

Marine mammal hotspots across the circumpolar Arctic

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Abstract

Aim: Identify hotspots and areas of high species richness for Arctic marine mammals.

Location: Circumpolar Arctic.

Methods: A total of 2115 biologging devices were deployed on marine mammals from 13 species in the Arctic from 2005 to 2019. Getis-Ord G_i^* hotspots were calculated based on the number of individuals in grid cells for each species and for phylogenetic groups (nine pinnipeds, three cetaceans, all species) and areas with high species richness were identified for summer (Jun-Nov), winter (Dec-May) and the entire year. Seasonal habitat differences among species' hotspots were investigated using Principal Component Analysis.

Results: Hotspots and areas with high species richness occurred within the Arctic continental-shelf seas and within the marginal ice zone, particularly in the "Arctic gateways" of the north Atlantic and Pacific oceans. Summer hotspots were generally found further north than winter hotspots, but there were exceptions to this pattern, including bowhead whales in the Greenland-Barents Seas and species with coastal distributions in Svalbard, Norway and East Greenland. Areas with high species richness generally overlapped high-density hotspots. Large regional and seasonal differences in habitat features of hotspots were found among species but also within species from different regions. Gap analysis (discrepancy between hotspots and IUCN ranges) identified species and regions where more research is required.

Main conclusions: This study identified important areas (and habitat types) for Arctic marine mammals using available biotelemetry data. The results herein serve as a benchmark to measure future distributional shifts. Expanded monitoring and telemetry studies are needed on Arctic species to understand the impacts of climate change and concomitant ecosystem changes (synergistic effects of multiple stressors). While efforts should be made to fill knowledge gaps, including regional gaps and more complete sex and age coverage, hotspots identified herein can inform management efforts to mitigate the impacts of human activities and ecological changes, including creation of protected areas.

KEYWORDS

Arctic continental shelf, biotelemetry, cetacean, distribution, Getis-Ord G_i^* hotspots, ice-associated, marginal ice zone, pinniped, polar bear, species richness

1 | INTRODUCTION

Climate change impacts have been documented in most ecosystems on Earth (e.g. IPCC, 2014; Scheffers et al., 2016). Shifts in species distributions and core habitats are ongoing and are predicted to continue throughout this century (Foote et al., 2013; Hazen et al., 2013; Poloczanska et al., 2016). These shifts are expected to alter trophic dynamics, cause mismatches between resource availability and consumers, alter species interactions and lead to species extirpations or extinctions (IPCC, 2014; Post et al., 2013). Impacts are likely to be especially severe in the Arctic, where air temperatures are rising 2–3 times faster than the global average and sea-ice extent is declining precipitously; a seasonally sea-ice free Arctic is predicted within a few decades (Meredith et al., 2019; Wang & Overland, 2012). Ongoing environmental change, particularly the loss of sea ice, has already caused considerable change in Arctic marine ecosystems (Meredith et al., 2019; Post et al., 2013). Sea-ice-associated species may have limited ability to shift their ranges in response to the ongoing changes (IPCC, 2014). Sea-ice loss represents direct habitat loss for ice-associated marine mammals, but such losses will likely also have many indirect effects through changes in their prey bases, increased presence of invasive species, temperate competitors and predators, altered disease risks and a variety of pressures associated with expanding human activities (IPCC, 2014; Meredith et al., 2019; Van Wormer et al., 2019). Due to low functional redundancy within Arctic ecosystems, impacts from species extirpations or range shifts are likely to be more severe in the Arctic than in more species-rich ecosystems (Post et al., 2009). Benchmark data on core habitats and migratory pathways are critical for detecting changes, performing risk assessments regarding impacts of human activities and informing spatial planning of protected areas.

Arctic marine mammals are dependent on sea ice for critical phases of their life cycles and their position near the top of the Arctic food web, in combination with being long-lived and slow to reproduce, means that they are sensitive to rapid changes in their environment (Kovacs et al., 2021; Reid et al., 2013; Tynan & DeMaster, 1997). Based on the boundaries defined by the Conservation of Arctic Flora and Fauna (CAFF; Figure 1), there are eleven marine mammal species that reside full time in the Arctic. Seven species are endemic to the Arctic and are tightly associated with sea ice for all or a significant part of the year: the bowhead whale (*Balaena mysticetus*), narwhal (*Monodon monoceros*), white or beluga whale (*Delphinapterus leucas*), ringed seal (*Pusa hispida*), bearded seal (*Erignathus barbatus*), walrus (*Odobenus rosmarus*) and polar bear (*Ursus maritimus*) (Kovacs et al., 2011; Laidre & Regehr, 2018). Four species of ice-associated seals, the hooded seal (*Cystophora cristata*), harp seal (*Pagophilus groenlandicus*), ribbon seal (*Histiophoca fasciata*) and spotted seal (*Phoca largha*), use drifting sea ice as a resting, pupping, nursing and moulting platform during winter and spring, but are generally found in open water or in subarctic areas for the rest of the year (Kovacs et al., 2011; Laidre & Regehr, 2018). Additionally, the harbour seal (*Phoca vitulina*) and

grey seal (*Halichoerus grypus*), which are generally considered temperate species, do have populations that reside year-round within the CAFF Arctic boundary.

One of the main challenges for evaluating environmental changes and their impacts in the Arctic marine ecosystem in a holistic manner is that the available data are spread across many sources and generally analysed at the species level using a wide range of methods. Therefore, large overall changes affecting multiple species may go undetected or are underrated. To address this data gap for marine mammals, biotelemetry data from 13 marine mammal species (collected by 33 scientific institutes) were synthesized to identify species hotspots and areas with high species richness across the circumpolar Arctic. Habitat features of the identified hotspots were also analysed to investigate the relative importance of different features and how these vary seasonally and across Arctic regions for individual species. Large-scale syntheses of biotelemetry data in other ecosystems have been successful in identifying multi-species hotspots, important ecosystem components and the magnitude of threats within these areas (e.g. Block et al., 2011; Hindell et al., 2020; Queiroz et al., 2019). This synthesis of Arctic marine mammal biotelemetry data provides information vital for: (1) determining the environmental and ecological drivers that shape Arctic marine ecosystems; (2) marine spatial planning for protected areas; (3) conducting environmental risk assessments that include cumulative effects for marine mammal populations (i.e. evaluating the overlap between important habitats and present or proposed human activities); and (4) identifying knowledge gaps.

2 | METHODS

2.1 | Study area and species

The study area comprised the circumpolar Arctic as defined by CAFF (Figure 1; CAFF, 2013). Biotelemetry data from all marine mammal species that spend most of their annual cycle within the CAFF Arctic boundary were included. Data came from 2115 biologging devices that were deployed on 13 species in the period 2005–2019 (Table 1). This time frame was chosen to represent recent species distributions during a period of rapid change in the Arctic.

2.2 | Locations

Data-handling and statistical analyses were conducted using R version 3.5.3 (R Core Team, 2019). Biologging devices provided ARGOS (CLS, 2016) or Fastloc GPS locations that were filtered to remove unlikely locations using the Douglas Argos-Filter (Douglas et al., 2012; walruses in East and West Greenland) or the SDA filter (argosfilter package; Freitas et al., 2008; for all other animals). Data sets were subsequently analysed using a continuous-time correlated random



FIGURE 1 Map of the circumpolar Arctic showing major place names and ocean areas (in italic font; top). Areas mapped in tan show the Conservation of Arctic Flora and Fauna (CAFF)'s Arctic region. Lower maps show recurrent polynyas (pink polygons; left) and the mean sea-ice frequency (%) from 2005 to 2019 in March and September

TABLE 1 Biotelemetry information for 13 marine mammal species included in the circumpolar Arctic hotspots analysis, including the number of animals tagged, time period, seasonal coverage and mean (\pm SD) and total tracking durations (d) for the different sampling regions. For details regarding animal capture and handling, biotelemetry devices used and permits see the references provided for the published datasets and the Supporting information for the unpublished datasets

Species	Region/sub-population	N	Time period	Seasonal coverage	Tracking duration (d; mean \pm SD)	Total number of tracking days	For details regarding animal handling deployment and permits see
Ringed seal	Svalbard (Norway)	51	2010–2018	Jul–May	184 \pm 62	9372	Hamilton et al. (2015), Hamilton et al. (2016)
	Northeast Greenland	20	2017–2018	Aug–Apr	147 \pm 55	2946	See Supporting information
	Melville Bay (Greenland)	12	2011–2012	Sep–May	216 \pm 51	2593	Yurkowski et al. (2016)
	Saglek Fjord (Canada)	13	2008–2012	Aug–Jun	157 \pm 75	2040	Brown et al. (2014)
	Baffin Bay (Canada)	17	2009–2019	Jul–May	127 \pm 94	2163	Yurkowski et al. (2016)
	Hudson Bay (Canada)	65	2006–2013	Aug–Jun	130 \pm 61	8465	Yurkowski et al. (2016)
	Holman (Canada)	9	2010–2010	Jul–Dec	139 \pm 10	1251	Yurkowski et al. (2016)
	Bering-Chukchi-Beaufort Seas (USA)	74	2007–2019	Jul–Jun	160 \pm 99	11,871	Crawford et al. (2012), Quakenbush et al. (2019), Von Duyke et al. (2019), Von Duyke et al. (2020)
	Kara Sea (Russia)	1	2016–2016	Aug–Nov	88	88	See Supporting information
	Total	263				40,789	
Bearded seal	Svalbard (Norway)	19	2005–2013	Jul–Jun	175 \pm 101	3322	Hamilton et al. (2018); Hamilton, Lydersen, et al. (2019)
	Bering-Chukchi-Beaufort Seas (USA)	62	2005–2018	Jul–Jun	150 \pm 80	9304	Boveng, and Cameron (2013), Cameron et al. (2018), Gryba et al. (2019), Von Duyke et al. (2019), Olnes et al. (2020)
	Total	81				12,626	
Walrus	Svalbard (Norway)	30	2014–2018	Jul–Jun	357 \pm 417	10,702	See Supporting information
	East Greenland	16	2008–2010	Jul–Jan	79 \pm 48	1269	See Supporting information
	West Greenland	23	2005–2008	Sep–Nov, Mar–Jun	38 \pm 20	866	Dietz et al. (2014)
	Smith Sound (Greenland/Canada)	49	2010–2015	May–Mar	66 \pm 39	3238	Heide-Jørgensen et al. (2017)
	Foxe Basin (Canada)	25	2010–2011	Sep–Dec	43 \pm 29	1074	See Supporting information
	Bering-Chukchi-Beaufort Seas (USA)	77	2010–2015	Jun–Oct	54 \pm 24	4138	Quakenbush et al. (2016)
	Pechora Sea (Russia)	28	2013–2018	Jul–Jun	64 \pm 70	1782	Semenova et al. (2019)
	Total	248				28,609	

