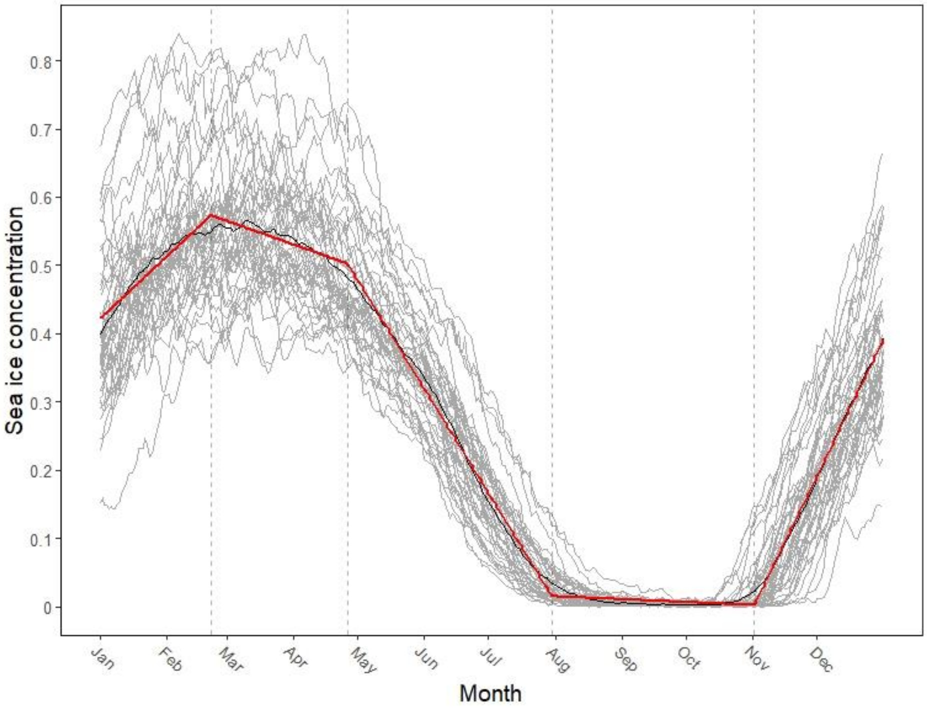

Figure 9: Daily sea ice concentration per year in Davis Strait from 1979-2021, with the segmented regression used to create sea ice seasons highlighted in red. Vertical dashed lines illustrate the start date for each season. These seasons were used to separate telemetry data into 4 seasons to analyze seasonal habitat selection for both species.

Table 12: Description of how seasonal oscillation means were incorporated into the analysis of each sea ice metric in Davis Strait (1979-2021)

	Same season	1 season lag	2 season lag	3 season lag	4 season lag	5 season lag
Retreat date						
	Break-up	Winter before	Freeze-up before	Ice-free before	Break-up before	Winter 2 years before
Advance date						
	Freeze-up	Ice-free before	Break-up before	Winter before	Freeze-up before	Ice-free 2 years before
Ice-free period duration						
	Ice-free	Break-up before	Winter before	Freeze-up before	Ice-free before	Break-up 2 years before
Mean summer concentration						
	Ice-free	Break-up before	Winter before	Freeze-up before	Ice-free before	Break-up 2 years before
Rate of decay						
	Break-up	Winter before	Freeze-up before	Ice-free before	Break-up before	Winter 2 years before

