FEATURE ARTICLE

Marine mammal hotspots in the Greenland and Barents Seas

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ABSTRACT: Environmental change and increasing levels of human activity are threats to marine mammals in the Arctic. Identifying marine mammal hotspots and areas of high species richness are essential to help guide management and conservation efforts. Herein, space use based on biotelemetric tracking devices deployed on 13 species (ringed seal *Pusa hispida*, bearded seal *Erignathus barbatus*, harbour seal *Phoca vitulina*, walrus *Odobenus rosmarus*, harp seal *Pagophilus groenlandicus*, hooded seal *Cystophora cristata*, polar bear *Ursus maritimus*, bowhead whale *Balaena mysticetus*, narwhal *Monodon monoceros*, white whale *Delphinapterus leucas*, blue whale *Balaenoptera musculus*, fin whale *Balaenoptera physalus* and humpback whale *Megaptera novaeangliae*; total = 585 individuals) in the Greenland and northern Barents Seas between 2005 and 2018 is reported. Getis–Ord G_i^* hotspots were calculated for each species as well as all species combined, and areas of high species richness were identified for summer/autumn (Jun–Dec), winter/spring (Jan–May) and the entire year. The marginal ice zone (MIZ) of the Greenland Sea and northern Barents Sea, the waters surrounding the Svalbard Archipelago and a few Northeast Greenland coastal sites were identified as key marine mammal hotspots and areas of high species richness in this region. Individual hotspots identified areas important for most of the tagged animals, such as common resting, nursing, moulting and foraging areas. Location hotspots identified areas heavily used by segments of the tagged
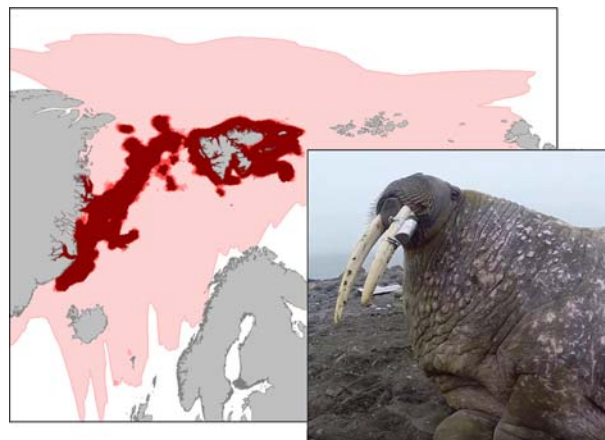
Getis–Ord G_i^* plots highlight marine mammal hotspots in the Barents region—walruses were one of 13 species studied (using new custom-GPS tags) *Photo: Kit M. Kovacs and Christian Lydersen; Image: C. D. Hamilton; NPI*

populations, including denning areas for polar bears and foraging areas. The hotspots identified herein are also important habitats for seabirds and fishes, and thus conservation and management measures targeting these regions would benefit multiple groups of Arctic animals.

KEY WORDS: Ice-associated marine mammals · Seasonal migrants · Marginal ice zone · Svalbard · East Greenland · Climate change · Arctic · Biotelemetry

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1. INTRODUCTION

The climate is changing faster in the Arctic than in any other area on Earth, with air temperatures increasing at a rate 2–3 times the global average and sea-ice extent declining at an alarming rate (IPCC 2018, Meredith et al. 2019). Arctic endemic marine mammals are all strongly ice-affiliated and hence are seriously threatened by these changes (see Laidre et al. 2008, Kovacs et al. 2011, Meredith et al. 2019 for details). Numerous consequences of climate change have already been documented for this species group. Declines in Arctic sea ice and associated environmental changes have been linked to shifts in species distributions (e.g. Higdon & Ferguson 2009, Hamilton et al. 2015, 2019a, Rode et al. 2015, Lone et al. 2018), changes in trophic relationships (e.g. Watt et al. 2016, Hamilton et al. 2017, Yurkowski et al. 2018) and increased risks of disease (e.g. Van Wormer et al. 2019). Concomitantly, levels of human activity, including shipping, tourism, commercial fishing, and oil and gas exploration and production, have increased and are likely to continue to do so in Arctic regions as sea-ice declines reduce logistical challenges for these industries (Reeves et al. 2014, Meredith et al. 2019). Thus, there is an acute need to identify important areas for marine mammals to allow for proper management and conservation of these species in the context of these multiple stressors (e.g. Kovacs et al. 2011, Reeves et al. 2014, Yurkowski et al. 2019).

Numerous marine mammal species inhabit the Greenland Sea and the northern Barents Sea. Three cetacean species (bowhead whale *Balaena mysticetus*, narwhal *Monodon monoceros* and white whale [beluga whale] *Delphinaterus leucas*) and the polar bear *Ursus maritimus* are Arctic endemic species that reside in these areas throughout the year (Kovacs et al. 2009, 2011). This region of the North Atlantic Arctic also contains 6 pinniped species. Three of these species (ringed seal *Pusa hispida*, bearded seal *Erignathus barbatus* and Atlantic walrus *Odobenus rosmarus rosmarus*) are endemic to the Arctic and live in close association with sea ice throughout the year. The harp seal *Pagophilus groenlandicus* and hooded seal *Cystophora cristata* are also dependent on sea ice. These species use the marginal ice zone (MIZ) in the Greenland Sea for pupping, nursing and moulting during the spring but are generally found in open water areas during the rest of the year (Kovacs et al. 2009, 2011). The harbour seal *Phoca vitulina* is generally considered to be a temperate seal species, but a population resides year round on the west coast of Svalbard (Lydersen & Kovacs 2010). A variety of cetacean species also use the Greenland and Barents Seas primarily during the summer and autumn as a foraging ground, including the killer whale *Orcinus orca*, the blue whale *Balaenoptera musculus*, the fin whale *Balaenoptera physalus*, the humpback whale *Megaptera novaeangliae*, the minke whale *Balaenoptera acutorostrata*, the sperm whale *Physeter macrocephalus*, the harbour porpoise *Phocoena phocoena* and the white-beaked dolphin *Lagenorhynchus albirostris* (Kovacs et al. 2009, Storrie et al. 2018).

Sea-ice extent is changing rapidly in the Greenland and Barents Seas, with the duration of sea-ice cover declining faster in the northern Barents Sea than in any other Arctic region (41.8 d decade^{-1}; Laidre et al. 2015a). Environmental conditions in Svalbard and the Barents Sea changed dramatically in the winter of 2005–2006, with the altered conditions persisting to the present day. The amount of land-fast ice forming in Svalbard's fjords declined sharply, especially along the west coast, and the location of the MIZ shifted northward (Hamilton et al. 2015, Pavlova et al. 2019). These changes were due in part to an increase in the temperature of Atlantic Water, in combination with more frequent penetration of Atlantic Water across the polar front, which, among other effects, has led to a 'borealization' of the fish and invertebrate communities in the Barents Sea (Fossheim et al. 2015, Tverberg et al. 2019). Levels of human activity in the Greenland and Barents Seas are increasing concomitant with the ongoing environmental changes. The Barents Sea (including the Svalbard Archipelago) is one of the most heavily trafficked regions in the High Arctic (Reeves et al. 2014). For example, the number of cruise vessels docking in Longyearbyen, the main settlement in Svalbard, tripled between 2007 and 2019 (Port of Longyearbyen 2020). Fishing activity is also expanding further north as sea ice recedes and currently occurs up to the northern ice edge, north of Svalbard (Reeves et al. 2014, ICES 2019). Hydrocarbon provinces are found throughout the Barents Sea and along the coast of East Greenland. Noise from air guns is already heard throughout the year in the western Fram Strait (Ahonen et al. 2017). Offshore oil and gas exploration and land-based mining are currently in the planning stage in East Greenland; some of these planned activities would involve extensive year-round shipping (Reeves et al. 2014).

The large-scale environmental changes and increasing levels of human activities in the Northeast Atlantic Arctic create a need to identify marine mam-

mal hotspots to help guide management and conservation efforts. Observational data are limited from these areas due to a combination of factors, including few human communities, large expanses of sea ice, low levels of light up to 6 mo of the year and the cryptic, dispersed nature of many marine mammal species. In this study, data from 585 biotelemetry instruments deployed on 13 species of marine mammals (2005–2019) in the Greenland and northern Barents Seas (by 11 scientific institutes) were collated in order to investigate the occurrence of marine mammal hotspots and areas of high species richness. Discrepancies between a species' range and hotspot coverage serve as a gap analysis that will help identify regions and species where more research effort is required. Threats to marine mammals within identified hotspots areas are also discussed.

2. MATERIALS AND METHODS

2.1. Study area

Biotelemetry data were collected from marine mammals tagged around the Svalbard Archipelago, in the northern Barents Sea, Fram Strait and along the northeast coast of Greenland (northwards of 68°N) during the last 15 years (2005–2019). The final area shown in the maps was from 58 to 90°N and 40°W to 100°E (Fig. 1).

The Greenland Sea (including the Fram Strait, Denmark Strait and the continental shelf of East Greenland) and the Barents Sea form the connection between the Northeast Atlantic Ocean and the Arctic Ocean (Fig. 1). The Barents Sea is moderately shallow (average depth: 230 m; maximum depth: ~500 m) whereas the Greenland Sea is deeper (average depth: 1444 m; maximum depth: 4846 m). The Barents Sea is also more exposed to warm Atlantic Water than the Greenland Sea. The West Spitsbergen Current (a branch of the North Atlantic Current) flows northwards along the west coast of Svalbard, on the eastern edge of the Greenland Sea, transporting warm Atlantic Water into the Arctic Ocean (Ingvaldsen & Loeng 2009). The East Greenland Current transports cold Arctic Water and sea ice southwards through the Fram Strait over the continental shelf of the east coast of Greenland (Rudels et al. 2002). The sea-ice maximum and minimum in this region occur in April and September, respectively (Fig. 1). The MIZ is defined as the area between the open ocean and the pack-ice with sea-ice concentrations between 15 and 80% (Fig. 1). It is a highly dynamic zone with large intra- and inter-annual variability in both its location and extent; it varies from being a few kilometres wide up to hundreds of kilometres wide. The summer productivity pulse makes the MIZ an important foraging area for many species (Sakshaug et al. 2009), including a variety of marine mammals.

2.2. Tagging information

Five hundred and eighty-five biotelemetry devices were deployed on animals from 13 species between 2005 and 2019 in and around Svalbard and Northeast Greenland (see Table 1, Fig. 2 and the text in the Supplement at www.int-res.com/articles/suppl/m659 p003_supp.pdf for capture and instrumentation details). The data include tags deployed on 10 species that are resident in this area throughout the year (ringed seal *Pusa hispida*, bearded seal *Erignathus barbatus*, harbour seal *Phoca vitulina*, walrus *Odobenus rosmarus*, harp seal *Pagophilus groenlandicus*, hooded seal *Cystophora cristata*, polar bear *Ursus maritimus*, bowhead whale *Balaena mysticetus*, narwhal *Monodon monoceros* and white whale *Delphinapterus leucas*) and 3 seasonally resident species (blue whale *Balaenoptera musculus*, fin whale *Balaenoptera physalus* and humpback whale *Megaptera novaeangliae*; see Table 1 & Fig. 2 for more details).