(Continues)

TABLE 1 (Continued)

Species	Region/sub-population	N	Time period	Seasonal coverage	Tracking duration (d; mean ± SD)	Total number of tracking days	For details regarding animal handling deployment and permits see
Bowhead whale	Greenland and Barents Seas (Norway/Greenland)	14	2017–2019	Jul–Jun	168 ± 120	2348	Kovacs et al. (2020)
	Baffin region (Greenland/Canada)	78	2005–2019	Jul–Jun	203 ± 190	15,822 ^a	Nielsen et al. (2015), Fortune et al. (2020), Teilmann et al. (2020)
	Bering–Chukchi–Beaufort Seas (USA)	63	2006–2019	Jul–Jun	188 ± 133	11,851	Citta, Okkonen, et al. (2018)
	Total	155				30,021	
White whale	Svalbard (Norway)	16	2013–2017	Jul–Feb	99 ± 52	1581	Vacquié-Garcia et al. (2018)
	Baffin Island (Canada)	13	2005–2010	Jul–May	166 ± 61	2152 ^a	Watt et al. (2016a)
	Hudson Bay (Canada)	9	2015–2015	Jul–Dec	117 ± 33	1051 ^a	Pirotta et al. (2018)
	Eastern Beaufort (Canada)	16	2005–2019	Jul–Jun	168 ± 119	2686 ^a	Citta et al. (2017), Storrie et al. (2022)
	Norton Sound (USA)	3	2012–2018	Jul–Jun	351 ± 75	1054	Citta et al. (2017)
	Bristol Bay (USA)	32	2006–2013	Jul–Jun	166 ± 62	5311 ^a	Citta et al. (2017)
	Anadyr Sea (Russia)	3	2006–2009	Jul–Jun	247 ± 94	740 ^a	Citta et al. (2017)
	Kara Sea (Russia)	1	2016–2016	Jul–Nov	106	106	See Supporting information
	Total	93				14,681	
Narwhal	East Greenland	39	2010–2017	Jul–Jun	142 ± 88	5531 ^a	Heide-Jørgensen et al. (2015)
	Baffin Bay (Greenland/Canada)	97	2005–2018	Jul–Jun	120 ± 87	11,636 ^a	Laidre et al. (2016), Watt et al. (2016b), Kenyon et al. (2018), Shuert et al. (2021)
	Northern Hudson Bay (Canada)	9	2006–2007	Aug–Jun	182 ± 88	1636 ^a	Watt et al. (2016b)
	Total	145				18,803	
Polar bear	Svalbard (Norway)	210	2005–2018	Jul–Jun	305 ± 210	63,977 ^a	Lone et al. (2018)
	East Greenland	21	2007–2010	Jul–Jun	334 ± 402	7016	Laidre et al. (2013), Laidre et al. (2015)
	Bering–Chukchi–Beaufort Seas (USA)	600	2005–2018	Jul–Jun	228 ± 233	136,859 ^a	Atwood et al. (2016), Wilson et al. (2016)
	Total	831				207,852	
Spotted seal	Bering–Chukchi–Beaufort Seas (USA)	95	2005–2018	Jul–Jun	177 ± 98	16,820	Gryba et al. (2019), Quakenbush et al. (2019), Von Duyke et al. (2019); See Supporting information
Ribbon seal	Bering–Chukchi–Beaufort Seas (USA)	39	2006–2016	Jul–Jun	136 ± 124	5313	See Supporting information

TABLE 1 (Continued)

Species	Region/sub-population	N	Time period	Seasonal coverage	Tracking duration (d; mean \pm SD)	Total number of tracking days	For details regarding animal handling deployment and permits see
Hooded seal	Greenland Sea (Norway/Greenland)	19	2008–2010	Jul–Jun	172 \pm 125	3276	Vacquié-García et al. (2017)
	Baffin Bay (Canada)	36	2005–2009	Jul–Jun	181 \pm 125	6533	Andersen et al. (2013)
	Total	55				9809	
Harp seal	Greenland Sea (Norway/Greenland)	20	2017–2018	Jul–Jun	178 \pm 143	3554	See Supporting information
Harbour seal	Svalbard (Norway)	60	2009–2011	Jul–Jun	187 \pm 107	11,230	Blanchet et al. (2014); Blanchet et al. (2016)
	Porsanger Fjord (Norway)	16	2009–2013	Sep–Jul	187 \pm 101	2999	Ramasco et al. (2017)
	Southern Greenland	9	2009–2011	Jul–Jun	187 \pm 136	1682 ^a	Rosing-Asvid et al. (2020)
	Total	85				15,911	
Grey seal	Iceland	5	2016–2017	Jul–Jun	242 \pm 122	1212	Baylis et al. (2019)
Total		2115				400,460	

^aTags were duty-cycled.

walk model (CTCRW model; crawl package; Johnson et al., 2008). References in Table 1 and in the Supporting Information provide details regarding capture methods, the specific type of biologging devices used, research permits and protocols for each deployment. A tag had to transmit locations for at least 14 days to be included in the analyses. Locations every 12 hours were predicted by the CTCRW models for each animal. Some biologging devices were duty-cycled (see Table 1); only days when the tag was transmitting were used in the analyses. CTCRW model-generated locations that were within transmission gaps greater than seven days were also removed from the analyses. Locations on land were moved to the closest in-water location in time for each species with the exception of polar bears. Given the grid size used in this analysis (30 x 30 km) and the large geographic extent (circumpolar), moving these locations had little or no effect on the hotspot locations.

Land and coastline shapefiles were downloaded from Natural Earth (large-scale data; <https://www.naturalearthdata.com/>), and polynya locations were downloaded from CAFF's GeoNetwork catalogue (CAFF, 2017). Tidewater glacier front shapefiles were retrieved from the Norwegian Polar Institute (NPI; Svalbard), Goliber et al. (2021; Greenland) and Cook et al. (2019; Canada). Water depth was extracted from the International Bathymetric Chart of the Arctic Ocean version 4.0 (Jakobsson et al., 2020). Mean sea-ice frequency shapefiles for March and September (2005–2019) were retrieved from NPI. Monthly mean sea surface temperatures (SST) (2005–2019) for March and September were obtained from NOAA's Optimum Interpolation SST version 2 (Reynolds et al., 2002). The range for each species was downloaded from the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2020).

2.3 | Marine mammal hotspots

Getis-Ord G_i^* hotspots (hereafter referred to as G_i^* hotspots/statistic) were calculated for each species or species group (i.e. all pinnipeds, all cetaceans, and all species) to identify areas with higher use by marine mammals (Getis & Ord, 1992; Ord & Getis, 1995). The G_i^* statistic measures the concentration of a variable at a point by comparing the local sum of values (i.e. a point and its neighbours within a specified distance) to an expected sum (i.e. random permutations drawn without replacement from all points in the dataset). A statistically significant positive z-score is assigned if the calculated local sum is larger than the expected sum and the difference is too large to be the result of random chance (Getis & Ord, 1992; Ord & Getis, 1995). The G_i^* statistic was calculated based on the number of individuals in 30 x 30 km grid cells throughout the study area. This approach identifies areas used by most of the tagged animals (i.e. individual hotspots). Hotspot maps based on the number of locations in grid cells, which identify heavily used areas, sometimes by only a few of the tagged animals (i.e. location hotspots), are presented in the Supporting Information (Figures S1–S8). The G_i^* statistic was calculated using

the *localG* function (spdep package, Bivand & Wong, 2018). The number of neighbours used for each species was found by calculating the global Getis-Ord G_i^* function in 30 km increments from 30–210 km, to identify the distance where global spatial autocorrelation was maximized (*globalG.test* function, spdep package; see Table S1; Bivand & Wong, 2018; Ord & Getis, 1995). Four hotspot contours were plotted: 99% ($z \geq 2.58$, $p \leq 0.01$), 95% ($z \geq 1.96$, $p \leq 0.05$), 90% ($z \geq 1.65$, $p \leq 0.1$) and 70% ($z \geq 1.15$, $p \leq 0.3$). Low use areas ($z < 1.15$, $p > 0.3$) were plotted as a continuous polygon that encompassed all areas used by each species or group. Species richness was calculated by identifying the number of species occurring in each grid cell. Hotspot areas and species richness were calculated for the entire year, for summer (Jun–Nov) and for winter (Dec–May).

Regions were defined for each species to account for differences in sample size across the circumpolar Arctic; each region was given an equal weighting when calculating the G_i^* statistic. The circumpolar range of a species was separated into regions based on where sub-populations occurred (i.e. based on IUCN delineations and current scientific knowledge) or where movement patterns and space use of animals was generally separate from animals tagged at adjacent tagging locations (see Table 1). Each individual, regardless of any existing finer stock structure, was given an equal weighting inside each region. For the analyses of all pinnipeds, all cetaceans and all species, each species and region received equal weight.

Null models were created to account for bias in tracking effort by showing where hotspots (and species richness) would be expected for each species and species group given the tagging locations and general movement patterns (see Supporting information for details; Queiroz et al., 2016; Yurkowski et al., 2019). The amount of overlap between high and null hotspot levels (95 and 99%) and high and null levels of species richness index areas (≥ 4 species) were calculated.