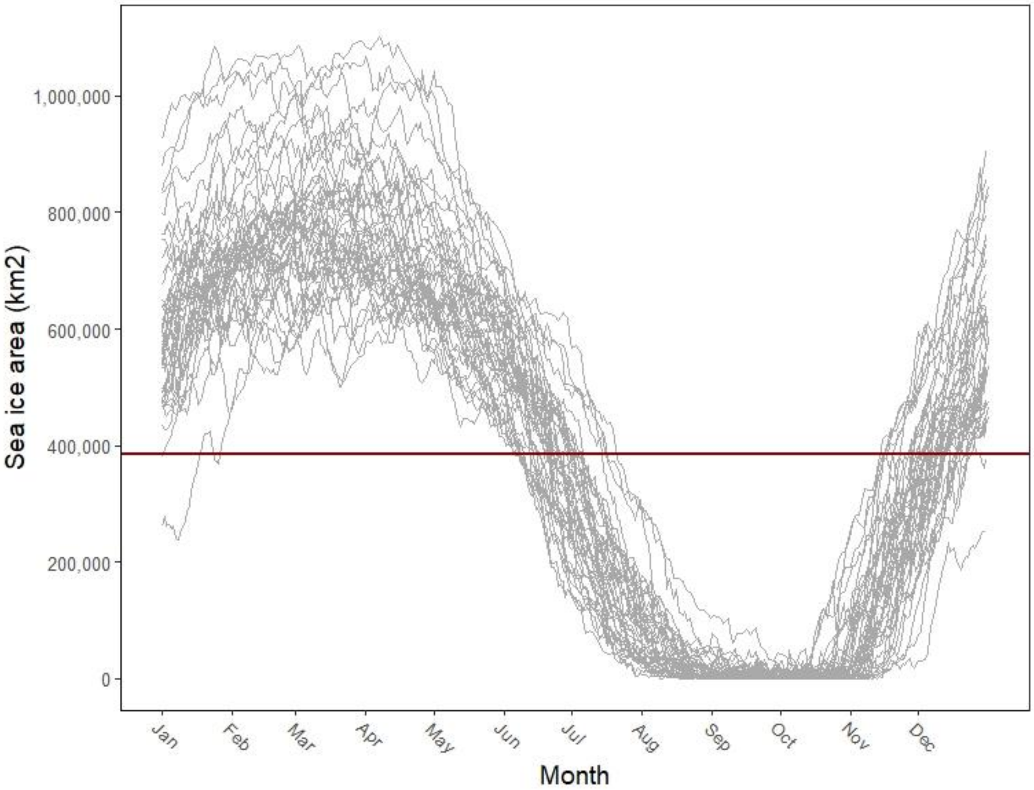

Figure 10: Daily sea ice area per year in Davis Strait from 1979-2021. The threshold (381,533 km^2) used to determine dates of retreat and advance is highlighted in red.

Table 13: AICc results for all sea ice models used to analyze trends in Davis Strait sea ice from 1979-2021, according to if AO or NAO was used*. Top models are bolded.

Model #	Dates of advance		Dates of retreat		Ice-free duration		Mean summer		Rate of Decay	
	AO	NAO	AO	NAO	AO	NAO	AO	NAO	AO	NAO
1**	326.92		320.81		366.45		-306.96		-485.43	
2	340.63	**328.12**	315.57	**306.20**	368.28	**336.97**	**-287.75**	-276.79	-472.43	**-486.70**
3	342.08	**315.35**	322.83	**322.05**	356.91	**354.96**	-279.39	**-291.38**	-484.92	**-486.61**
4	**329.21**	334.32	315.56	**305.90**	368.52	**365.36**	-287.11	**-289.10**	**-473.34**	-461.92
5	341.72	**336.26**	313.66	**306.25**	359.61	**347.36**	**-282.31**	-273.39	**-473.73**	-463.69
6	335.29	**321.08**	309.26	**309.01**	358.86	**347.63**	**-279.37**	-274.17	-463.08	**-477.82**
7	335.30	**328.39**	314.87	**314.17**	**351.16**	355.84	-271.77	**-281.17**	**-474.19**	-473.47
8	329.34	**312.08**	312.60	**305.93**	364.25	**334.77**	**-308.31**	-292.60	-470.64	**-486.67**
9	328.85	**306.32**	319.14	**318.34**	**352.87**	352.85	-296.72	**-305.58**	-483.79	**-485.10**
10	**317.91**	326.09	313.46	**303.59**	364.06	**359.70**	-304.88	**-310.65**	**-471.97**	-460.99
11	328.89	**319.18**	311.89	**304.59**	355.51	**342.51**	**-296.87**	-291.21	**-472.58**	-462.12
12	321.23	**302.73**	**307.15**	307.22	355.73	**344.83**	**-296.28**	-289.34	-461.53	**-475.63**
13	322.43	**314.91**	312.53	**312.10**	**348.54**	352.59	-288.92	**-296.22**	-472.46	**-472.48**
% top models:	16.67	83.33	8.33	91.67	25.00	75.00	50.00	50.00	41.67	58.33
	Total AO vs NAO top models:				AO:	17/60	28.33%	NAO:	43/60	71.67%

* See Table 1 for the predictor variables included in each model. Note that the number of ice-covered days is not included here as this metric was only analyzed with one model.

** Note: Model 1 for each metric does not include AO or NAO as the predictor variables include only the ice data and year. See Table 1.