Positions were calculated by the Argos satellite system (CLS 2016) or transmitted via the Argos or Iridium satellite systems (Iridium Satellite Communications) in the case of GPS data (Table 1). The single exception was walrus GPS data from Svalbard, which were transmitted to logging stations positioned at 7 terrestrial haul-out sites. All pinnipeds, except walruses, transmitted haul-out data either as the start and end times of individual haul-out events (tags produced by Sea Mammal Research Unit Instrumentation, University of St Andrews, St Andrews, Scotland) or as the proportion of time hauled out each hour (tags produced by Wildlife Computers, Redmond, WA). All tracking data from the summer of 2005 until 31 December 2018 were included in the analyses herein.

Animal handling and tagging procedures in Norwegian territories were approved by the Norwegian Animal Research Authority (before 2015) or the Norwegian Food Safety Authority (from 2015), and for animals captured in Svalbard, permits were also issued by the Governor of Svalbard. Animal handling and tagging procedures in Greenland were approved by the Greenland Institute of Natural Resources and the Government of Greenland.
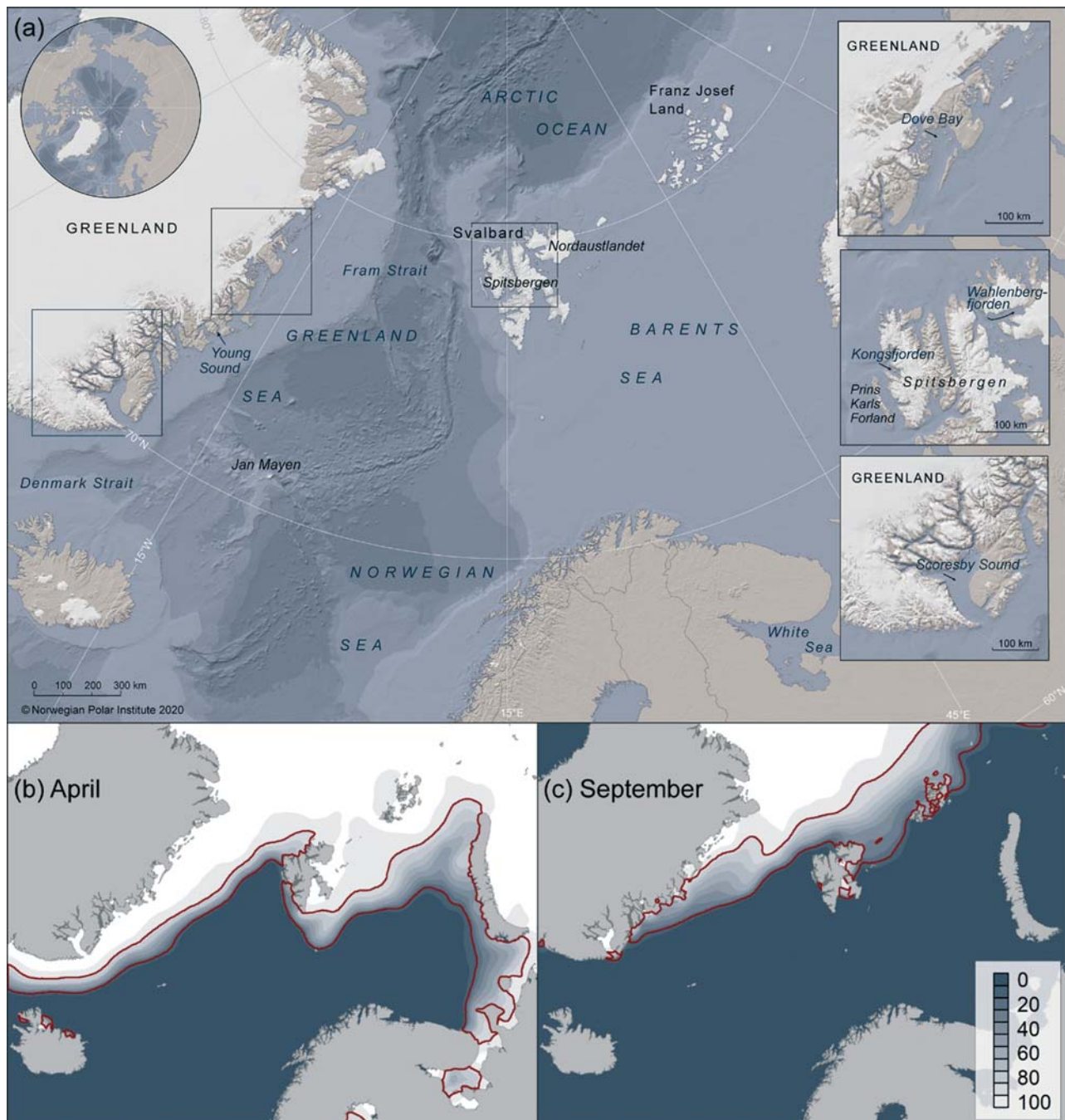
Fig. 1. Map of the study area showing (a) the major place names, ocean areas (in italic font), islands and fjords mentioned in the main text and (b,c) mean sea-ice concentrations (0–100%) for April and September from 2005 to 2018. The 2 red lines indicate the margins of the 15% and 80% sea-ice concentrations (i.e. they encompass the marginal ice zone). Sea-ice data were not available for some coastal areas in this region, shown in dark grey

2.3. Location filtering

All data handling and statistical analyses were performed using R version 3.5.3 (R Core Team 2019). Argos positions were filtered using the SDA filter (argosfilter package; Table S1 in the Supplement; Freitas et al. 2008) for all species, except for walruses, blue whales, bowhead whales and fin whales. Walruses from Svalbard transmitted GPS locations and walruses from East Greenland had Argos locations that were filtered using the Douglas Argos filter (Douglas et al. 2012). SDA filter results for blue

Table 1. Overview of the species included in the hotspot analyses including the number of tags deployed and number of animals tagged in different tagging locations, time period of tracking, seasonal coverage, age classes, tag manufacturers, position type (Argos, GPS or both) and sources (including references for published data sets) for marine mammals tagged around Svalbard and Northeast Greenland. Age classes include pups (P), sub-adults (S) and adults (A). Note: some polar bears were tagged multiple times in Svalbard; 1 ringed seal in Svalbard was also tagged 2 times. Tag manufacturers include Sea Mammal Research Unit Instrumentation (SMRU), Wildlife Computers (WC), Sirtrack, Telonics and Advanced Telemetry Systems (ATS)

Species	Tagging location	No. of tags deployed	No. of animals tagged	Time period	Seasonal coverage	Age classes	Tag manufacturer	Position type	Source
Ringed seals	Svalbard	53	52	2010–2018	Jul–May	S/A	SMRU	Both	Hamilton et al. 2015, 2016
	Northeast Greenland	20	20	2017–2018	Aug–May	S/A	SMRU/WC	Both	Supplement
Bearded seals	Svalbard	20	20	2005–2013	Jun–May	P/A	SMRU	Both	Hamilton et al. 2018, 2019b
Harbour seals	Svalbard	60	60	2009–2011	Jun–May	P/S/A	SMRU	Argos	Blanchet et al. 2014, 2016
Walruses	Svalbard	33	33	2014–2018	Jun–May	A	Sirtrack	GPS	Supplement
	Northeast Greenland	18	18	2008–2010	Jul–Jan	A	WC	Argos	Supplement
Harp seals	Greenland Sea	20	20	2017–2018	Jun–May	P	SMRU/WC	Both	Supplement
Hooded seals	Greenland Sea	20	20	2007–2009	Jun–May	P/S/A	SMRU	Argos	Vacquié-Garcia et al. 2017a
Polar bears	Svalbard	214	142	2005–2019	Jun–May	S/A	Telonics, Sirtrack, ATS	GPS	Lone et al. 2018
	Northeast Greenland	21	21	2007–2009	Jun–May	S/A	Telonics	GPS	Laidre et al. 2013, 2015b
Bowhead whales	Greenland/ Fram Strait	23	23	2010, 2017–2019	Jun–May	A	WC	Argos	Lydersen et al. 2012, Kovacs et al. 2020b
Narwhals	Northeast Greenland	39	39	2010–2017	Jun–May	A	WC	Both	Heide-Jørgensen et al. 2015
White whales	Svalbard	18	18	2013–2017	Jul–Feb	A	SMRU	Argos	Vacquié-Garcia et al. 2018
Blue whales	Svalbard	10	10	2014–2018	Aug–Dec	A	WC	Argos	Supplement
Fin whales	Svalbard	6	6	2015–2018	Sep–Dec	A	WC	Argos	Supplement
Humpback whales	Barents Sea	10	10	2018–2019	Sep–Dec	A	WC	Argos	Supplement
Total (13 species)		585	512	2005–2019	Jun–May				

whales, bowhead whales and fin whales were deemed to be too conservative, despite trying different maximum movement speeds and turning angles, so locations for these 3 species were filtered by removing quality Z locations (i.e. invalid locations) and manually removing large location spikes resulting from Argos error. All species and location types (Argos and GPS) were subsequently filtered using the continuous-time correlated random walk model (CTCRW model, crawl package; Johnson et al. 2008) with a stopping model incorporated to account for time spent hauled out for all pinnipeds except walruses. Locations every second hour were interpolated from the CTCRW model for each animal. Interpolated locations that occurred during gaps in transmitted

locations over 5 d long were removed from the dataset. The narwhal data had duty cycles of varying lengths beginning in either September or October (see Heide-Jørgensen et al. 2015 for details); locations were used only from days when transmissions occurred.

A land shapefile for the NE Atlantic was made by combining 3 sources: (1) the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) full-resolution coastline shapefile (version 2.3.7; Wessel & Smith 1996); (2) a coastline shapefile for Svalbard (Norwegian Polar Institute; www.npolar.no); and (3) a coastline shapefile for Greenland (Danish Geodata Agency; www.eng.gst.dk). On-land locations were moved to the closest 'in water' loca-
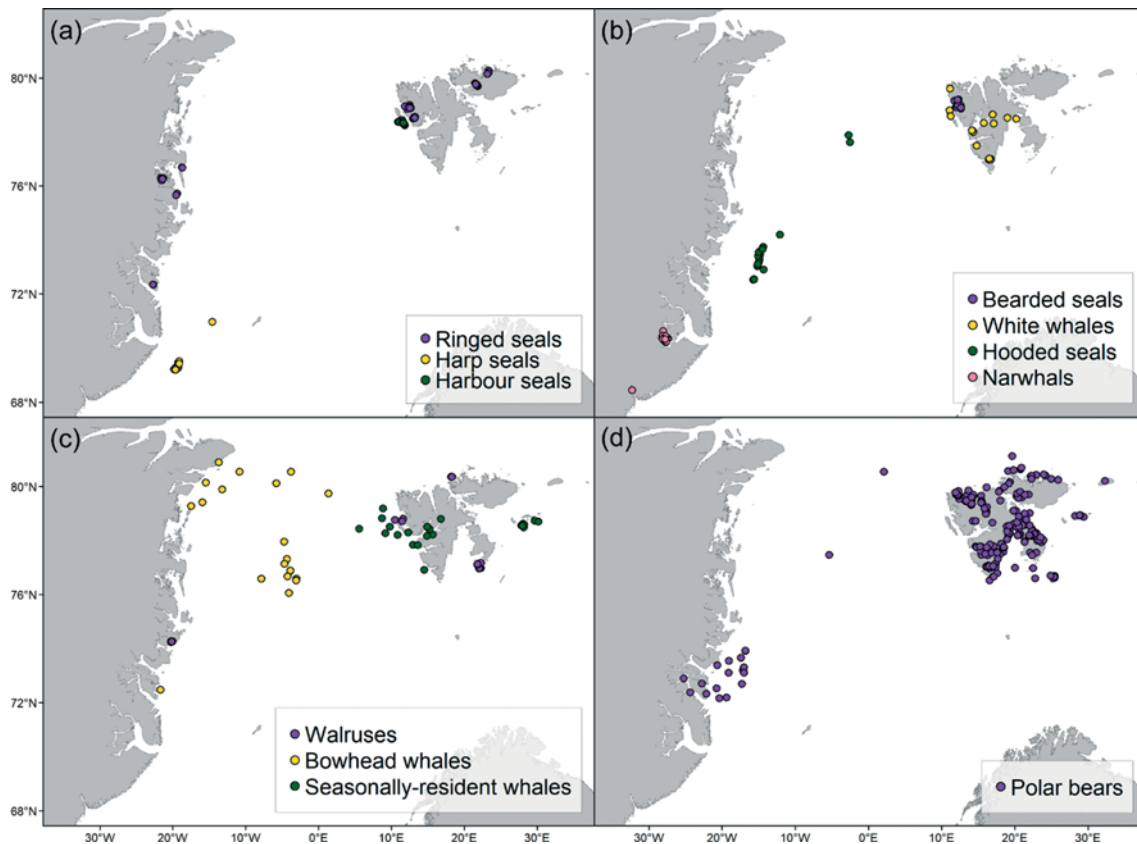
Fig. 2. Capture locations for 13 marine mammal species (including 3 seasonally resident whale species) used in the analysis of marine mammal hotspots in the Greenland and northern Barents Seas. (a) Ringed seals, harp seals and harbour seals; (b) bearded seals, white whales, hooded seals and narwhals; (c) walruses, bowhead whales and seasonally-resident whales; (d) polar bears