2.4 | Hotspot habitat

To explore the similarities and differences in the habitat features within marine mammal hotspots across the circumpolar Arctic, principal component analysis (PCA) was conducted on standardized habitat variables extracted from the G_i^* hotspots (70–99% statistical significance) for each species (*prcomp* function). These variables included distance to the coast (km), distance to the nearest tidewater glacier front (km), water depth (m), sea-ice frequency (% of days during a month that an area had sea ice), sea surface temperature (SST; °C) and distance to the nearest polynya (km; winter only). Sea-ice frequency and SST values were extracted from March and September means (2005–2019). March and September correspond to the periods of maximum (winter) and minimum sea-ice extent (summer) throughout most of the circumpolar Arctic. It is important to note that using a 14-year mean of monthly sea-ice data may not

reflect the sea ice available to the animals during the time frame of their respective biotelemetry device deployments. However, this index should be sufficient for identifying broad-scale patterns in sea-ice use. While these variables may not cover all possible environmental conditions of potential importance, they are highly relevant and have been used frequently in previous habitat modelling for marine mammals (e.g. Cameron et al., 2018; Hamilton, Lydersen, et al., 2019; Hauser et al., 2018; Laidre et al., 2015; Matthews et al., 2020). Because preliminary analysis showed that SST had very little influence on the PCA plots, this variable was excluded from further analyses. The range of each species was divided into three regions (where applicable) as data exploration showed large regional differences in hotspot habitats for some species. The regions were defined as: (1) Bering-Chukchi-Beaufort (BCB) region; (2) Canadian Arctic Archipelago and West Greenland and; (3) East Greenland and the Barents Sea region.

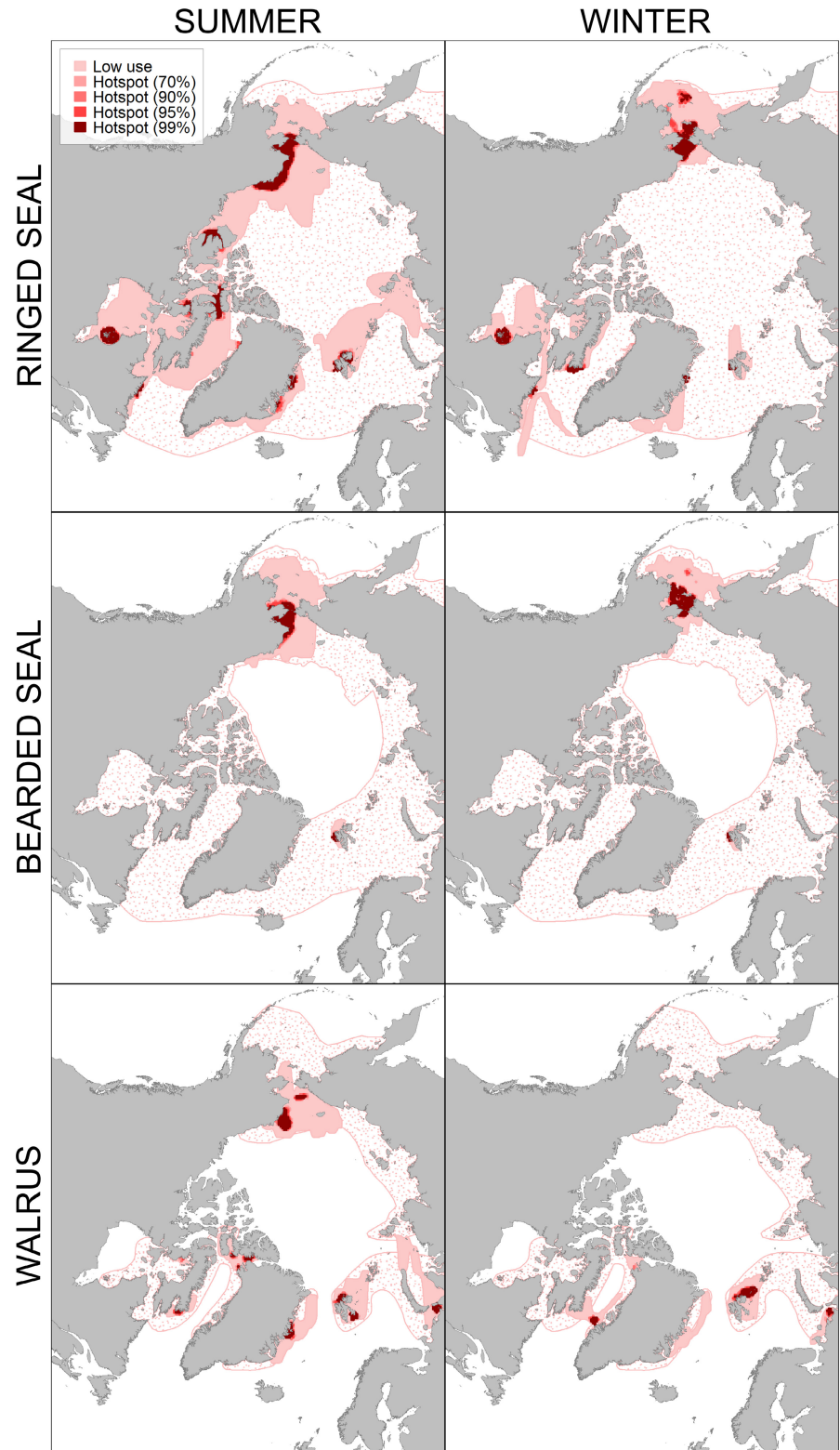
3 | RESULTS

A total of 400,460 tracking days from 2115 biologging devices were available for 13 marine mammal species from 2005 to 2019. Data were available for most of the year for most species and regions, although exceptions did occur, notably for walruses and white whales because winter data were sparse (see Table 1). Discrepancies between the IUCN global range and hotspot locations also identify spatial data gaps for each species (Figures 2–5 and Table 1). Age and sex were not included in these analyses due to species and regional differences in individuals that were tagged. For example, the majority of tagged polar bears were female polar bears, all walruses in Svalbard and the Pechora Sea were male walruses while most of the walruses from the Bering-Chukchi-Beaufort region (BCB) were female walruses, the majority of bearded seals from the BCB were juveniles and all harp seals tagged in the Greenland Sea and all grey seals tagged in Iceland were pups.

3.1 | Ringed seals

Hotspots occurred in coastal and offshore areas around the circumpolar Arctic (Figures 2, S1, S9, Table 1). In particular, they occurred in northern Svalbard, East Greenland (between Scoresby Sound and Dove Bay), West Greenland (i.e. Melville Bay), around Saglek Bay, eastern Hudson Bay, around Baffin Island (including Cumberland Sound, Lancaster Sound and around Melville Peninsula), east of Victoria Island (including the Amundsen Gulf) and in the BCB (including the northern Bering Sea, Bering Strait, the eastern Chukchi Sea (including Kotzebue Sound) and much of the Beaufort Sea). Summer hotspots were generally more widespread and further north in the Pacific Arctic and Canadian Arctic Archipelago than winter hotspots (Figures 2, S1). Hotspots were not calculated for the Kara Sea

FIGURE 2 Getis-Ord G_i^* hotspots for ringed seals, bearded seals and walrus in the circumpolar Arctic during the summer (Jun-Nov) and winter (Dec-May) based on the number of individuals per grid cell. Increasing intensities of red indicate hotspots of increasing level of significance. The red dotted polygon shows the global range of the species (IUCN Red List)



region because only one ringed seal was tagged in this region. The null model hotspots occurred in the vicinity of where ringed seals were tagged and overlapped high hotspot levels (95 and 99%) by 34% (Figures S15, S16).

3.2 | Bearded seals

Hotspots occurred in coastal regions of northwest Svalbard and in the BCB (in the northern Bering Sea (including Norton Sound and

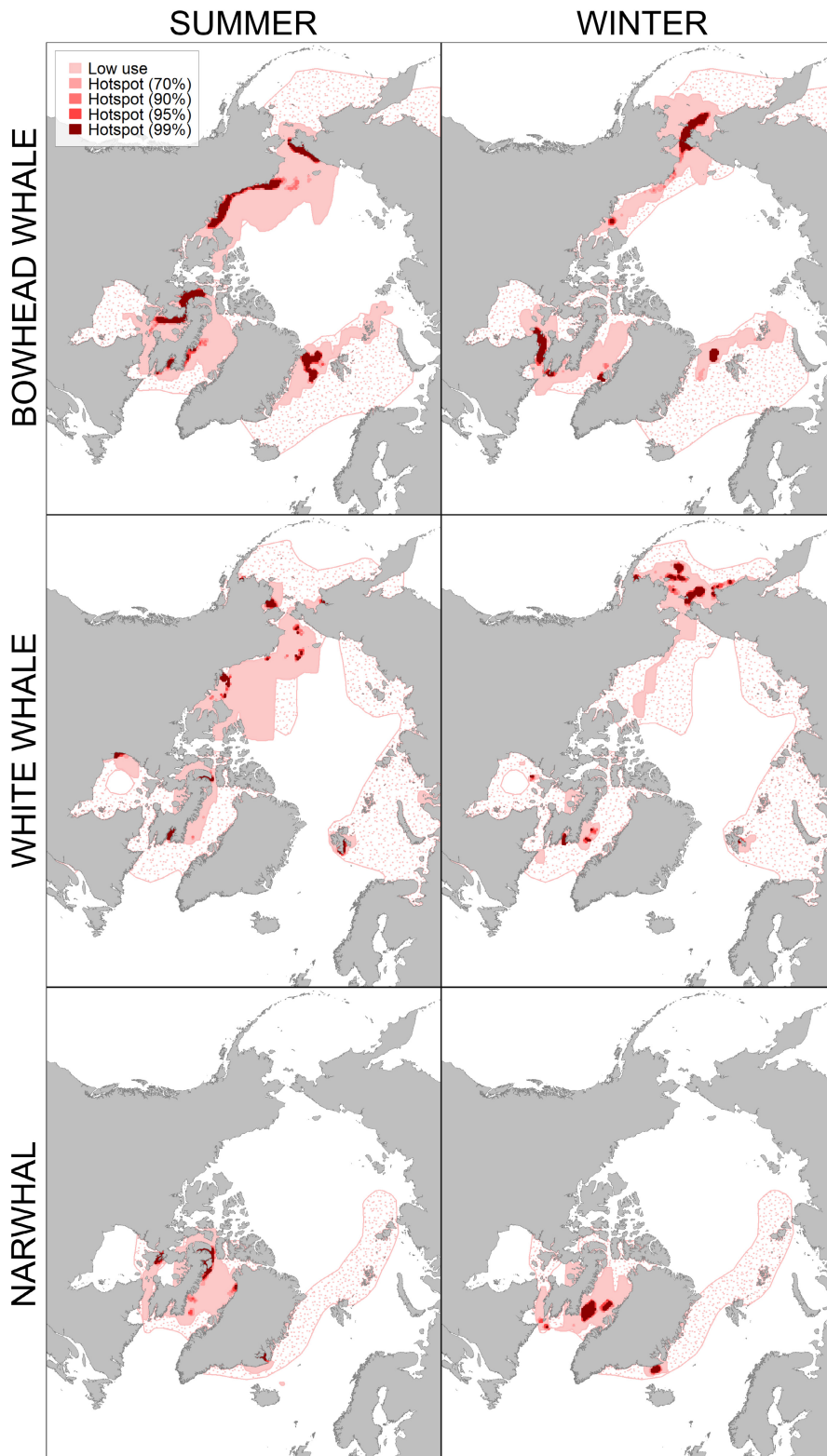


FIGURE 3 Getis-Ord G_i^* hotspots for bowhead whales, white whales and narwhals in the circumpolar Arctic during the summer (Jun-Nov) and winter (Dec-May) based on the number of individuals per grid cell. Increasing intensities of red indicate hotspots of increasing level of significance. The red dotted polygon shows the global range of the species (IUCN Red List)

Bering Strait) and in the eastern Chukchi Sea (including Kotzebue Sound); **Figures 2**, S1, S9, **Table 1**). Winter hotspots were slightly further south and more offshore than summer hotspots in the BCB (**Figure 2**). The null model hotspots occurred in the vicinity of where bearded seals were tagged and overlapped high hotspot levels (95 and 99%) by 32% (**Figures S15**, S16).