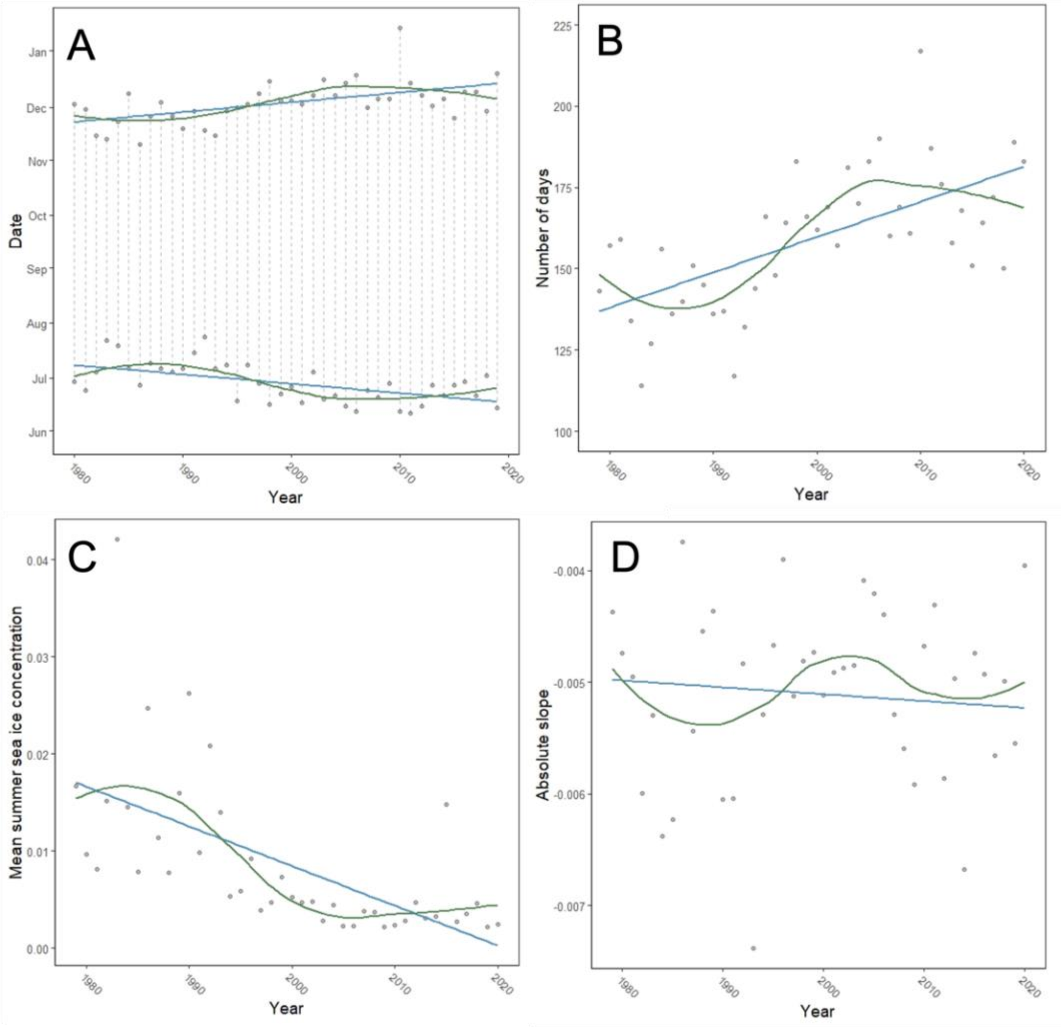

Figure 11: Analysis of Davis Strait sea ice from 1979-2021, including: A) dates of sea ice retreat and advance, B) ice-free season duration, C) mean summer sea ice concentration, and D) rate of sea ice decay. Linear regressions are illustrated in blue and non-linear in green.

Appendix B

Davis Strait polar bear home range analysis

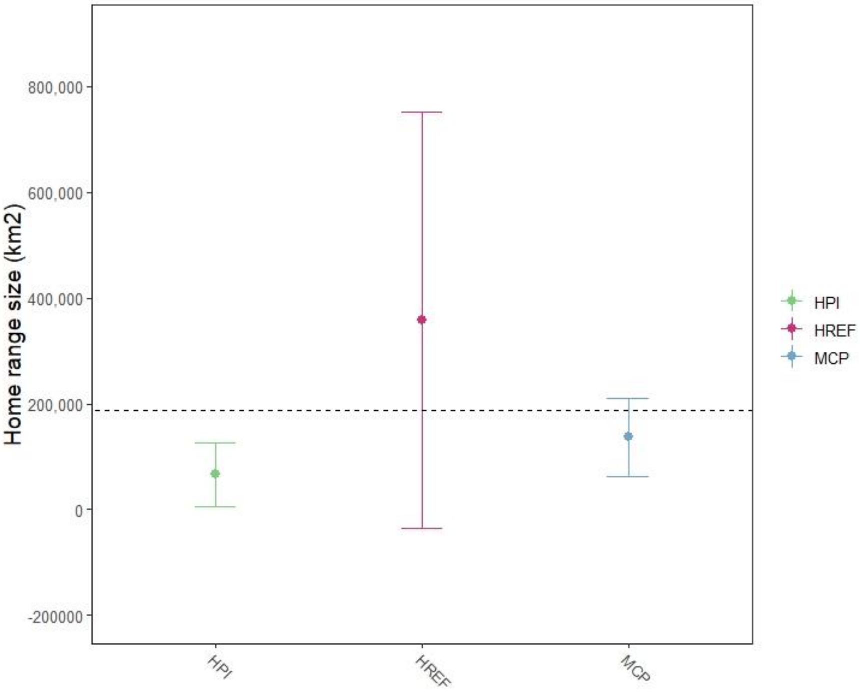

Figure 12: Home range sizes (95%) for female polar bears in Davis Strait from 1991-2001, including the second-generation plug-in KDE (HPI; green), the first-generation reference KDE (HREF; pink), and the minimum convex polygon (MCP; blue). The dashed horizontal line indicates the mean of all three metrics (187,300.3 km^2).