tion (in time) for each individual (except for polar bears). Locations were subsequently rasterized into a 10 × 10 km grid, and the number of individuals of each species (individual hotspots analysis), the number of locations for each species (location hotspots analysis) and the number of species (species richness) in each grid cell were calculated. A 10 × 10 km grid was chosen as a compromise between showing large-scale patterns across the Greenland and Barents Seas and showing patterns within small fjords in Svalbard and Greenland (e.g. Kongsfjorden, a fjord in Svalbard with high tagging effort, is ~5 × 20 km).

2.4. Marine mammal hotspots

Marine mammal hotspots were calculated in order to identify areas that are heavily used by different marine mammal species in the Greenland and northern Barents Seas. Hotspot analyses were run for the whole year as well as for summer/autumn (Jun–Dec) and winter/spring (Jan–May) periods to account for

intra-annual variation in sea-ice extent (Fig. 1) and species' movement and behaviour patterns on a seasonal basis. Various hotspot methods were explored including the percent volume method (Citta et al. 2018), the lattice-based density estimator (Barry & McIntyre 2011), the kernel home range method (package adehabitatHR; Calenge 2006) and the Getis–Ord G_i^* method (Getis & Ord 1992, Ord & Getis 1995). The Getis–Ord G_i^* method was chosen because it includes values of neighbouring points, has a rapid computational run time and excludes land areas.

Individual and location hotspots, based on the number of individuals and locations in grid cells, were calculated using the Getis–Ord G_i^* statistic (Getis & Ord 1992; e.g. Queiroz et al. 2016, Yurkowski et al. 2019). The Getis–Ord G_i^* statistic identifies local spatial patterns in a dataset by measuring the concentration of a variable around a point. It compares the local sum of values within a specified distance of a point (i.e. a point and its neighbours) to an expected local sum (drawn without replacement from all points in the dataset). If the calculated local

sum is larger than the expected local sum, and the difference is too large to be the result of random chance, a statistically significant positive z-score is assigned to that point (Getis & Ord 1992, Ord & Getis 1995). Individual hotspots identify areas used by the majority of the tagged animals, while location hotspots identify areas heavily used, sometimes by only a small portion of the tagged animals.

All individuals and locations were given equal weighting in the hotspot analysis conducted for each species. The equal-weighting option was chosen to avoid relying on potentially erroneous assumptions about the representativeness of the data in different locations and time intervals. Ringed seal, walrus and polar bear hotspots were calculated separately for animals tagged in Svalbard and Northeast Greenland due to these areas having separate populations; sample sizes also differed in the 2 areas (see Figs. S1–S3 in the Supplement for hotspot results when analyses were run for Svalbard and Northeast Greenland combined). For the 'all species' hotspot analysis, each species was given an equal weight when calculating the number of individuals and locations in each grid cell. The localG function in the spdep package (Bivand & Wong 2018) was used to calculate the Getis–Ord $G_i^\star$ statistic. The number of neighbours for each grid cell was defined as the number of grid cells within the distance that maximized spatial autocorrelation for each species, found by calculating the global Getis–Ord $G_i^\star$ statistic in 10 km increments from 10 to 200 km (globalG.test function in spdep package, Table S2 in the Supplement; Ord & Getis 1995, Bivand & Wong 2018).

Four hotspot levels 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% ($z \geq 1.15$, $p \leq 0.3$), following Getis & Ord (1992). Low-use areas ($z < 1.15$, $p > 0.3$) were plotted as a continuous polygon that encompassed all areas used by each species. Coldspots (i.e. areas with significant negative autocorrelation) were not plotted as they indicate areas infrequently used by tracked animals, not necessarily areas infrequently used by the species. The range for each species was downloaded from the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2020) and plotted to show the hotspots in the context of where each species is likely to be found in the study area. The amount of overlap between high hotspot levels (i.e. 95% and 99%) and high levels of species richness (≥4 species for annual and summer/autumn, ≥2 species for winter/spring) was also calculated.

Null models were created for the Getis–Ord $G_i^\star$ statistic for each species and all species combined to represent where individual and location hotspots would be expected given the tagging locations and movement patterns of each species (see Queiroz et al. 2016, Yurkowski et al. 2019). The basis for the null models comprised simulated correlated random walks created for each species using Weibell distributed step lengths and Von Mises distributed turning angles. The step lengths and turning angles for each species were used to create the relevant distributions for the simulated tracks. The maximum step length for each species was used to set an upper limit on the step lengths

Table 2. Total, mean (±SD) and maximum tracking duration (d) and the month of tagging for animals in each of the 13 marine mammal species tagged around Svalbard and Northeast Greenland

| Species	Total tracking duration (d)	Tracking duration (d; mean ± SD)	Maximum tracking duration (d)	Tagging month
Ringed seals	12 452	171 ± 66	305	Jul–Aug
Bearded seals	3625	181 ± 106	367	Pups: May Adults: Jul–Aug
Harbour seals	11 369	189 ± 107	392	Pups: Jun–Jul Sub–adults/adults: Aug–Sep
Walruses	12 033	236 ± 351	1485	Jul–Aug
Harp seals	3559	178 ± 143	400	Apr
Hooded seals	3280	164 ± 128	424	Mar & Jul
Polar bears	72 710	309 ± 236	1192	Mar–Apr & Aug
Bowhead whales	3164	144 ± 152	613	Jun & Sep
Narwhals	5577	143 ± 88	420	Aug–Sep
White whales	1585	88 ± 59	191	Jul–Aug
Blue whales	244	27 ± 19	61	Aug–Oct
Fin whales	193	32 ± 22	64	Sep
Humpback whales	894	89 ± 31	118	Sep
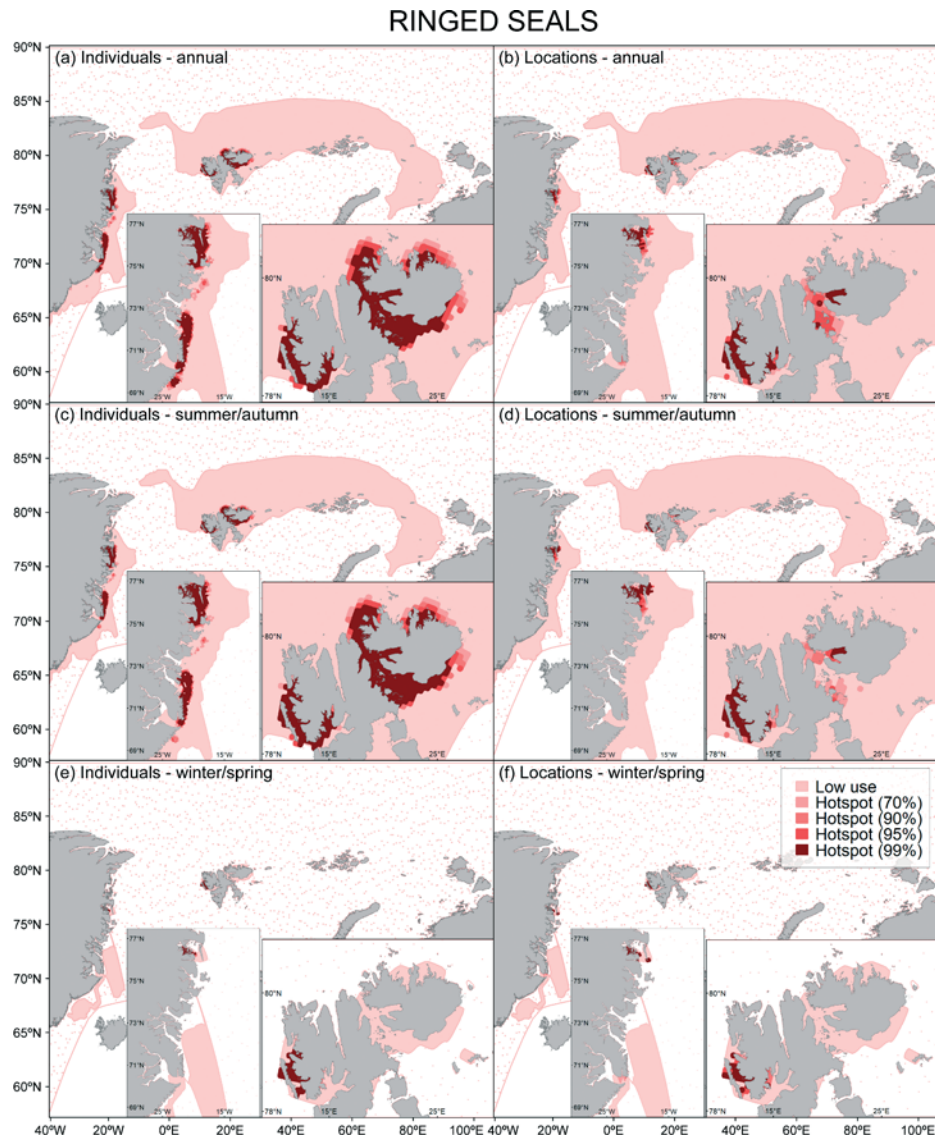
Fig. 3. Getis−Ord $G_i^{\ast}$ (a,c,e) individual hotspots and (b,d,f) location hotspots for 73 ringed seals tagged in Svalbard and North-east Greenland over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Inset maps show hotspots in East Greenland (left) and northern Svalbard (right). Increasing intensities of red indicate hotspots of different levels of statistical significance; the pink dotted polygon shows the species' range. The analysis was run for ringed seals tagged in Svalbard and Northeast Greenland separately

selected for the simulations. One correlated random walk was simulated for each individual in each species; the simulated track had the same starting location and the same number of steps as the individual's observed track. The simulated tracks for each species (except for polar bears) were constrained to the ocean. A null model for species richness was also made from the simulated correlated random walks. The amount of overlap between high marine mammal hotspot levels and high null model hotspot levels (i.e. 95% and 99%) was also calculated.