3.3 | Walrus

Hotspots occurred in shallow regions along the northern and southern coasts of the Svalbard Archipelago, East Greenland (i.e. Young Sound and Dove Bay), Davis Strait region, Smith Sound, northern Foxe Basin, Chukchi Sea and the Pechora Sea (**Figures 2**, S2, S9,

FIGURE 4 Getis-Ord G_i^* hotspots for polar bears, spotted seals and ribbon seals in the circumpolar Arctic (polar bears) and the Pacific Arctic (spotted and ribbon seals) during the summer (Jun-Nov) and winter (Dec-May) based on the number of individuals per grid cell. Increasing intensities of red and orange (polar bears only) indicate hotspots of increasing level of significance. The red hotspots are from data included in the analyses herein while the orange hotspots are from Yurkowski et al. (2019). The red dotted polygon shows the global range of the species (IUCN Red List)

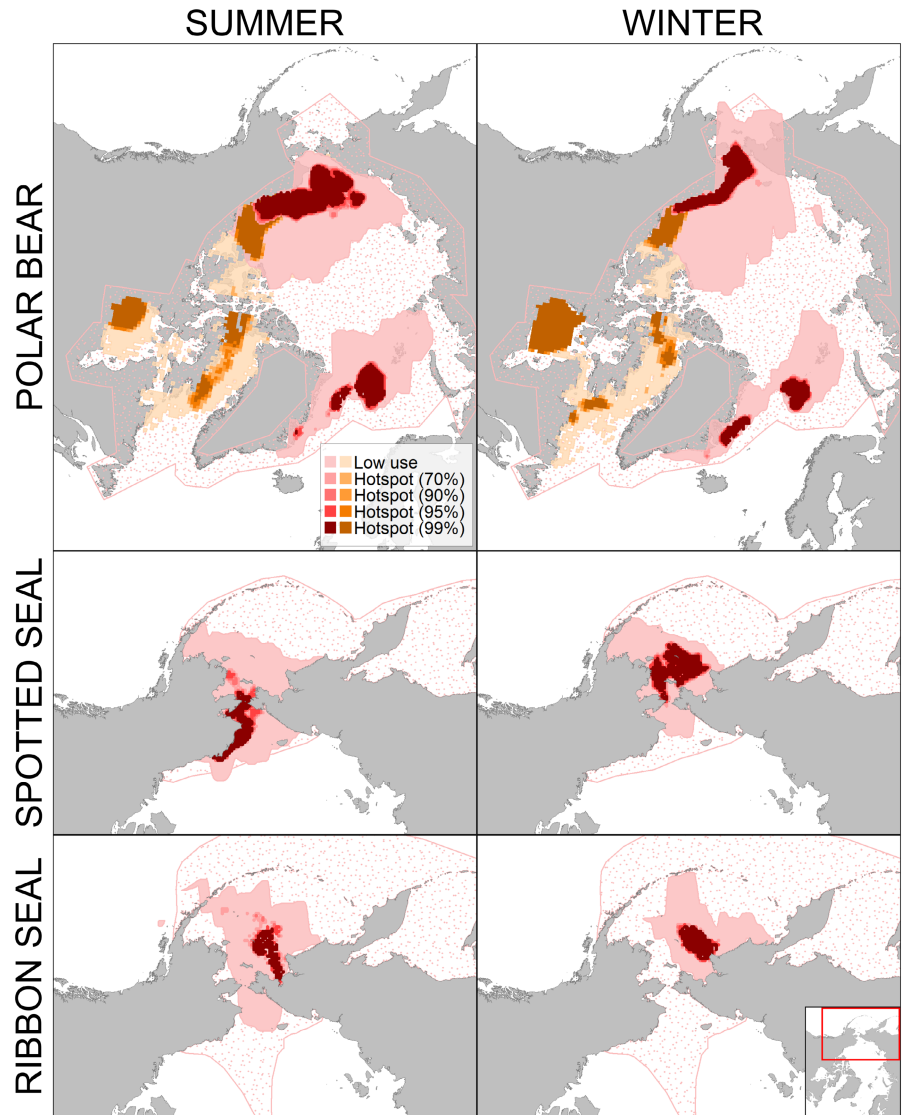


Table 1). Null model hotspots occurred in the vicinity of where walrus were tagged and overlapped high hotspot levels (95% and 99%) by 55% (Figures S15, S16).

3.4 | Bowhead whales

Hotspots occurred in the Greenland and northern Barents Seas between Northeast Greenland and Franz Josef Land (Russia), Disco Bay, around Baffin Island (including Cumberland Sound, Hudson Strait, Foxe Basin and Gulf of Boothia), Amundsen Gulf and the BCB (including the Beaufort Sea and the western Chukchi Sea in summer and the Bering Strait and the western Bering Sea in winter; Figures 3, S2, S10, Table 1). Hotspots based on the number of locations also occurred around the Franz Josef Land Archipelago and further south in the Bering Sea (Figure S2). Summer hotspots were located further north than winter hotspots in the BCB and in

the Canadian Arctic Archipelago, whereas the Greenland-Barents Sea population displayed the opposite pattern (Figure 3). Null model hotspots occurred in the vicinity of where tags deployed on bowhead whales transmitted their first locations and overlapped high-density hotspot levels (95 and 99%) by 32% (Figures S15, S17).

3.5 | White whales

Hotspots occurred around southern Svalbard, Baffin Bay, regions around Baffin Island (including Cumberland Sound and Admiralty Inlet), eastern Hudson Bay, Viscount Melville Sound (annual hotspots only), Amundsen Gulf and in the BCB (including Bristol Bay, Norton Sound, Gulf of Anadyr and in the Bering and Chukchi Seas; Figures 3, S3, S10, Table 1). Summer hotspots were generally located further north than winter hotspots in the BCB and Canadian Arctic

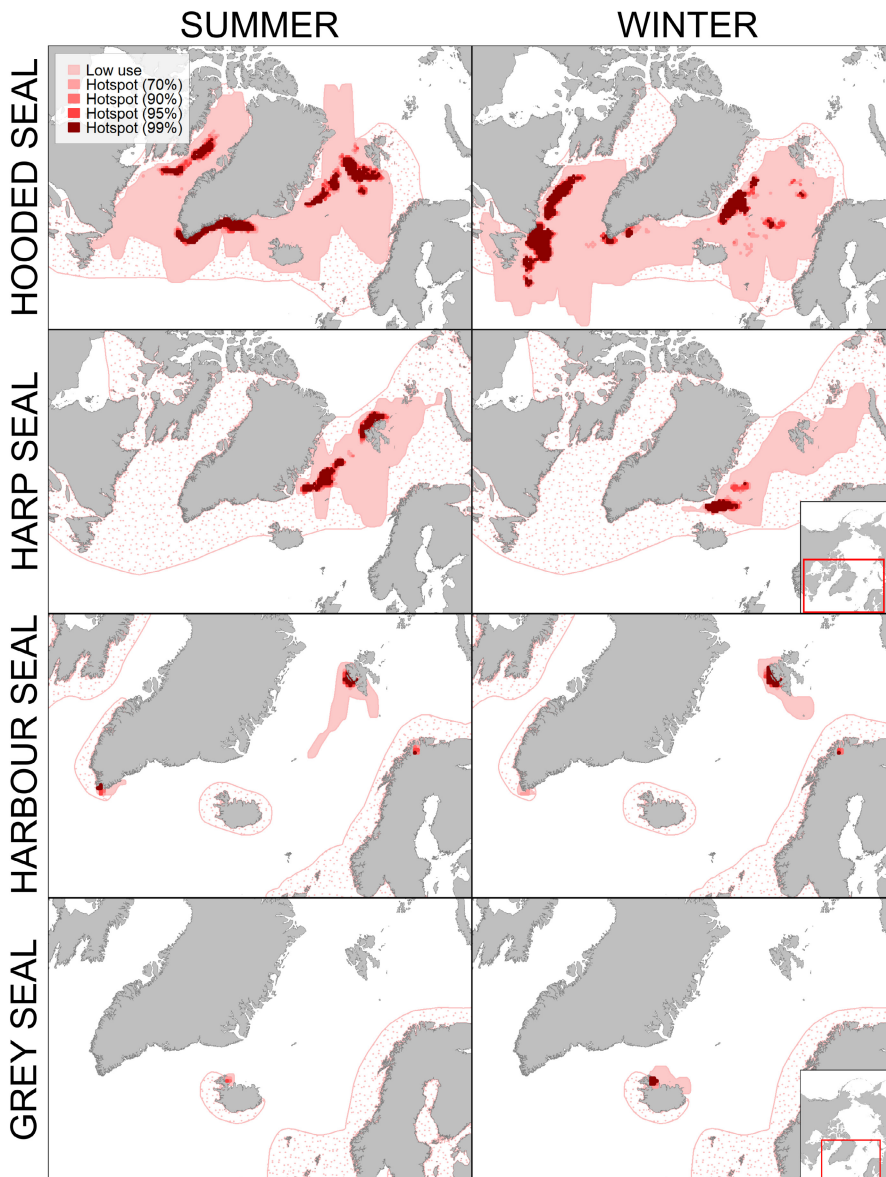


FIGURE 5 Getis-Ord G_i^* hotspots for hooded seals, harp seals, harbour seals and grey seals in the Atlantic Arctic during the summer (Jun-Nov) and winter (Dec-May) based on the number of individuals per grid cell. Increasing intensities of red indicate hotspots of increasing level of significance. The red dotted polygons show the global range of the species (IUCN Red List)

Archipelago (Figure 3). Hotspots were not mapped for the Kara Sea because only one white whale was tagged in this region. Null model hotspots occurred in the vicinity of where white whales were tagged and overlapped high hotspot levels (95 and 99%) by 34% (Figures S15, S17).