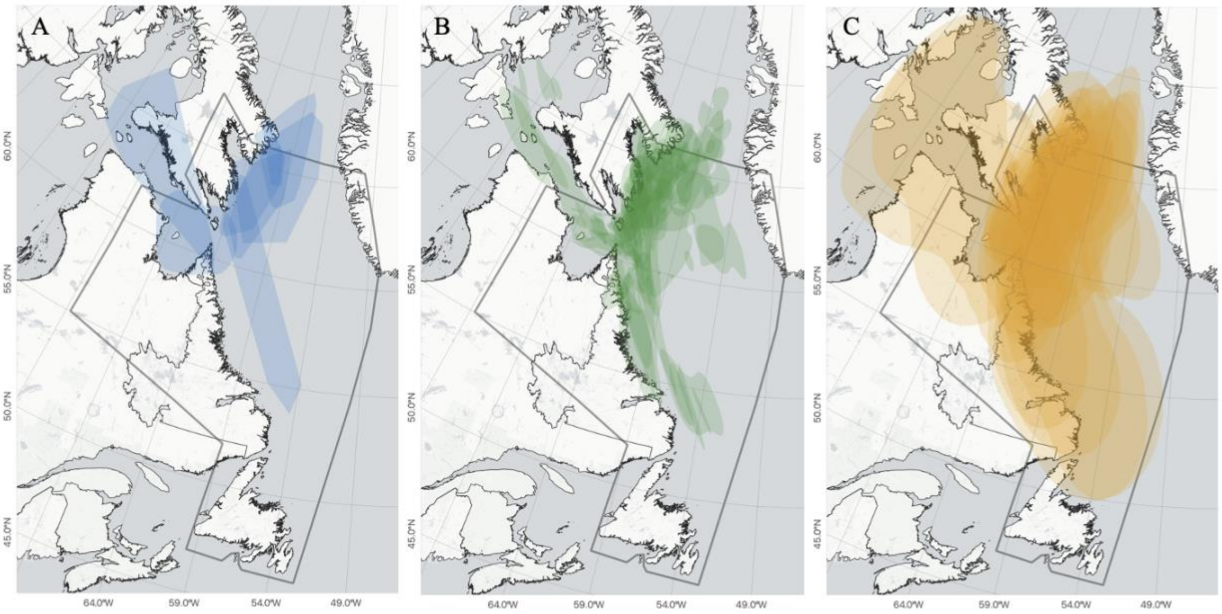

Figure 13: Annual 95% home ranges for female polar bears in Davis Strait (1991-2001) using three metrics: A) minimum convex polygons (MCP; blue); B) first-generation reference KDE (HREF; green); and C) second-generation plug-in KDE (HPI; orange). The DS management area was digitized from a map of polar bear subpopulations (Environment and Climate Change Canada 2018) and the basemap was obtained from QGIS Quickmap Services.

Appendix C

Seasonal resource selection function results for polar bears and harp seals in Davis Strait

Table 14: Pearson correlation coefficients (*r*) for the covariates used in the Davis Strait polar bear (1991-2001) and harp seal (1999-2005) resource selection functions. Note that seal resource selection was not analyzed for the winter season.

	Bears				Seals		
Freeze-up							
	ICE	DEPTH	LAND		ICE	DEPTH	LAND
ICE	--	--	--	ICE	--	--	--
DEPTH	0.484	--	--	DEPTH	-0.020	--	--
LAND	-0.294	**-0.831**	--	LAND	-0.427	-0.251	--
WATER	0.220	0.186	-0.252	WATER	0.022	0.092	-0.345
Winter							
	ICE	DEPTH	LAND				
ICE	--	--	--				
DEPTH	0.247	--	--				
LAND	0.031	**-0.714**	--				
WATER	0.140	0.330	-0.425				
Break-up							
	ICE	DEPTH	LAND		ICE	DEPTH	LAND
ICE	--	--	--	ICE	--	--	--
DEPTH	-0.144	--	--	DEPTH	0.011	--	--
LAND	0.242	-0.549	--	LAND	-0.170	-0.448	--
WATER	-0.050	0.151	-0.320	WATER	0.045	0.051	-0.161

Table 15: Coefficients (β), standard errors (SE), and p-values (P) of covariates for each top resource selection model used to analyze Davis Strait polar bear resource selection (1991-2001).

Model #	Covariate	Scaled values		
		β	SE	*p*
Freeze-up (all points)				
5b	DEPTH	0.595	0.111	<0.001
	ICE	-0.976	0.272	<0.001
	ICE^2	0.430	0.285	0.131
Freeze-up (without low ice)				
null	ID	NA	NA	NA
Winter (all points)				
5b	DEPTH	0.508	0.081	<0.001
	ICE	-1.180	0.179	<0.001
	ICE^2	0.761	0.205	<0.001
Winter (without low ice)				
null	ID	NA	NA	NA
Break-up (all points)				
8b	ICE	-0.698	0.127	<0.001
	ICE^2	0.657	0.161	<0.001
	LAND	-0.159	0.066	0.017
Break-up (without low ice)				
3	LAND	-0.155	0.063	0.014

Table 16: Coefficients (β), standard errors (SE), and p-values (P) of covariates for each top resource selection function model used to analyze Davis Strait harp seal resource use (1993-2005).