3. RESULTS

3.1. Species distributions

3.1.1. Ringed seals *Pusa hispida*. Ringed seals mainly occupied coastal areas in Northeast Green-land and Svalbard (Fig. 3, Tables 1 & 2), though some ringed seals from Svalbard took trips offshore in the summer and autumn, ranging as far east as the Kara Sea and as far north as the Arctic Ocean north of the Fram Strait. Some of the ringed seals from Northeast Greenland also used offshore areas on the East
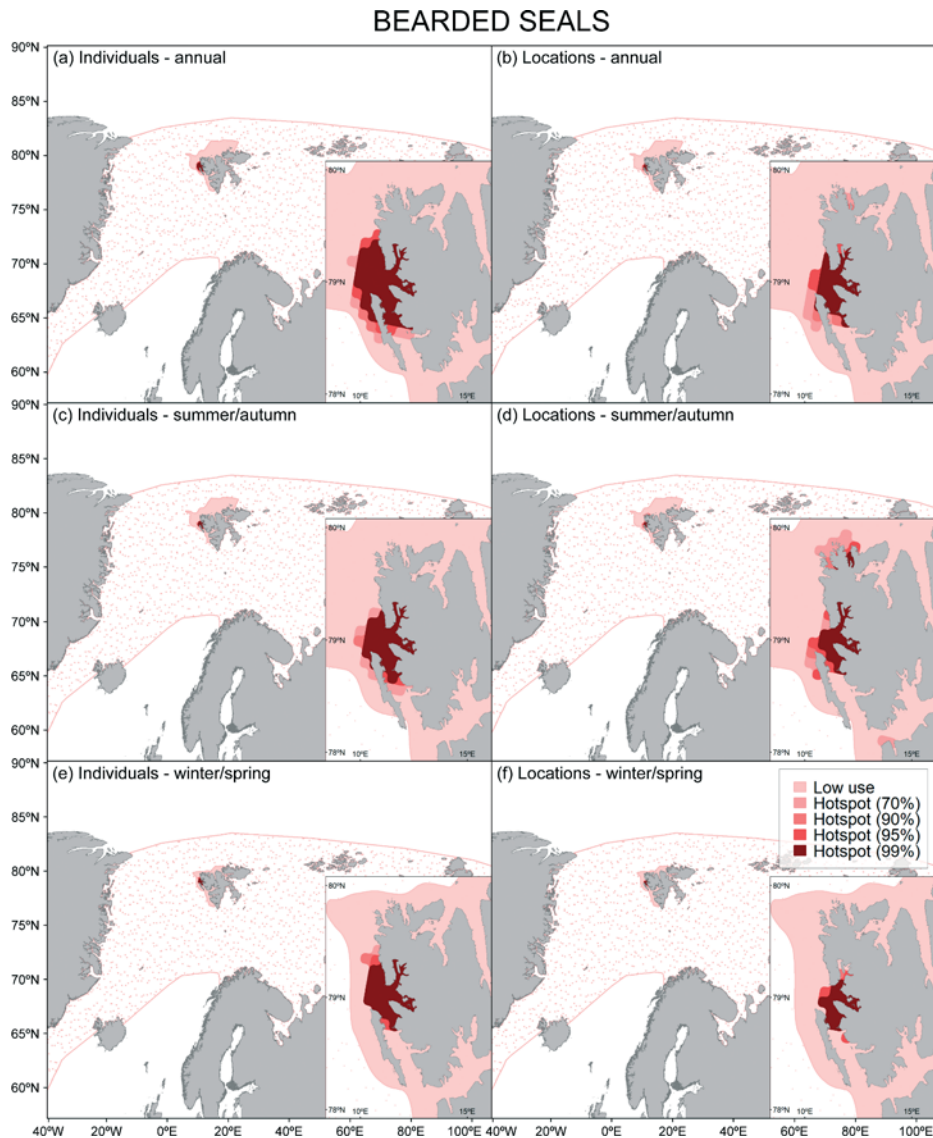
Fig. 4. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for 20 bearded seals tagged in Svalbard over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Inset maps show hotspots in north-western Svalbard. Details as in Fig. 3 legend

Greenland continental shelf. Ringed seals had wider distributions in the summer/autumn than in the winter/spring (Fig. 3). Hotspots (both individual and location) were found in coastal regions of Svalbard and Northeast Greenland (Fig. 3). Null model hotspots for ringed seals were in northwestern Svalbard, in Wahlenbergfjorden (a fjord in Nordaustlandet, NE Svalbard) and in Dove Bay (Greenland), in the vicinities where tagging took place for this species (Fig. 2a, Fig. S4a,b in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped ringed seal hotspots (95% and 99%) by 21% and 59% for individual and location hotspots, respectively (Table 3).

3.1.2. Bearded seals *Erignathus barbatus*. Bearded seals were located in shallow areas along the western and northern coasts of Svalbard and hotspots (both individual and location) were located in north-western Svalbard (Fig. 4, Tables 1 & 2). Null model hotspots for bearded seals were also located in north-western Svalbard, near the area where the animals were tagged (Figs. 2b, S4c,d). Highly significant null model hotspot levels (95% and 99%) overlapped bearded seal hotspots (95% and 99%) by 81% and 90% for individual and location hotspots, respectively (Table 3).

3.1.3. Harbour seals *Phoca vitulina*. Harbour seals were located mainly in western Svalbard, both in
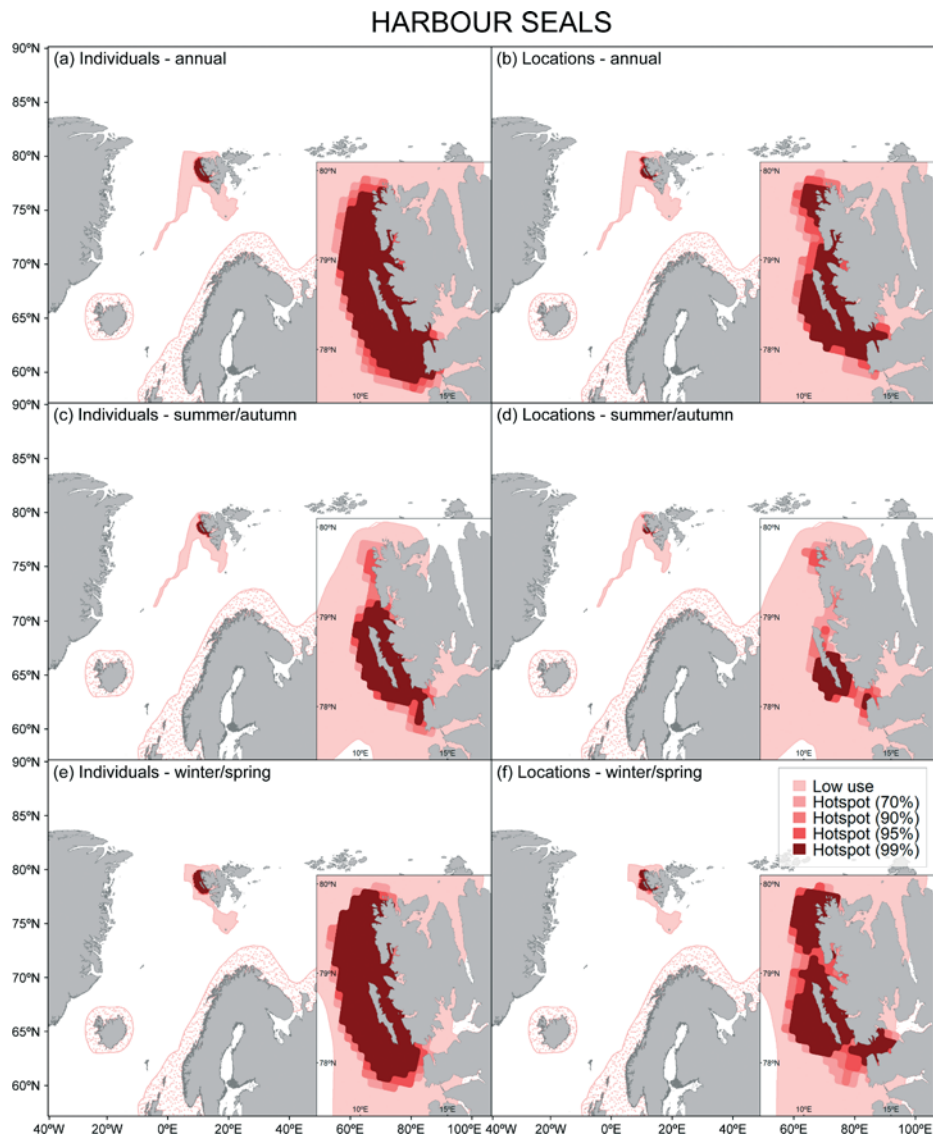
HARBOUR SEALS

Fig. 5. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for 60 harbour seals tagged in Svalbard over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Inset maps show hotspots in north-western Svalbard. Details as in Fig. 3 legend

coastal areas and over the continental shelf. Some harbour seals travelled to northern Svalbard and south as far as Bjørnøya (Fig. 5, Tables 1 & 2). Hotspots (both individual and location) were located in north-western Svalbard. Individual hotspots and winter/spring hotspots covered a larger area than location hotspots and summer/autumn hotspots (Fig. 5). Null model hotspots for harbour seals were located in western Svalbard, west of their tagging area in Forlandsøyene, just west of Prins Karls Forland (Fig. 2a, Fig. S4e,f in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped harbour seal hotspots (95% and 99%) by

65% and 60% for individual and location hotspots, respectively (Table 3).