3.6 | Narwhals

Hotspots occurred in East Greenland (i.e. inside and south of Scoresby Sound), West Greenland (i.e. Melville Bay), northern Baffin Island (including Eclipse Sound and Admiralty Inlet) and southern Foxe Basin (including north of Southampton Island; Figures 3, S3, S10, Table 1). Summer hotspots were more coastal (all regions) and further north (only Baffin Region) than winter hotspots (Figure 3). Null model hotspots occurred in the vicinity of where narwhals were tagged and overlapped high hotspot levels (95 and 99%) by 67% (Figures S15, S17).

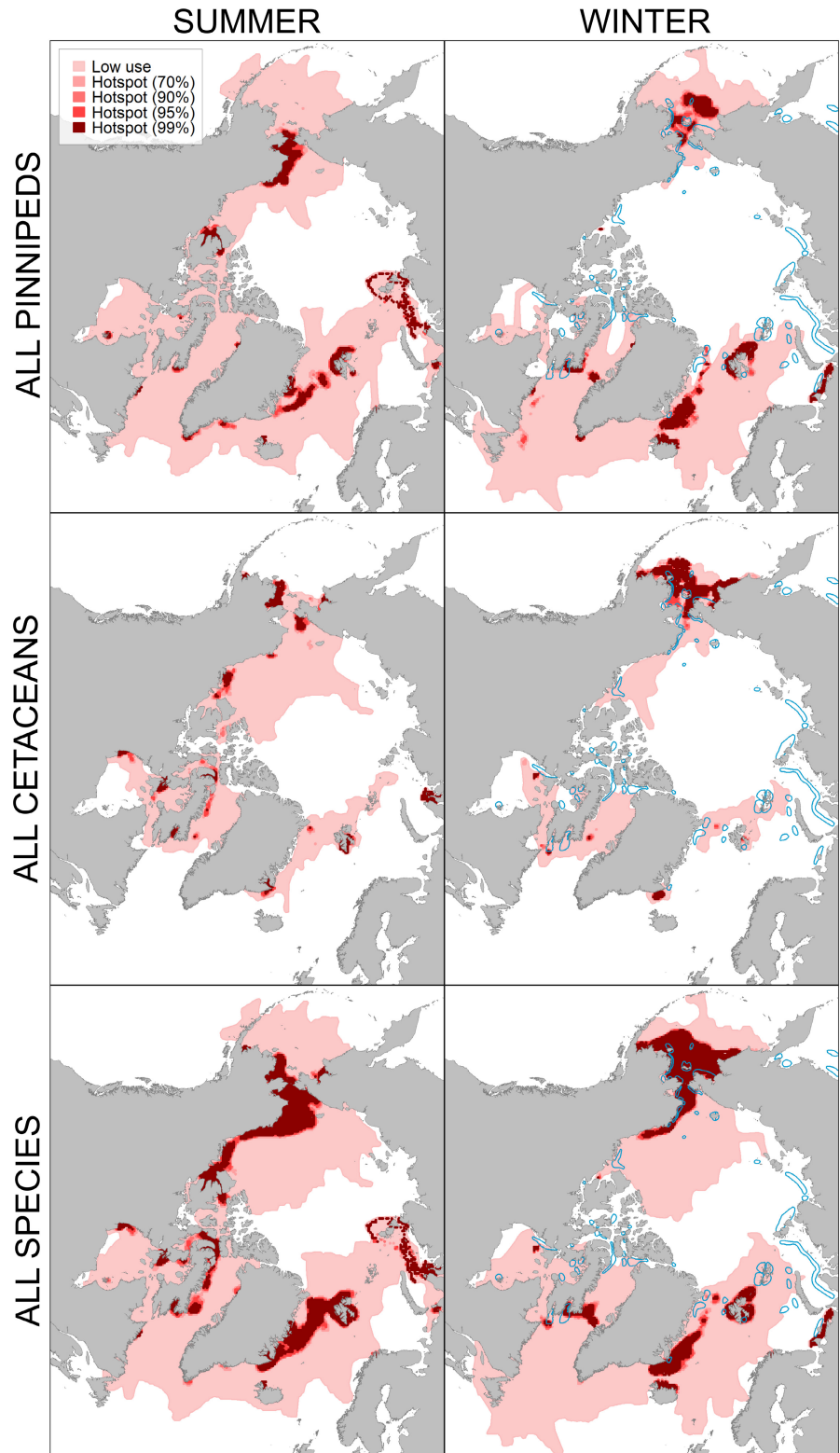
3.7 | Polar bears

Hotspots occurred around the Svalbard Archipelago, along the marginal ice zone (MIZ) of the Greenland Sea, East Greenland coastline, Baffin Bay, Davis Strait, Labrador Sea, Hudson Bay, Beaufort Sea, Chukchi Sea and around Wrangel Island (Figures 4, S4, S11, Table 1). Summer hotspots occurred slightly further north than winter hotspots in most regions (Figure 4). Additional hotspot data were available from Yurkowski et al. (2019) for the Canadian Arctic (i.e. orange hotspots in Figures 4, S4, S11). Null model hotspots occurred in the vicinity of where polar bears were tagged and overlapped high hotspot levels (95 and 99%) by 58% (Figures S15, S18).

3.8 | Spotted seals

Hotspots in the BCB region were generally offshore in the central Bering Sea in winter and along the eastern Chukchi Sea, including

FIGURE 6 Getis-Ord G_i^* hotspots for nine pinniped, three cetacean and the combined 13 marine mammal species (cetaceans, pinnipeds and the polar bear) in the circumpolar Arctic during the summer (Jun-Nov) and winter (Dec-May) based on the number of individuals per grid cell. Increasing intensities of red indicate hotspots of increasing level of significance. Polynya locations are shown on the winter hotspots maps as blue polygons



Kotzebue Sound, in summer (Figures 4, S5, S11, Table 1). Coastal hotspots also occurred along the Bering Strait region and the north-west Alaska coast in the Chukchi Sea (Figure 6). Winter hotspots were generally further south and further offshore than summer hotspots (Figure 4). Null model hotspots were found near tagging locations for spotted seals and overlapped high hotspot levels (95 and 99%) by 31% (Figures S19, S20).

3.9 | Ribbon seals

Hotspots occurred in the Bering Sea, including in the Gulf of Anadyr (Figures 4, S5, S11, Table 1). Hotspots were generally offshore, except for in the Gulf of Anadyr (Figures 4, S11). Null model hotspots occurred in the vicinity of where ribbon seals were tagged and overlapped high hotspot levels (95 and 99%) by 63% (Figures S19, S20).

3.10 | Hooded seals

Hotspots occurred along the south and west coasts of the Svalbard Archipelago, Norwegian Sea, Greenland Sea (including the MIZ), Davis Strait, coastal regions of southeast Greenland, the Labrador Sea, Davis Strait and Baffin Bay (Figures 5, S16, S12, Table 1). Hotspots based on the number of locations were also found in southern portions of the Norwegian Sea and southeast of Iceland (Figure S6). Summer hotspots generally occurred further north than winter hotspots (Figure 5). Null model hotspots occurred in the vicinity of where hooded seals were tagged and overlapped high hotspot levels (95 and 99%) by 23% (Figures S19, S20).

3.11 | Harp seals

Hotspots occurred in the MIZ of the Greenland Sea, northern Barents Sea and around the Svalbard Archipelago (Figures 5, S6, S12, Table 1). Hotspot maps based on the number of locations also occurred south of Svalbard and in fjords in western Svalbard (Figure S6). Summer hotspots were located further north than winter hotspots (Figure 5). Null model hotspots occurred in the vicinity of where harp seals were tagged and overlapped high hotspot levels (95 and 99%) by 25% (Figures S19, S20).

3.12 | Harbour seals

Hotspots occurred in south Greenland, Porsanger Fjord (northern Norway) and along western Svalbard (Figures 5, S7, S12, Table 1). Summer and winter hotspots were located in similar areas in the North Atlantic (Figure 5). Null model hotspots occurred in the vicinity of where harbour seals were tagged and overlapped high hotspot levels (95 and 99%) by 86% (Figures S19, S21).

3.13 | Grey seals

Hotspots occurred in northwest Iceland (Figures 5, S7, S12, Table 1). Summer and winter hotspots were located in similar areas around northern Iceland (Figure 5). Null model hotspots occurred in the vicinity of where grey seals were tagged and overlapped high hotspot levels (95 and 99%) by 75% (Figures S19, S21).

3.14 | Species groups

Hotspots calculated for species groups (all pinnipeds, all cetaceans and all species) and the species richness index highlight regions across the circumpolar Arctic that are important for Arctic marine mammals (Figures 6, 7, S4, S8, S13). These included predominantly continental-shelf habitats in the Svalbard Archipelago, the MIZ in the northern Barents and Greenland Seas, East Greenland, regions

around Baffin Island, Foxe Basin, much of the BCB, as well as areas within the Kara and Pechora Seas (Figures 6, 7, S13). Summer hotspots were generally found further north than winter hotspots in the BCB and in the Canadian Arctic Archipelago (Figures 6, 7). Winter data for some cetacean species were quite limited.

Particularly, high values of species richness were found in the "Arctic gateways" in the North Atlantic (Fram Strait) and North Pacific (Bering Strait) (Figures 7, S14). Overlap between high levels of species richness (≥ 4 species) and high hotspot levels (95 and 99%) was generally quite high, especially during the winter (Figures 7, S14). There were some areas with high species richness near Franz Josef Land and in central Baffin Bay that did not have high hotspot levels (Figures 7, S14). Null model hotspots and the highest null species richness index areas occurred in the vicinity of where animals were tagged (Figures S22, S23). High null model hotspot levels (95 and 99%) overlapped high marine mammal hotspots levels (95 and 99%) by 42% (all pinnipeds), 40% (all cetaceans) and 59% (all species). High null species richness (≥ 4 species) overlapped high marine mammal species richness (≥ 4 species) by 41%.