Model #	Covariate	Scaled values		
		β	SE	*p*
Freeze-up				
12c	DEPTH	0.091	0.031	0.003
	ICE	-0.053	0.036	0.134
	WATER	0.456	0.077	<0.001
	$WATER^2$	-0.167	0.055	0.002
Break-up				
13b	DEPTH	0.128	0.031	<0.001
	LAND	-0.047	0.028	0.099
	WATER	-0.219	0.204	0.284
	$WATER^2$	0.171	0.023	<0.001

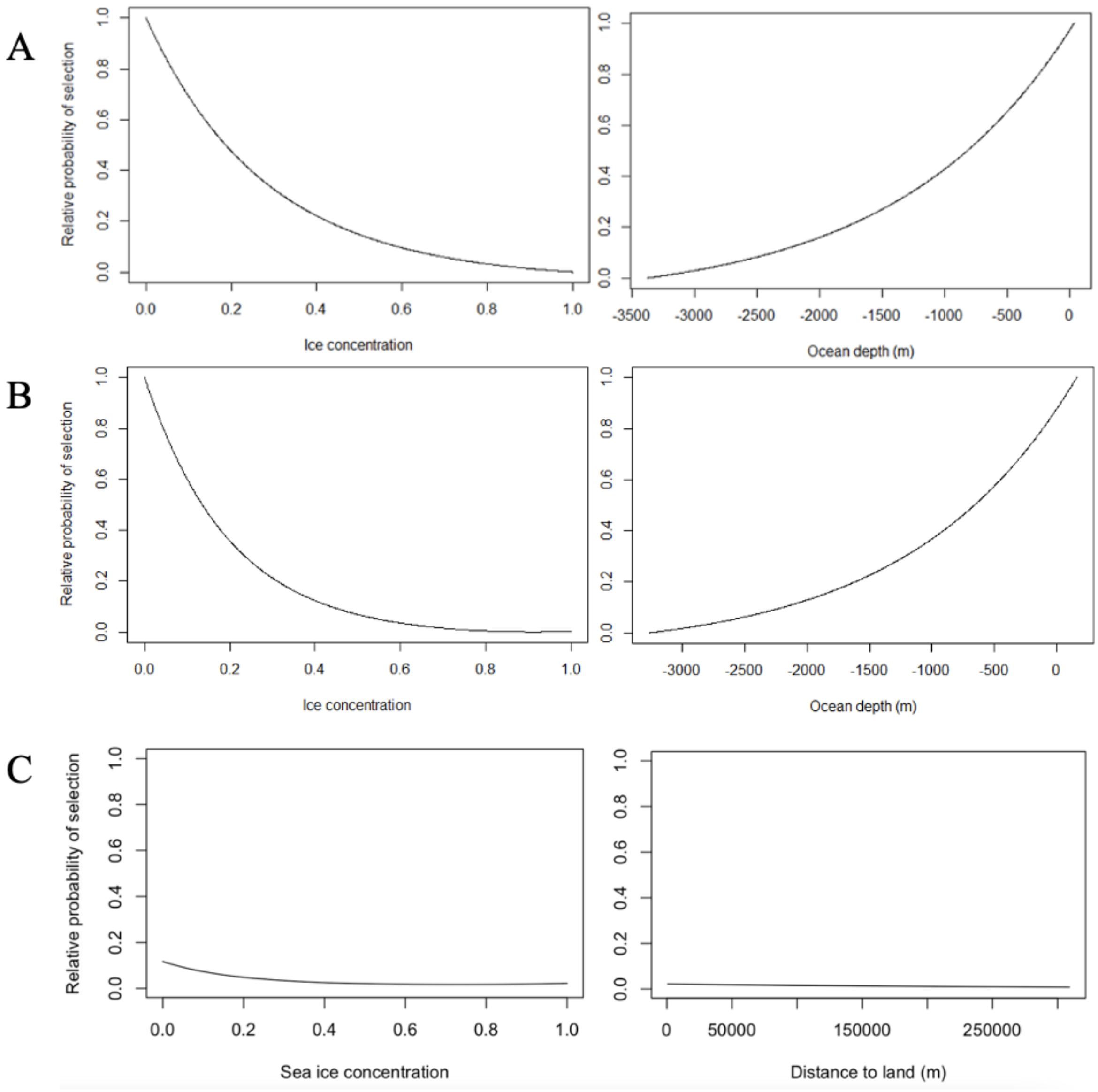

Figure 14: Relative probability of selection for each of the covariates (sea ice concentration and ocean depth) used in the seasonal polar bear resource selection functions where all points were used (i.e., ≤15% sea ice concentration included), including A) freeze-up; B) winter; and C) break-up. For each curve, all other covariate values were held to their median value.