3.1.4. Walruses *Odobenus rosmarus*. Walruses were located in coastal areas of Northeast Greenland and in the northern Barents Sea. Hotspots (both individual and location) were located along the northeastern coast of Greenland between 74 and 81° N, in southern and northern Svalbard, and in Russian waters between Svalbard and Franz Josef Land (Fig. 6, Tables 1 & 2). Individual hotspots covered a wider geographical area than location hotspots (Fig. 6). Location hotspots were also located in Northeast Greenland (i.e. in the Northeast Water Polynya)
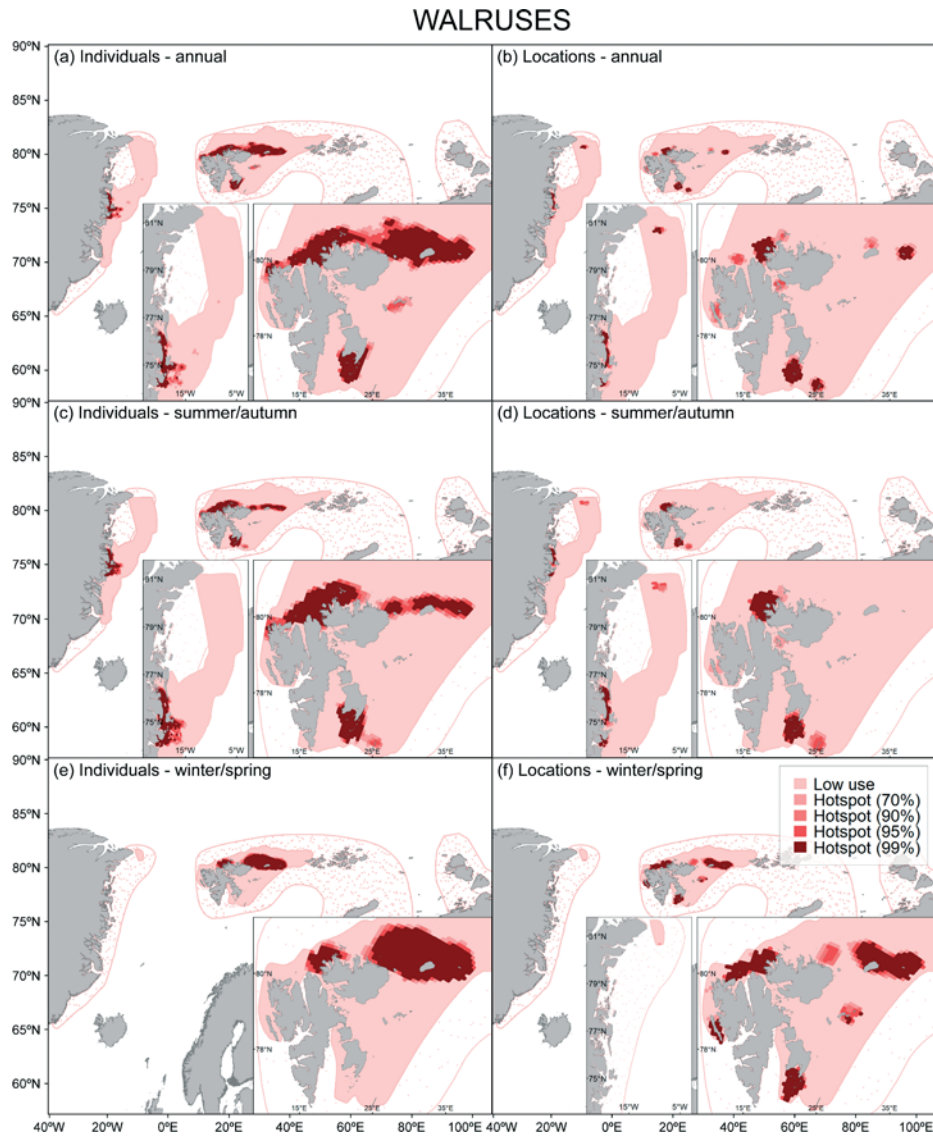
WALRUSES

Fig. 6. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for 51 walruses tagged in Svalbard and Northeast Greenland over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Inset maps show hotspots in East Greenland (left) and Svalbard (right). There were no individual hotspots during the winter/spring for walruses tagged in East Greenland. Details as in Fig. 3 legend. The analysis was run for walruses tagged in Svalbard and Northeast Greenland separately

Table 3. Amount (%) that null models of Getis−Ord G_i^* hotspots (95% and 99%) overlapped hotspots (95% and 99%) made from tracks of 13 marine mammals (including 3 seasonally resident whale species) in the Greenland and Barents Seas

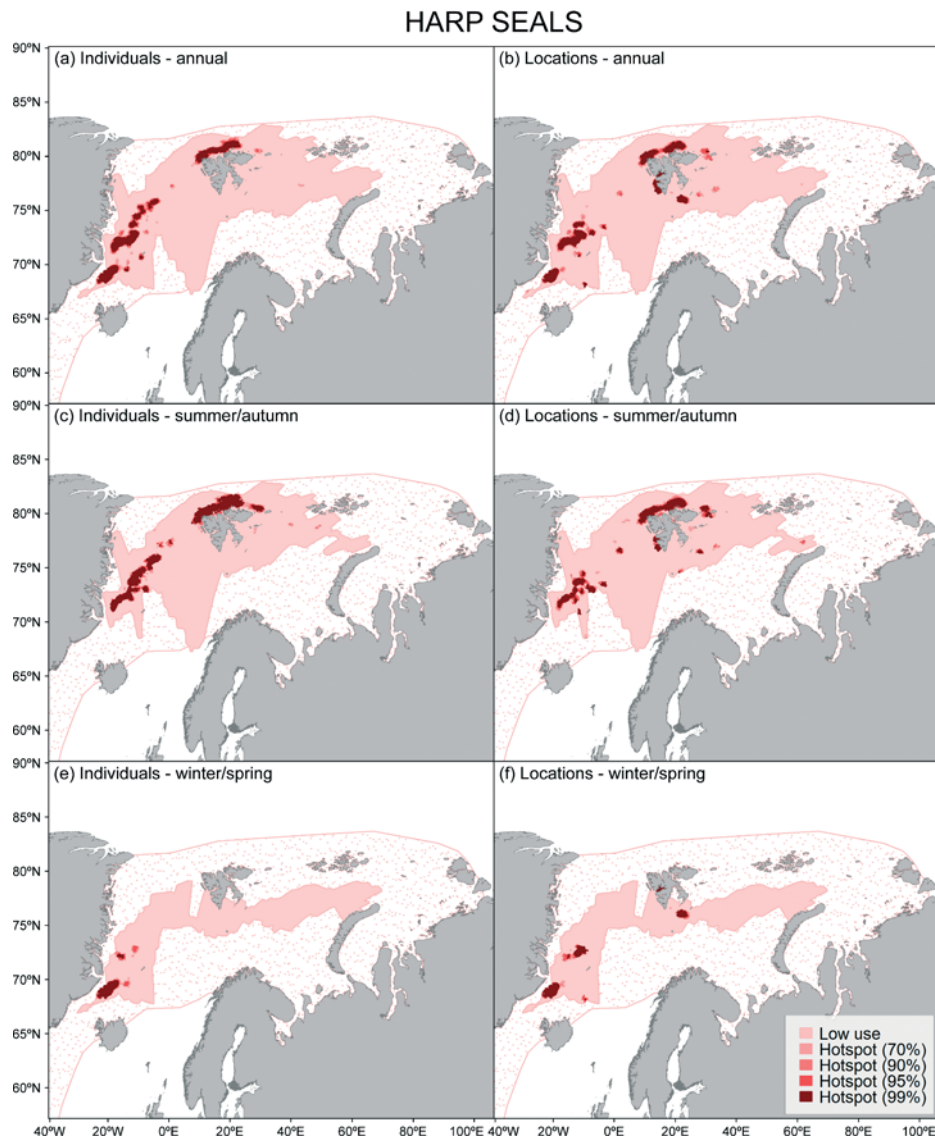| Species	Overlap (%) Individual hotspots	Location hotspots	Species	Overlap (%) Individual hotspots	Location hotspots
Ringed seals	21	59	Polar bears	31	70
Bearded seals	81	90	Bowhead whales	5	2
Harbour seals	65	60	Narwhals	43	34
Walruses	20	39	White whales	13	9
Harp seals	18	9	Seasonally resident whales	26	29
Hooded seals	20	18	All species	30	34

HARP SEALS

Fig. 7. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for 20 harp seals tagged in the Greenland Sea over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Details as in Fig. 3 legend

in the summer/autumn, in western Svalbard in the winter/spring and covered a wider distributional area in the winter/spring around the Svalbard Archipelago than in the summer/autumn (Fig. 6). A lack of hotspots for walruses in Northeast Greenland in the winter/spring is due to only 2 of the 18 walruses transmitting location data after December, with both of these data streams terminating in January. Null model hotspots for walruses were mainly situated around northern and south-eastern Svalbard and around Young Sound in East Greenland, near the area where the walruses were tagged (Fig. 2c, Fig. S5a,b in the Supplement). Highly significant null

model hotspot levels (95% and 99%) overlapped walrus hotspots (95% and 99%) by 20% and 39% for individual and location hotspots, respectively (Table 3).

3.1.5. Harp seals *Pagophilus groenlandicus.* Harp seals occupied the Greenland Sea and the northern Barents Sea (Fig. 7, Tables 1 & 2). Hotspots (both individual and location) were concentrated in the MIZ in the Greenland Sea and in northern Svalbard. Location hotspots were also found in western and southern Svalbard (Fig. 7). Summer/autumn hotspots covered a larger area in the Barents Sea than winter/spring hotspots. Null model hotspots for harp
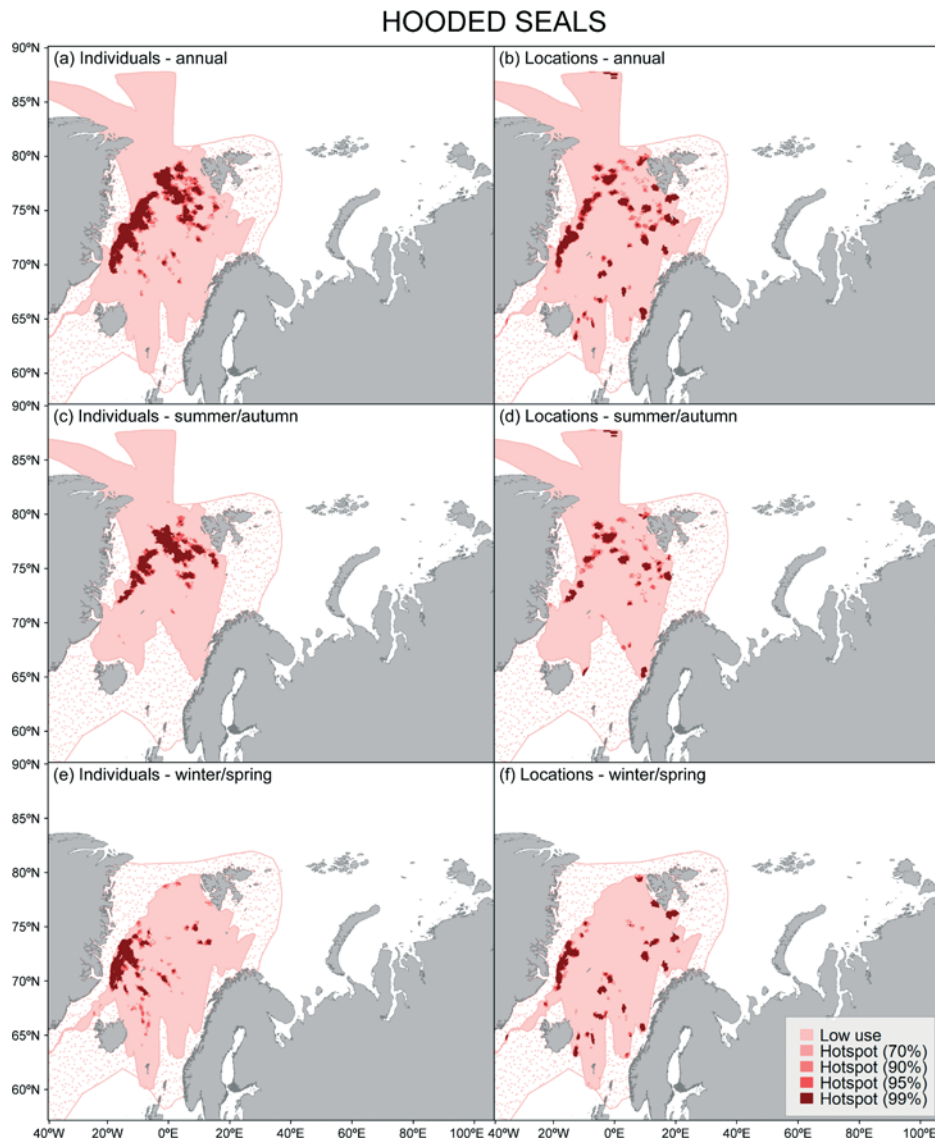
HOODED SEALS

Fig. 8. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for 20 hooded seals tagged in the Greenland Sea over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Details as in Fig. 3 legend

seals were situated in the Greenland Sea near the areas where they had been tagged (Fig. 2a, Fig. S5c,d in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped harp seal hotspots (95% and 99%) by 18% and 9% for individual and location hotspots, respectively (Table 3).