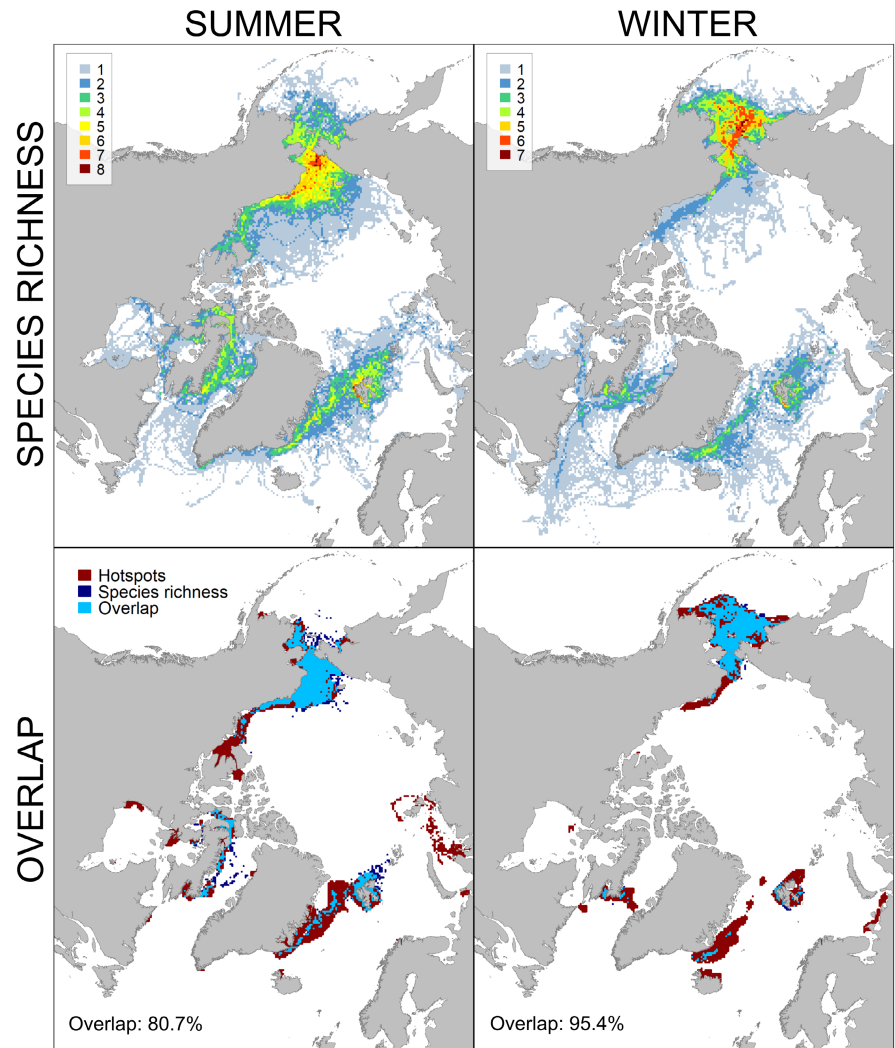
3.15 | Hotspot habitat

Large regional differences in the habitat features within hotspots for marine mammals occurred across the circumpolar Arctic (Figures 8, 9, Tables S2, S3). Hotspots in Svalbard, Greenland and the eastern Canadian Arctic Archipelago were generally in areas with tidewater glacier fronts, whereas this habitat is absent in the BCB (Figures 8, 9, Table S2). Sea-ice frequency was higher in the winter hotspots than the summer hotspots for all species, although a large range of sea-ice frequencies were used during the winter period (Table S2). Hooded, harp, ribbon, harbour and grey seals were generally found in areas with less sea ice than the other marine mammal species during the winter months (Figures 8, 9, Table S2). Ringed seal, bearded seal and white whale hotspots had less sea ice in the East Greenland and Barents Sea region than the other regions during the winter (Figures 8, 9, Table S2). Distance to the coast and water depth were variable among species, largely reflecting whether species had coastal or open ocean distributions (Figures 8, 9, Table S2). Positive water depths (i.e. land) reflected tight coastal distributions in some regions for some species (Table S2). Most marine mammal species were generally further away from polynyas in the winter in the Canada/West Greenland region than the other regions (Figures 8, 9, Table S2).

4 | DISCUSSION

Arctic marine mammal hotspots and areas of high species richness occurred across the Arctic continental-shelf seas and in the MIZ, in regions previously identified as important habitats for Arctic marine mammals (Citta, Lowry, et al., 2018; Hamilton et al., 2020; Yurkowski et al., 2019). The seasonal presence of sea ice is a defining feature for most hotspot areas identified, with most Arctic marine mammal

FIGURE 7 Species richness and overlap between high levels of Getis-Ord G_i^* all species hotspots (95 and 99%) and high species richness (≥ 4 species) for 13 marine mammal species in the circumpolar Arctic during the summer (Jun-Nov) and winter (Dec-May). Blue to red colour scale indicates an increasing number of species (species richness)



hotspots having >10% sea-ice frequency during both the summer and winter periods. Sea ice serves a variety of functions for Arctic marine mammals: it is a pupping, nursing and moulting platform for seals; a hunting platform and transport corridor between hunting and maternity denning areas for polar bears; and a resting platform, near benthic foraging areas, for walrus. It also offers protection from storm events and aquatic predators and ice edges are important foraging areas for all species (Kovacs et al., 2011; Laidre et al., 2008). Seasonally sea-ice-covered regions have high primary production from ice-algae and phytoplankton blooms that begin under the ice in spring, providing nutritional support for zooplankton, benthic fauna and fish upon which marine mammals depend (Ardyna et al., 2020; Kovacs et al., 2011; Sakshaug, 1997). Spring and summer blooms follow the MIZ as it retreats northwards in the summer, making these high-productivity areas broad and generally predictable in both space and time. Correspondingly, summer hotspots were generally located further north than winter hotspots for many (but not all) species and regions and had lower sea-ice frequencies. Bowhead whales in the Greenland and Barents Seas are an outlier to this general pattern as they have the opposite movement pattern, migrating north in the winter and south in the summer (Kovacs et al., 2020). In

the Canadian Arctic, several marine mammal species utilize a more east-west movement pattern than south-north pattern in their winter to summer movements. In addition, defined seasonal movements are also not characteristic for several, but not all, species in Svalbard, East Greenland and the eastern Canadian Arctic (e.g. harbour seals, white whales, ringed seals, bearded seals) that have coastal distributions throughout the year. The differences in movement patterns and habitat types within and among species may need to be considered when designing conservation and management measures around important areas (e.g. migratory pathways, over-wintering areas, nursing areas).

The selected summer (June–November) and winter (December–May) seasons corresponded to migration and seasonal residency patterns for most, but not all, species and regions. Seasonal hotspot designations are therefore not equally representative for all species and regions. For example, Amundsen Gulf is a summering area for bowhead whales in the BCB. Bowhead whales are predicted to remain in summer areas for longer periods of the year due to environmental changes and they have recently been documented over-wintering in Amundsen Gulf (Insley et al., 2021). However, the winter hotspot in Amundsen Gulf in the analyses herein is not due to

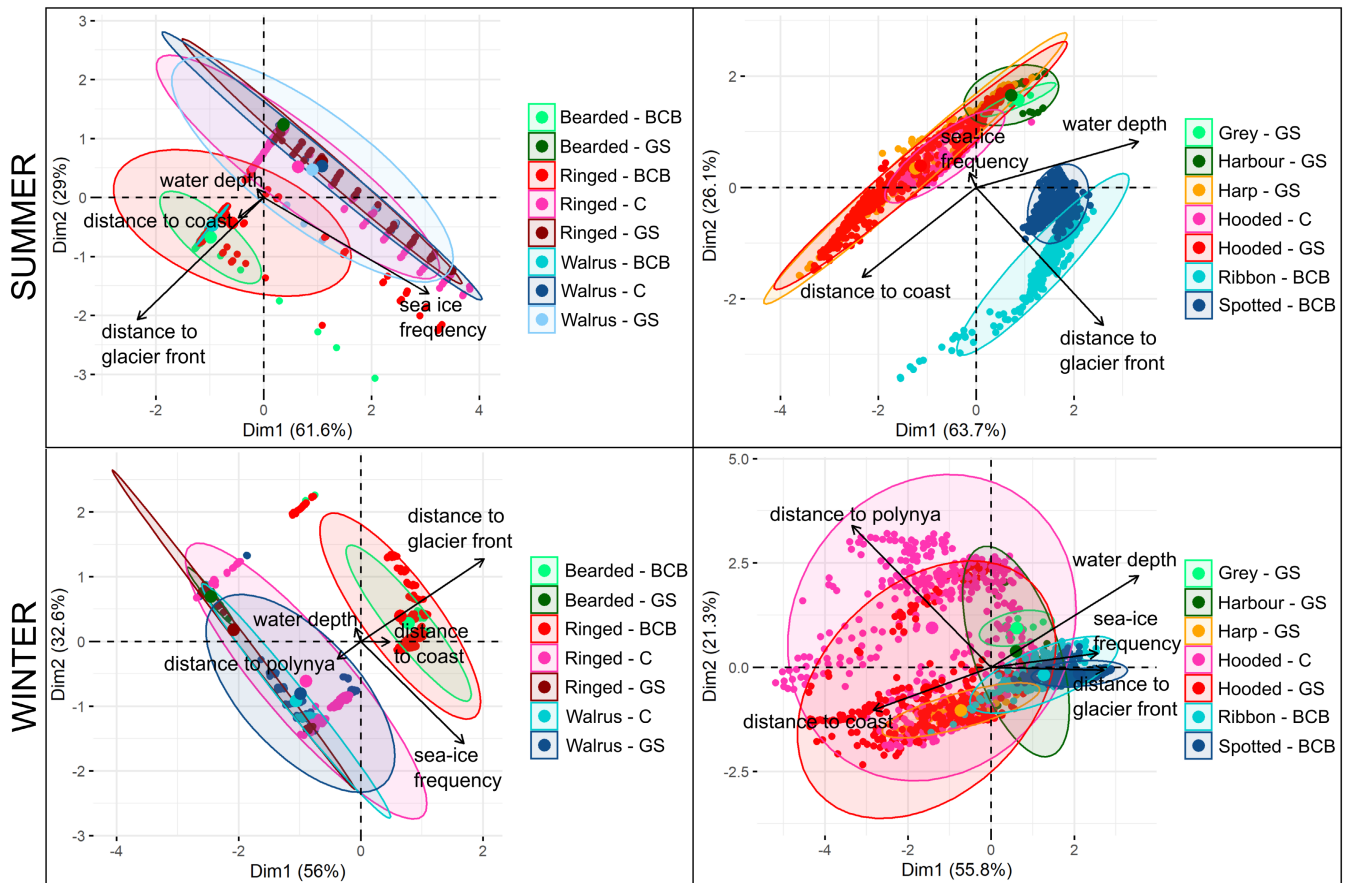


FIGURE 8 PCA plots for habitat variables in Getis-Ord G_i^* hotspots (70%–99%) for nine pinniped species (bearded seal, ringed seal, walrus, grey seal, harbour seal, harp seal, hooded seal, ribbon seal and spotted seal) in the circumpolar Arctic during the summer (Jun–Nov) and winter (Dec–May). The circumpolar range of each species was split into regions (BCB: Bering–Chukchi–Beaufort region; C: Canadian Arctic Archipelago and West Greenland; GS: East Greenland and Barents Sea region)