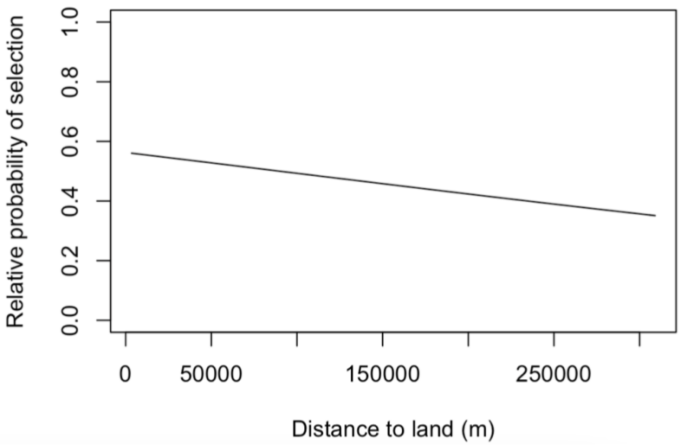

Figure 15: Relative probability of selection for the covariate (distance to land) used in the break-up polar bear resource selection function where points with ≤15% sea ice concentration were not included. Note that the top models for winter and freeze-up were the null.

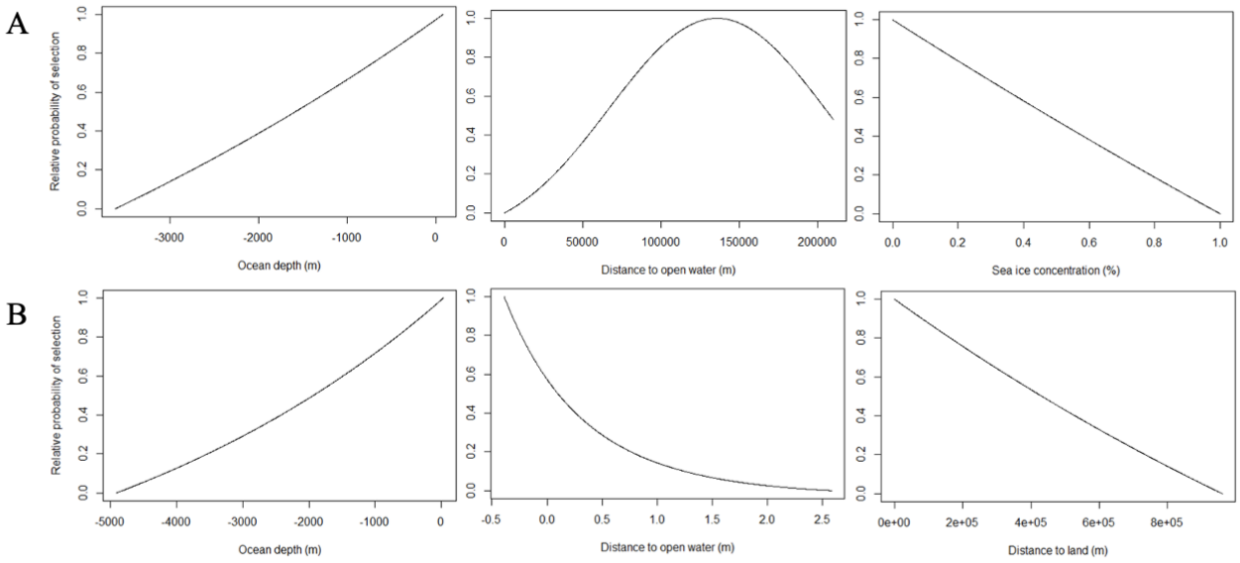

Figure 16: Relative probability of selection for each of the covariates (sea ice concentration and ocean depth) used in the seasonal harp seal resource selection functions, including A) freeze-up; and B) break-up.