3.1.6. Hooded seals *Cystophora cristata.* Hooded seals were mainly located in the Greenland Sea and off the west coast of Svalbard (Fig. 8, Tables 1 & 2). Hotspots (both individual and location) were mainly in the deep areas of the Greenland Sea. Location hotspots were also found on the continental shelf

west and south of Svalbard and close to the Norwegian coast (Fig. 8). Null model hotspots for hooded seals were located in the Greenland Sea in the vicinity of where they had been tagged (Fig. 2b, Fig. S5e,f in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped hooded seal hotspots (95% and 99%) by 20% and 18% for individual and location hotspots, respectively (Table 3).

3.1.7. Polar bears *Ursus maritimus.* Polar bears were found in the Greenland Sea, northern Barents Sea and Arctic Ocean (Fig. 9, Tables 1 & 2). Hotspots (both individual and location) were found in coastal
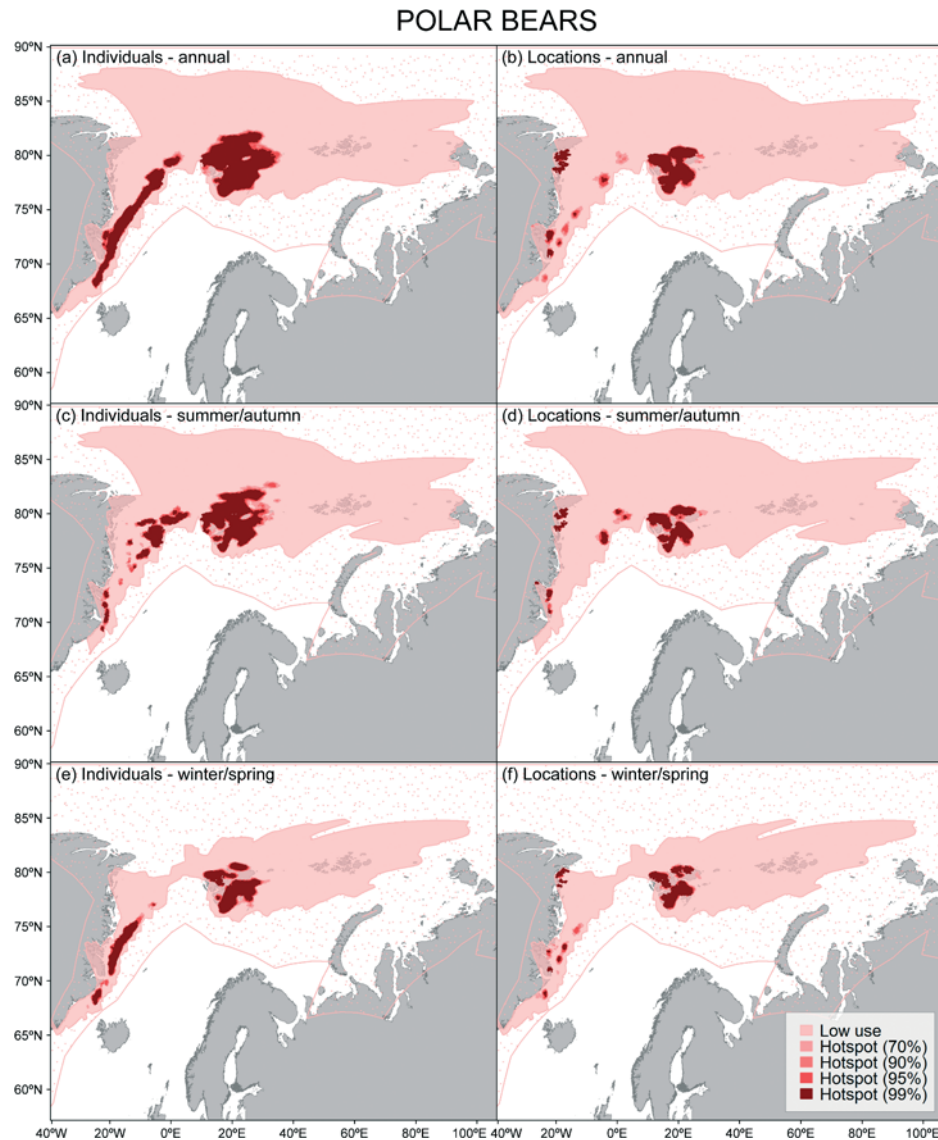
POLAR BEARS

Fig. 9. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for 235 polar bears tagged around Svalbard and Northeast Greenland over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Details as in Fig. 3 legend. The analysis was run for bears tagged in Svalbard and Northeast Greenland separately

and offshore areas of Northeast Greenland and around the Svalbard Archipelago (Fig. 9). Most of the coastal hotspots in Northeast Greenland corresponded to denning locations identified in Laidre et al. (2015b). Summer−autumn hotspots covered a wider area around the Svalbard Archipelago and were found further north in the MIZ in the Greenland Sea compared to winter/spring hotspots (Fig. 9). Note that most of the biotelemetry data from Northeast Greenland were from bears tagged in offshore areas; of the 21 bears tagged in 2007 and 2008, only 5 were instrumented on coastal land-fast ice in fjords. Many polar bears in Northeast Greenland reside

year-round in coastal regions and show strong site fidelity (Boertmann & Mosbech 2012, Laidre et al. 2015b, 2018). Null model hotspots for polar bears were situated around the Svalbard Archipelago and in the Greenland Sea (Fig. 2d, Fig. S6a,b in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped polar bear hotspots (95% and 99%) by 31% and 70% for individual and location hotspots, respectively (Table 3).

3.1.8. Bowhead whales *Balaena mysticetus*. Bowhead whales were located mainly in the northern Barents and Greenland Seas, within the MIZ (Fig. 10, Tables 1 & 2). Hotspots were located in Northeast
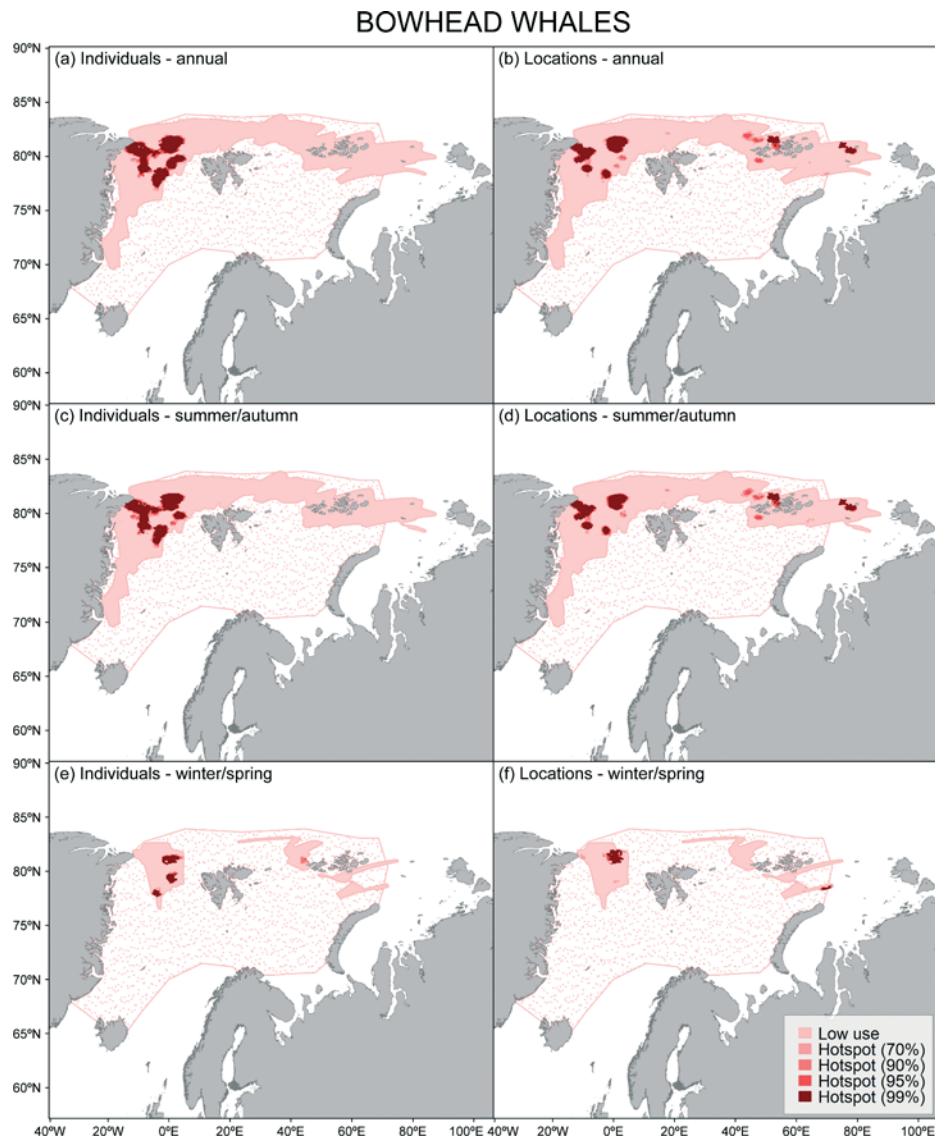
BOWHEAD WHALES

Fig. 10. Getis–Ord $G_i{}^*$ (a,c,e) individual hotspots and (b,d,f) location hotspots for 22 bowhead whales tagged in the marginal ice zone in the Fram Strait and off of north-eastern Greenland over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Details as in Fig. 3 legend

Greenland (both individual and location hotspots) and around Franz Josef Land (mainly location hotspots; Fig. 10). Summer/autumn hotspots covered a larger geographical area than winter/spring hotspots (Fig. 10). Null model hotspots for bowheads were found in Northeast Greenland and in the Fram Strait (Fig. 2c, Fig. S6c,d in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped bowhead whale hotspots (95% and 99%) by 5% and 2% for individual and location hotspots, respectively (Table 3).

3.1.9. Narwhals *Monodon monoceros.* Narwhal hotspots (both individual and location) were found

within Scoresby Sound (summer hotspots) and at the edge of the continental shelf outside of the fjord (winter hotspots) (Fig. 11, Tables 1 & 2). Null model hotspots for narwhals were found in Scoresby Sound, the main area where the animals had been tagged (Fig. 2b, Fig. S6e,f in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped narwhal hotspots (95% and 99%) by 43% and 34% for individual and location hotspots, respectively (Table 3).