over-wintering. It is rather an artefact of the winter season definition as bowhead whales arrive in the Amundsen Gulf in May at the end of their spring migration. Similarly, the Beaufort Sea is used by white whales in the summer but is included in the winter hotspots because of white whales that migrate in May with the bowhead whales. Each season also encompasses multiple biological stages for all species. For example, the winter period includes over-wintering behaviour, birth and nursing (either entirely for most pinnipeds or a proportion for cetaceans and polar bears) for most species; different areas and habitats are likely favoured for different life-history events. Another caveat is that in some regions, multiple stocks exist for some species and biotelemetry data are usually not evenly split among the different stocks (e.g. white whales in the BCB region). In these cases, hotspots will be biased towards the areas that are used by the stocks with the most tracking data. Logistical challenges when undertaking fieldwork, and the variable ecologies of the ages and sexes in many marine mammal species, also means that tracking datasets usually do not contain an equal representation of the different age classes and sexes. In extreme cases, only one age class or one sex has been tagged (e.g. Greenland Sea harp seal data includes only pups, the vast majority of tagged polar bears are females). Thus, extrapolating results to the species level should be done with caution.

Areas with high species richness were generally found within high hotspot levels for all species (overlap >80%). Because each species-region combination received an equal weight in the all species analysis, some regions (i.e. western Hudson Bay, Kara Sea), had high hotspots levels but low species richness. These regions are known to be important marine mammal areas, but biotelemetry data were lacking for them. Similarly, there were a few regions with high species richness that did not have high hotspots levels. This discrepancy is likely the result of areas that are used by multiple species for transit or only used intensively by subsets of the tagged populations. The species richness and hotspot results should be used in tandem for conservation and management purposes.

The two “Arctic gateways” in the north Atlantic and Pacific oceans were especially species rich and they generally had high hotspot levels (also see CAFF 2017). These regions transport heat, nutrients and plankton into the Arctic Ocean (Basedow et al., 2018) and are also regions with rich fish stocks (Christiansen et al., 2014). Both regions are experiencing warming trends and exhibiting reductions in Arctic ecosystem components (Fossheim et al., 2015; Huntington et al., 2020). Regional differences in hotspot habitats were also found in many cases, likely reflecting not only the different environmental features present but also the ecosystem differences

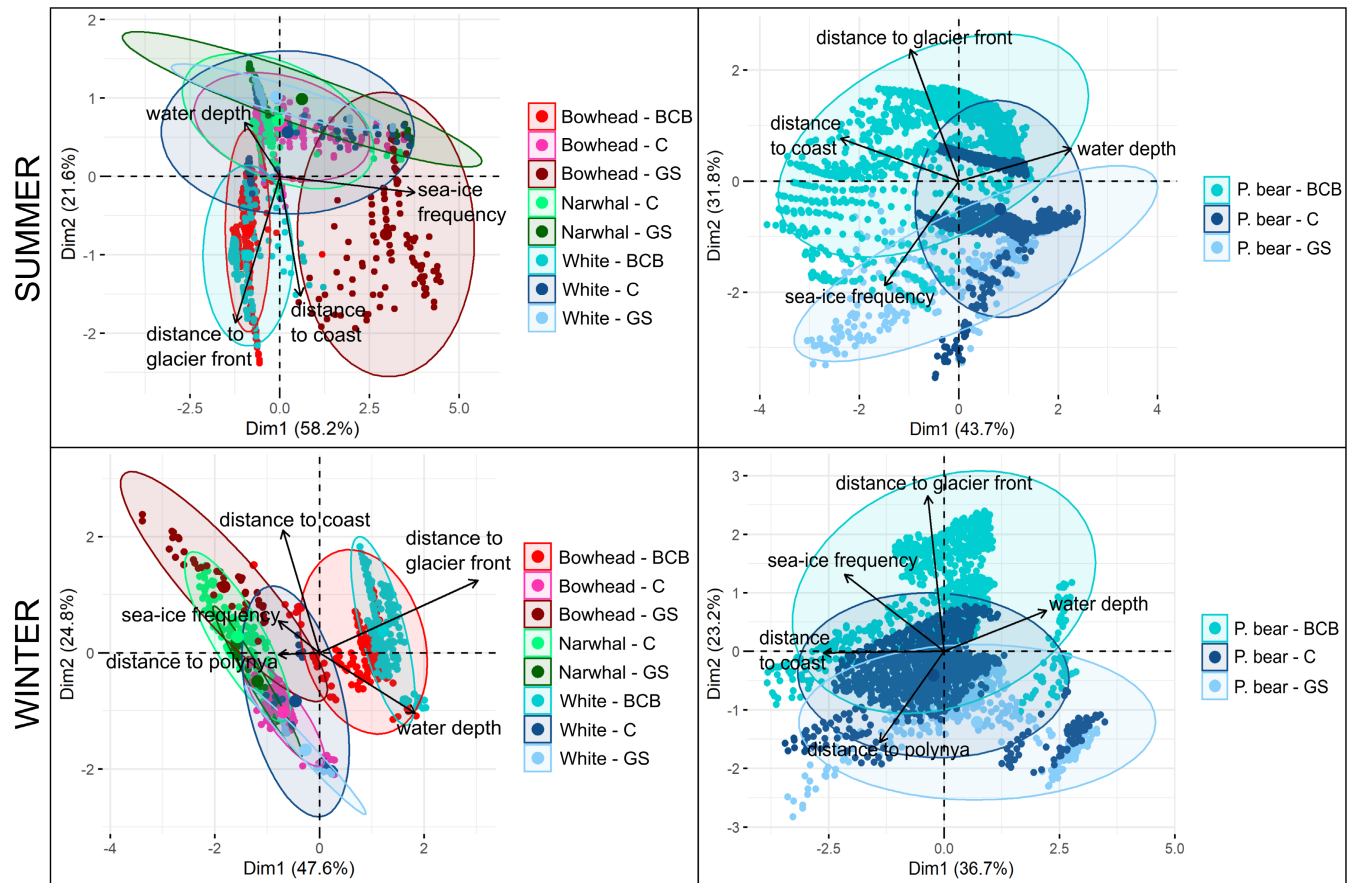


FIGURE 9 PCA plots for habitat variables in Getis-Ord G_i^* hotspots (70%–99%) for three cetacean species (bowhead whale, narwhal and white whale) and polar bears in the circumpolar Arctic during the summer (Jun–Nov) and winter (Dec–May). The circumpolar range of each species was split into regions (BCB: Bering–Chukchi–Beaufort region; C: Canadian Arctic Archipelago and West Greenland; GS: East Greenland and Barents Sea region)

across the circumpolar Arctic (e.g. Bluhm et al., 2015; Stenson et al., 2020). This indicates that environmental changes might have different impacts on species' distribution and behaviour across the circumpolar Arctic. The long-term impacts of these ecological trends on Arctic marine mammals, concomitant with other threats including increased presence of temperate marine mammal species, increased levels of human activities and changing trophic interactions are concerning.

Recurrent polynyas overlapped many marine mammal hotspots in the winter period (Figure 6). Polynyas can be important for marine mammals as over-wintering and foraging areas; at times thousands of marine mammals from multiple species occupy these areas (Born & Knutsen, 1992; Kovacs et al., 2020; Laidre et al., 2008). The hotspots of some species, such as bearded seals, bowhead whales, white whales and spotted seals, were closer to polynyas than hotspots of other species explored herein, although regional differences in polynya use were apparent. Several recurrent polynyas did not overlap with identified hotspots, despite these areas being known to be important for marine mammals. This is likely a sampling artefact reflecting where biotelemetry data are lacking such as from the North Water Polynya, the Great Siberian Polynyas and polynyas within the Canadian Arctic Archipelago (Heide-Jørgensen et al., 2016; Speer

et al., 2017). Similarly, the finding that winter hotspots were generally further from polynyas in the Canadian and West Greenland region than the other regions may be due to lack of biotelemetry data from polynya areas in this region. The winter distribution of sea ice has moved north of some well-known recurrent polynyas, further demonstrating effects of climate change on important marine mammal habitats.

Tidewater glacier front habitat is important for several Arctic marine mammal species, but is prevalent only in some Arctic regions, including Greenland, Svalbard, Franz Josef Land and Novaya Zemlya in the Russian Arctic (Laidre et al., 2016; Lydersen et al., 2014). Correspondingly, distance to tidewater glacier fronts was a defining feature of regional differences in hotspot habitat. Close association with tidewater glacier fronts was identified in the hotspots of many species in the Canada/West Greenland and the East Greenland/Barents regions, but cannot be considered important in the regions where it does not occur (i.e. in the BCB region). Upwelling and circulation patterns driven by katabatic winds and freshwater discharge lead to high concentrations of lower trophic level prey near the glacier terminus creating important foraging habitats for ringed seals, bearded seals, white whales and narwhals (Hamilton et al., 2016, 2018; Laidre et al., 2016; Lydersen et al., 2014; Meire et al., 2017).