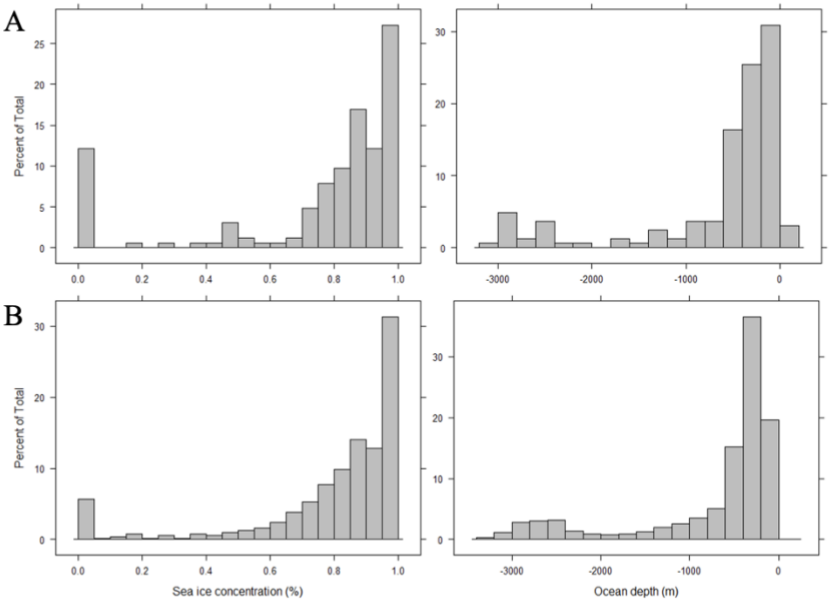

Figure 17: Percentage of use histograms for polar bear resource selection during the freeze-up period in Davis Strait (1991-2001), including all data (i.e., including sea ice <15% in concentration), where A) used and B) available data.

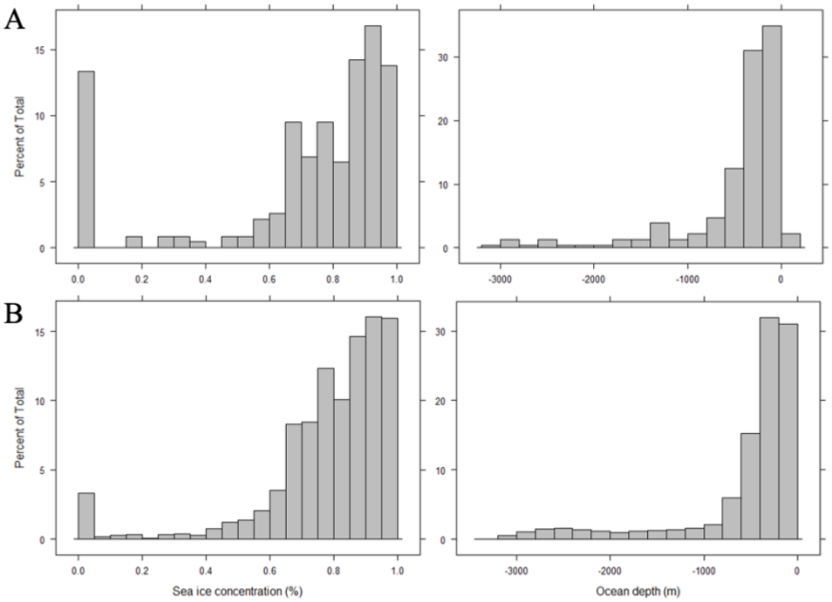

Figure 18: Percentage of use histograms for polar bear resource selection during the winter period in Davis Strait (1991-2001), including all data (i.e., including sea ice <15% in concentration), where A) used and B) available data.

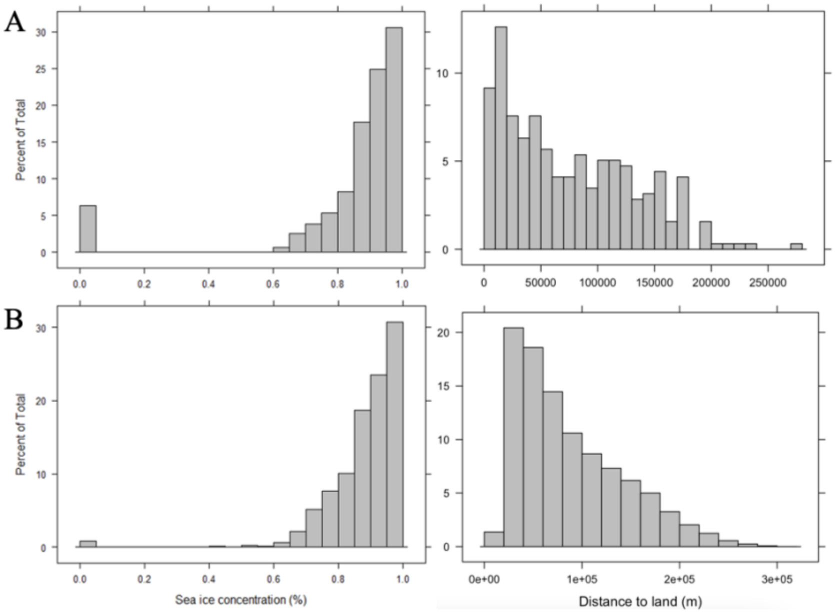

Figure 19: Percentage of use histograms for polar bear resource selection during the break-up period in Davis Strait (1991-2001), including all data (i.e., including sea ice <15% in concentration), where A) used and B) available data.