3.1.10. White whales *Delphinapterus leucas.* White whales were found in coastal regions of Svalbard (Fig. 12, Tables 1 & 2). Hotspots (both individual
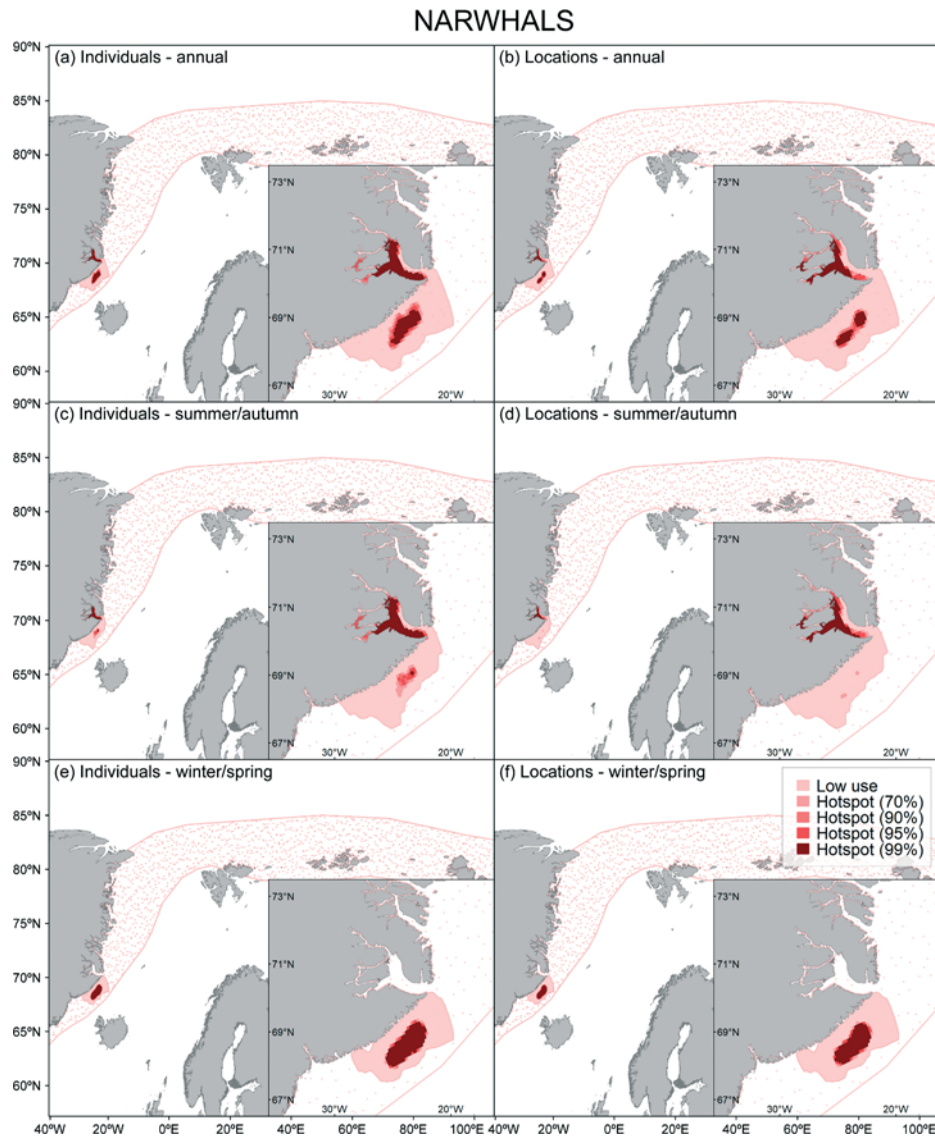
NARWHALS

Fig. 11. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for 39 narwhals tagged in Northeast Greenland over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Inset maps show hotspots in Northeast Greenland. Details as in Fig. 3 legend

and location) were found in both south-eastern and south-western Svalbard (Fig. 12). Location hotspots were also found in northern Svalbard fjords (Fig. 12). Null model hotspots for white whales were in western Svalbard, extending over the continental shelf break into the Greenland Sea (Fig. 2b, Fig. S7a,b in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped white whale hotspots (95% and 99%) by 13% and 9% for individual and location hotspots, respectively (Table 3).

3.1.11. Seasonally resident whales. Seasonally resident whales were found in the Barents Sea, Greenland Sea and Norwegian Sea (Fig. 13, Tables 1 & 2).

Hotspots were located around the Svalbard Archipelago and near Jan Mayen (Fig. 13). Location hotspots were also found within Svalbard fjords, while individual hotspots were found mainly in coastal areas (Fig. 13). Null model hotspots for seasonally resident whales were found in western Svalbard and south-east of Nordaustlandet, near the areas where these species had been tagged (Fig. 2c, Fig. S7c,d in the Supplement). Highly significant null model hotspot levels (95% and 99%) overlapped seasonally resident whale hotspots (95% and 99%) by 26% and 29% for individual and location hotspots, respectively (Table 3).
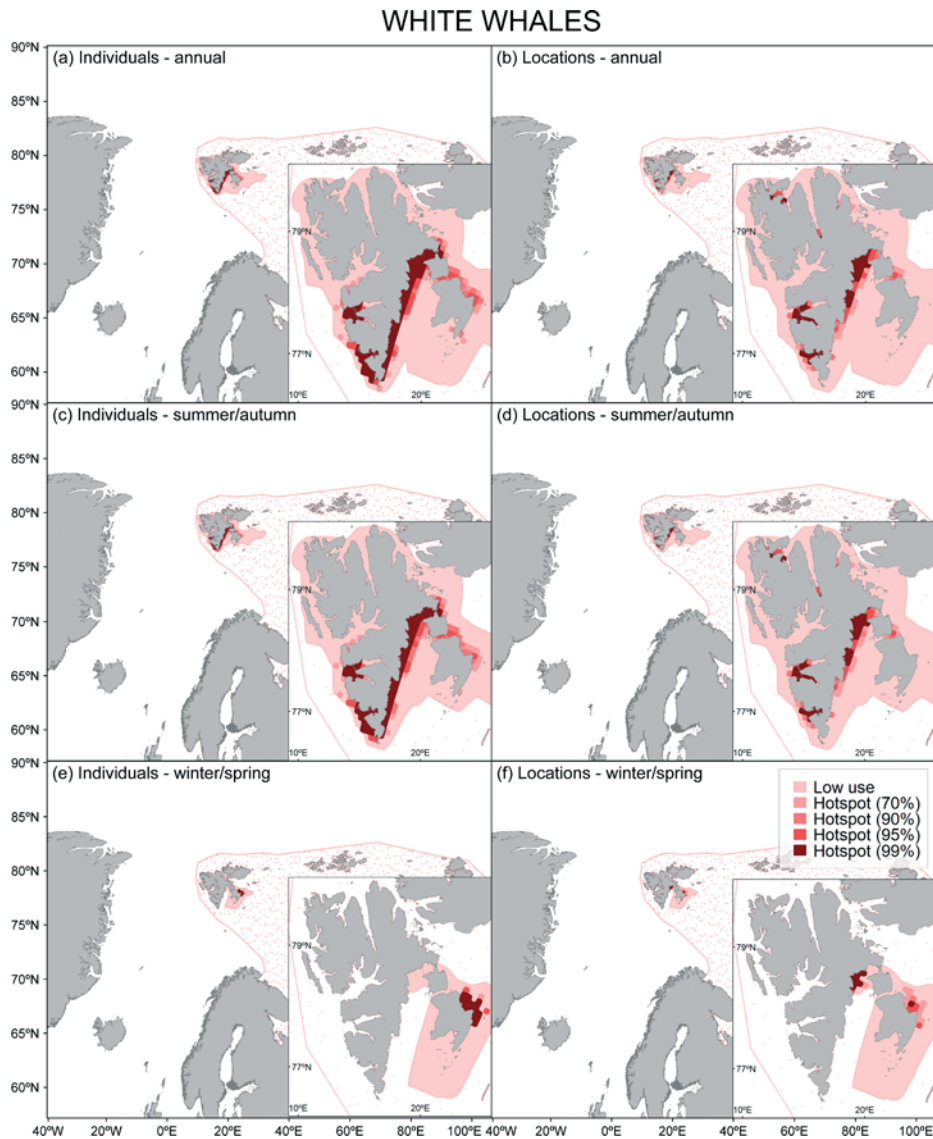
WHITE WHALES

Fig. 12. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for 18 white whales tagged in Svalbard over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Inset maps show hotspots around the Svalbard Archipelago. Details as in Fig. 3 legend
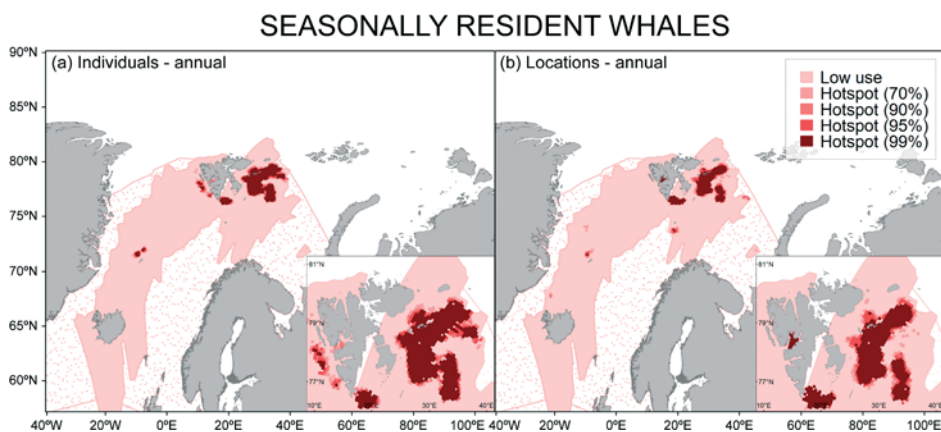
SEASONALLY RESIDENT WHALES

Fig. 13. Getis−Ord G_i^* (a) individual hotspots and (b) location hotspots for blue, fin and humpback whales (total n = 26 seasonally resident whales) tagged around Svalbard. These species were only present in the study area during the summer/autumn. Inset maps show hotspots around the Svalbard Archipelago. Details as in Fig. 3 legend
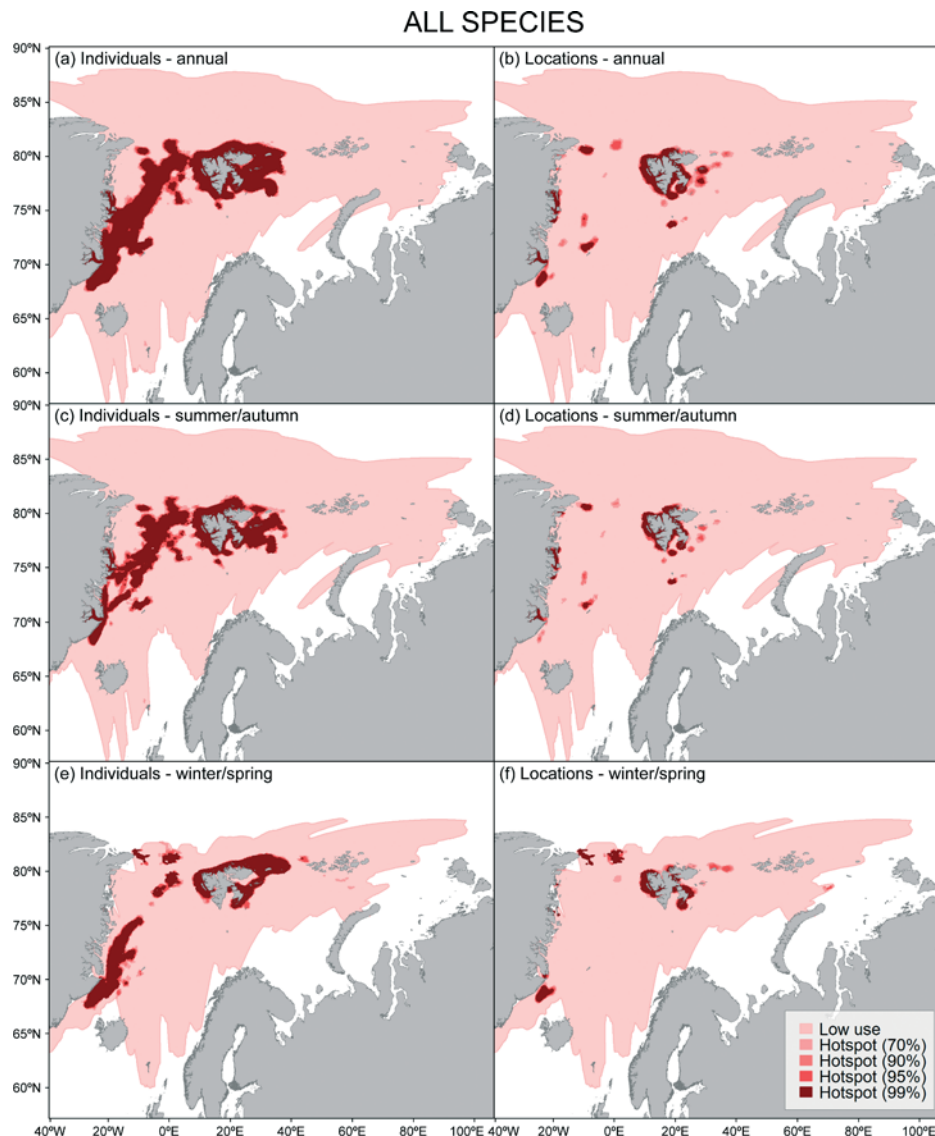
Fig. 14. Getis−Ord G_i^* (a,c,e) individual hotspots and (b,d,f) location hotspots for the 13 species tagged around Svalbard and Northeast Greenland over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring. Details as in Fig. 3 legend