Tidewater glacier fronts are also important pupping and denning areas for ringed seals and polar bears (in some locations) and provide hunting areas for polar bears in the spring (Freitas et al., 2012; Laidre & Stirling, 2020; Lydersen et al., 2014). In the BCB, where there are no tidewater glaciers and also in other Arctic regions, ringed seals use shore-fast ice for pupping and polar bears use sea ice, barrier islands and land for denning (Crawford et al., 2012).

The hotspot method (based on the number of individuals of each species in a grid cell) used herein identified areas used by most of the tagged animals in a region and include common birthing, nursing, resting, foraging and moulting sites. Other important areas used by only segments of a population may be missed by this method such as foraging sites for species that forage either singly or in small to medium sized groups across large regions. Polar bear denning locations might also be missed. Null models were created to address bias due to tracking effort; they show where hotspot locations would be expected based on tagging locations and general movement patterns of the species. The amount of overlap between high levels of null model hotspots and marine mammal hotspots varied by species group (Table 2). Overlap was generally less for species that had large-scale or directed movements away from tagging locations. Biases are undoubtedly introduced by fieldwork being carried out in areas where species are known to occur and that are accessible. Additional biases likely result from duty-cycling and short attachment times that limit the amount of data available for certain periods of the year.

Sea-ice declines and associated environmental changes are likely the largest current threat to Arctic marine mammals. These threats may operate directly through the loss of birthing, nursing and resting areas or transport corridors, or indirectly through changes in space use, prey composition, abundance and distribution, or the presence

of interspecific competitors and predators (Kovacs et al., 2011; Laidre et al., 2008; Matthews et al., 2020; Reid et al., 2013; Stenson et al., 2016). Large-scale sea-ice declines and ecosystem changes are underway in many of the hotspot areas identified in this study (e.g. Fosshem et al., 2015; Huntington et al., 2020; Vihtakari et al., 2018; Yurkowski et al., 2018). Arctic marine mammals have reacted to past glacial and interglacial periods by changing their distributions (Foote et al., 2013; Harington, 2008; Louis et al., 2020). However, there is a limit to how far Arctic marine mammals can shift their distribution northward into the Arctic Ocean Basin given their strong affiliation with the highly productive continental-shelf habitats demonstrated by our hotspots analyses. The potential for northward shifts is likely variable among species and between regions. Productivity in the Arctic Ocean Basin is lower than the Arctic continental-shelf seas and it is unknown how productivity and fish distribution will change as the Arctic continues to warm.

Sea-ice declines have not led to direct changes in habitat use for all species. For some species, including narwhals, white whales, bowhead whales, walrus, hooded seals and bearded seals, habitat use appears to be more directly linked to bathymetric features than to sea-ice concentration for some regions and times of year (e.g. this study, Andersen et al., 2013; Hauser et al., 2018; Kenyon et al., 2018; Olnes et al., 2020). Some species are making greater use of open water areas as environmental changes occur and new prey species become available (Hamilton, Vacqu e-Garcia, et al., 2019). However, habitat use, foraging behaviour and location of hotspots may be indirectly impacted through changes in the prey base and the increased presence of interspecific competitors and predators (Breed et al., 2017; Hauser et al., 2018; Matthews et al., 2020). In particular, the increased presence of killer whales has the potential for substantial impacts, both directly through predation and indirectly through predator avoidance behaviour (Breed et al., 2017; Higdon & Ferguson, 2009; Matthews et al., 2020).

Economic interest in the Arctic continental-shelf seas and the Arctic Ocean Basin is increasing as decreasing sea-ice extent reduces logistical challenges for industries. Increased human activity (e.g. shipping, fishing, oil and gas exploration and production, mining and tourism) pose multiple threats to Arctic marine mammals including risk of ship strikes, gear entanglement, bycatch, prey competition, effects of noise (e.g. avoidance, hearing loss, disruption of prey), oil spills, pollution, displacement and changes in behaviour (e.g. Citta et al., 2014; Hauser et al., 2018; Reeves et al., 2014; Rode et al., 2018). The overall potential for population-level impacts will vary depending on the proportion of the population impacted and the magnitude of a given effect. Impacts could be severe if human activities interrupt key processes (such as migration) or critical time periods (e.g. breeding) (e.g. Heide-J rgensen et al., 2013).

TABLE 2 Amount (%) that null model Getis-Ord G_i^* hotspots (95% and 99%) overlap the marine mammal hotspots (95% and 99%) for each species and species group

Species	Overlap (%)
Ringed seal	34.3
Bearded seal	31.9
Walrus	55.3
Bowhead whale	32.0
White whale	34.1
Narwhal	67.1
Polar bear	58.4
Spotted seal	31.0
Ribbon seal	62.6
Hooded seal	23.2
Harp seal	24.6
Harbour seal	86.1
Grey seal	74.5
All species	58.9
All pinnipeds	42.4
All cetaceans	39.9

4.1 | Future research needs and recommendations

Global climate predictions suggest that many high-use areas identified herein will likely become less favourable habitat during this

century, which is likely to result in distributional shifts and to impact the long-term persistence of Arctic marine mammals (e.g. Durner et al., 2009; Øigård et al., 2014; Reimer et al., 2019). Ideally, biotelemetry studies should be expanded across the distributional range of species with sample sizes that will document movement and behaviour patterns of various age and sex groups in each region to ensure that important areas for critical life stages are identified (e.g. Fortune et al., 2020; Sequeira et al., 2019).

A gap analysis is implicit in the identification of Arctic marine mammal hotspots, because discrepancies between hotspots and IUCN ranges highlight where, and for which species, more research is required. This comparison also highlights regions where IUCN species ranges need to be revised because biotelemetry data extend beyond the IUCN borders of species occupancy in some cases. More biotelemetry data are needed particularly for the Russian Arctic. For example, identification of the western Chukchi Sea and East Siberian Sea as low use areas for polar bears is likely due to limited tagging effort. Data are also lacking for some species in East and West Greenland, the eastern Svalbard Archipelago and for some areas within the Canadian Arctic Archipelago. Additionally, data are lacking from some stocks in the larger regional areas (e.g. eastern Chukchi belugas in the BCB), influencing the identification of hotspot locations in these regions. Numerous species also require more tagging effort; limited data are available for bearded seals, white whales, walruses, narwhals and harp seals. Additional tagging efforts should also try to attain greater seasonal coverage for some species (see Table 1). For species that generally have had short attachment durations (e.g. whales, walruses in some regions), portions of the year with sparse or no data limits the detection of seasonal hotspots. Location data are also generally lacking for the moulting periods of seals, an energetically costly period, when seals may be particularly vulnerable. Addressing these gaps will require innovative new attachment methods. Efforts should also be made to continue time series (including re-tagging individuals when possible) to quantify changes in behaviour, distribution and habitat use due to climate change. Integration of behavioural data (e.g. dive and activity data) from the tags in future large-scale studies along with complementary data from many sources (e.g. diet, body condition, prey availability, passive acoustic data) will undoubtedly improve our understanding of marine mammal habitat use and how it is likely to be impacted by climate change and concomitant changes in human activities. In some Arctic regions, Indigenous Knowledge will provide information to help fill identified knowledge gaps (Gryba et al., 2021; Huntington et al., 2017; Loseto et al., 2018).

Effective conservation and management measures for Arctic marine mammals rely on comprehensive data from biotagging initiatives and syntheses across species to identify important areas. Minimizing man-made stressors may reduce the overall impacts and allow some species time to adjust to environmental changes. Protected areas, including Marine Protected Areas, nature reserves and national parks, need to be expanded and protecting areas that extend across international boundaries should be considered (Hussey et al., 2016). Numerous examples exist of where biotelemetry data and identified

hotspot regions have influenced policy and management decisions, including defining protected areas, reducing the risk of vessel strikes and in risk assessments for proposed human activities (e.g. Hays et al., 2019). Greater use of movement data is needed to help protect species against the variety of threats they face, including complications arising from transboundary management (e.g. Hays et al., 2016, 2019; Sequeira et al., 2019; Tittley et al., 2021). Given the current rate of change in the Arctic, spatially and temporally dynamic protected areas should be evaluated (D'Aloia et al., 2019; Hyrenbach et al., 2000). Specific examples where dynamic protected areas might be most effective include avoidance of disturbance to pinniped pupping, nursing and moulting areas during these life-history events, polynyas during winter and spatial adjustments relative to large intra- and inter-annual variations in the MIZ. Monitoring marine mammal use of hotspots through biotelemetry in near-real time could support dynamic boundary delimitations and active management (Hobday et al., 2011; Sequeira et al., 2019).

5 | CONCLUSIONS

The Arctic continental-shelf seas and MIZ were identified as regions with a high density of hotspots and high species richness. The "Arctic gateways" of the North Pacific and North Atlantic were particularly species rich. Hotspots differed by species, but some common areas were identified, such as coastal areas around the Svalbard Archipelago, the East Greenland continental shelf, waters surrounding Baffin Island and coastal and continental-shelf areas throughout the BCB region. Habitat features of marine mammal hotspots differed seasonally, regionally, within and among species. Environmental changes associated with sea-ice declines and increases in human activity are currently taking place in many of the identified hotspots. Biotelemetry research is needed in regions and on populations where data are lacking. Efforts also need to be directed to continuing telemetry time series and incorporating behavioural data and Indigenous Knowledge where applicable. Although there are regional, sex and age gaps in the data at hand, the hotspots identified in this study do represent key marine mammal areas that can serve as a benchmark for spatial management to mitigate anthropogenic disturbances and reduce stress on marine mammal populations. Arctic marine mammals are currently facing multiple threats and the findings of this study can inform management efforts to help mitigate pressures related to these threats and assist this species group in adjusting to future environmental changes.

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KMK, CL designed the study. CDH processed the data, performed statistical analyses. CDH, KMK, CL interpreted the results. CDH wrote the first draft, all authors provided data, contributed to manuscript revision.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Getis-Ord G_i^* hotspot shapefiles are available from the Norwegian Polar Data Centre (doi: <https://doi.org/10.21334/npolar.2022.c919170d>).

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BIOSKETCH

The authors are marine mammal scientists and Inuit co-leads whose research focuses on distribution and movements of marine mammals in the Arctic via the deployment of satellite-linked transmitters. Together, our studies cover much of the circumpolar Arctic.

Author contributions: K.M.K. and C.L. designed the study. C.D.H. processed the data and performed statistical analyses. C.D.H., K.M.K. and C.L. interpreted the results. C.D.H. wrote the first draft and all authors provided data and contributed to manuscript revision.

SUPPORTING INFORMATION

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