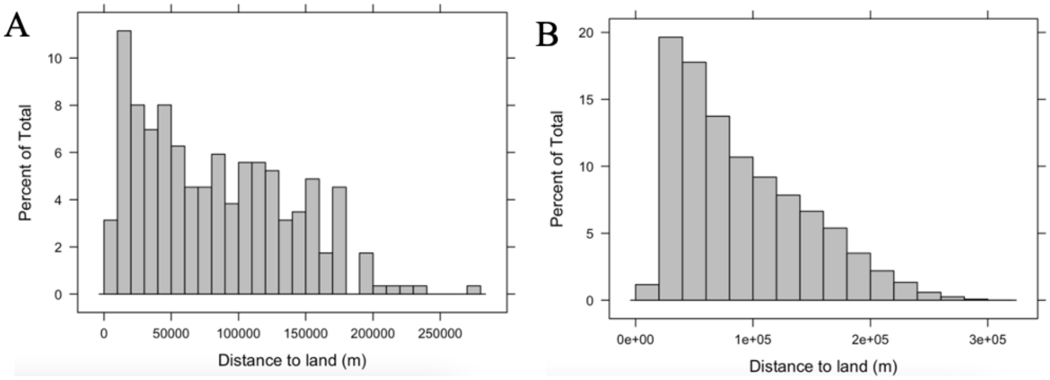

Figure 20: Percentage of use histograms for polar bear resource selection during the break-up period in Davis Strait (1991-2001), where sea ice <15% in concentration was removed, including A) used and B) available data.

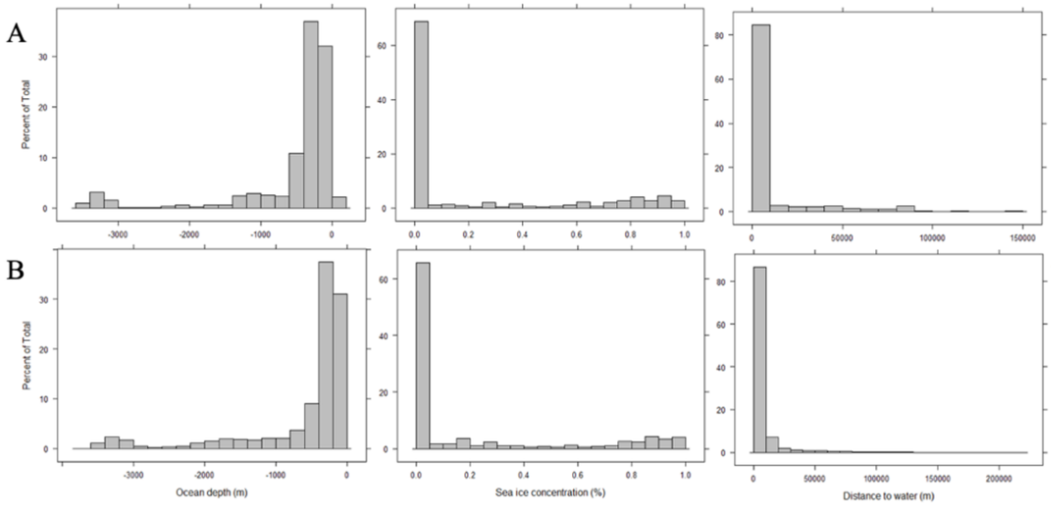

Figure 21: Percentage of use histograms for harp seal resource selection during the freeze-up period in Davis Strait (1993-2005), including A) used and B) available data.

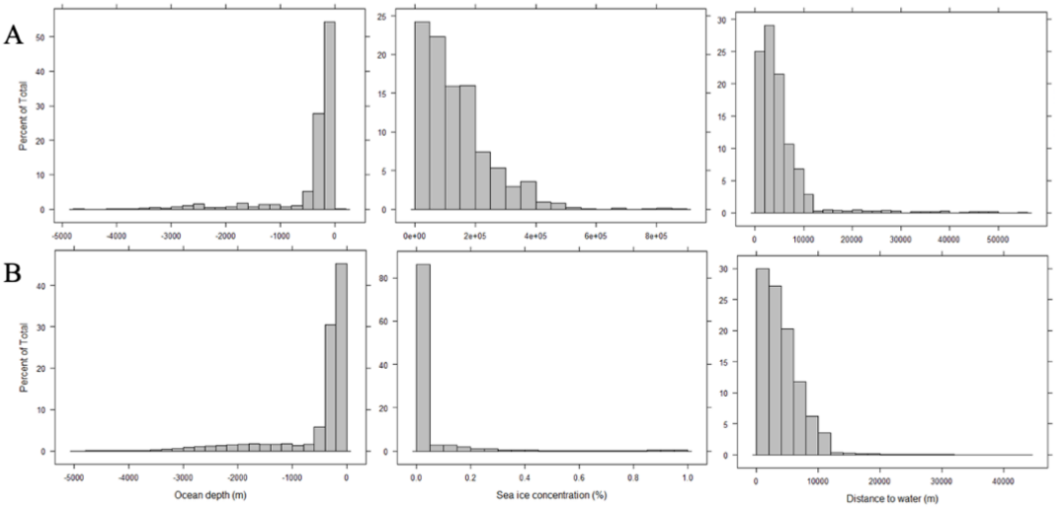

Figure 22: Percentage of use histograms for harp seal resource selection during the break-up period in Davis Strait (1993-2005), including A) used and B) available data.