3.2. All species hotspots and species richness

Hotspots (both individual and location) for all 13 marine mammal species were found around the Svalbard Archipelago, in coastal areas of Northeast Greenland and in the MIZ of the Greenland and northern Barents Seas (Fig. 14). These areas coincided with areas that had the greatest species richness (Figs. 15, 16). Up to 90% of the highest values of species richness occurred within high individual hotspot levels (95% and 99%; Table S3 in the Supplement). Overlap between high values of species richness and high hotspot levels was generally less

for location hotspots compared to individual hotspots and for the winter/spring period compared to summer/autumn and annual data (Table S3 in the Supplement). Null model hotspots for all species were found mainly around western and south-eastern Svalbard and in the Greenland Sea, near the tagging areas for the different species (Fig. 2, Fig. S7e,f in the Supplement). Highly significant null model hotspot levels (95 and 99%) overlapped all species hotspots (95 and 99%) by 30% and 34% for individual and location hotspots, respectively (Table 3). The highest values for the species richness null model were also located west of Svalbard (Fig. S8 in the Supplement).

4. DISCUSSION

The MIZ of the Greenland Sea and the northern Barents Seas and coastal areas in Northeast Greenland and around the Svalbard Archipelago were found to be hotspots for a wide range of marine mammal species in the Northeast Atlantic Arctic, as well as being areas of high species richness. The individual versus location hotspots results identified a few important differences. Individual hotspots identified areas important to the majority of tagged individuals. Examples of individual hotspot areas include common resting, moulting, breeding and foraging areas. Prins Karls Forland and the adjacent continental shelf are the main breeding, moulting, resting and foraging locations for harbour seals *Phoca vitulina* in Svalbard (Lydersen & Kovacs 2010). Similarly, drift ice areas within the MIZ are used for breeding, moulting and resting by harp seals *Pagophilus groenlandicus* and hooded seals *Cystophora cristata* (Folkow et al. 2004, Vacquié-Garcia et al. 2017a). Walruses *Odobenus rosmarus* predominantly forage near terrestrial haul-out sites (Lowther et al. 2015), and ringed seals *Pusa hispida* are found throughout the year in close association with tidewater glacier fronts (Hamilton et al. 2016). In contrast, location hotspots identified areas that are used heavily, in some cases by only a few of the tagged individuals. Location hotspots were similar to individual hotspots for some species, including ringed seals, harbour seals and harp seals. However, differences in individual versus location hotspots were also found, revealing a discrepancy for some species and regions between areas frequented by many animals (i.e. individual hotspots) and areas that are highly used (not necessarily by the majority of tagged individuals; i.e. location hotspots). For these species, areas where tagged animals congregate (e.g. pupping, nursing and breeding locations) may not be the same locations in which individuals spend the majority of their time. In general, individual and location hotspot results differed for species where individuals or small groups forage in different locations across a wide geographic area or for species that perform important life-history behaviours in different locations across their range. For example, location hotspots identified areas that were previously identified as being foraging areas for hooded seals and bowhead whales *Balaena mysticetus* (Vacquié-Garcia et al. 2017a, Kovacs et al. 2020a). Previous analyses of the polar bear *Ursus maritimus* data show that many location hotspots in Northeast Greenland are denning sites (Laidre et al. 2015b). Location hotspots
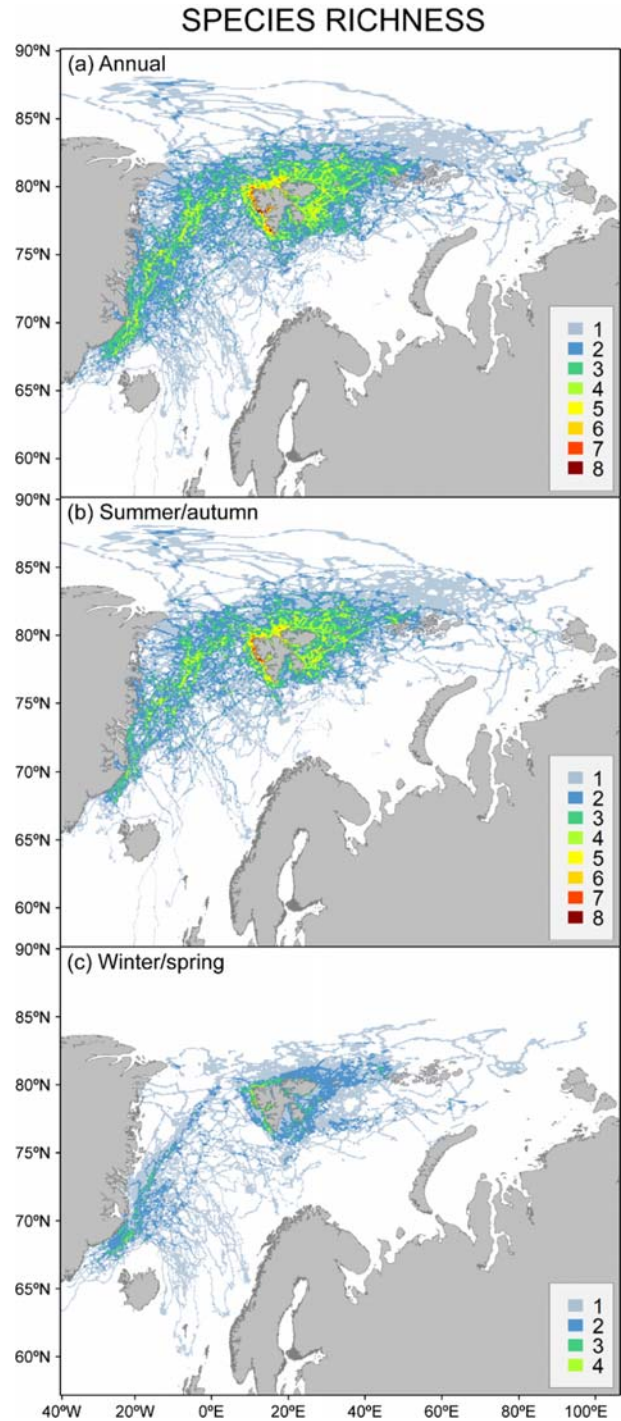

Fig. 15. Species richness (number of species in each grid cell) for the 13 species of marine mammals tagged around Svalbard and Northeast Greenland over (a) the entire year, (b) during the summer/autumn and (c) during the winter/spring

were also found further north in the Svalbard Archipelago than individual hotspots for white whales and bearded seals, and further west for walruses, indicating that these areas were used heavily by only a few
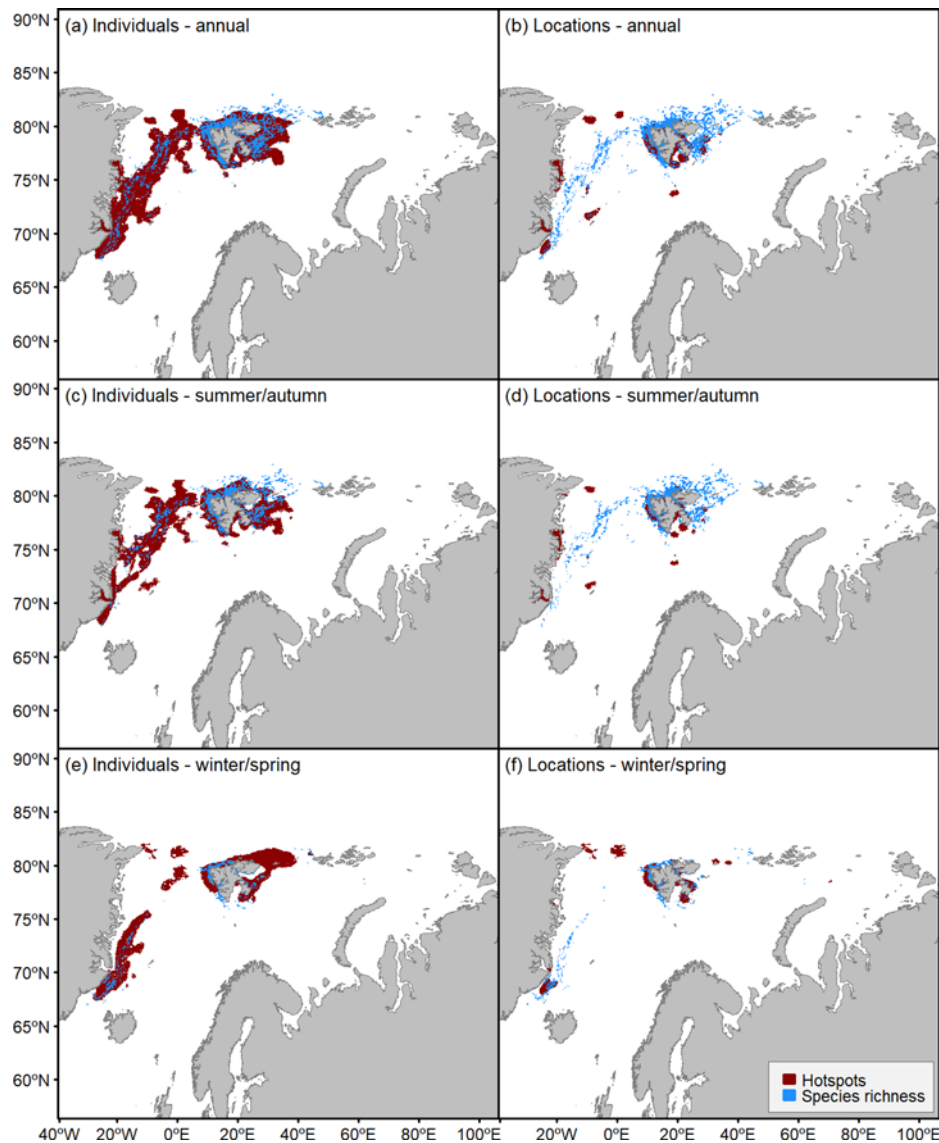
Fig. 16. Areas where overlap occurs between high values of Getis−Ord G_i^* hotspots (95 % and 99 %) and areas of high species richness (4−8 species for annual and summer/autumn analyses and 2−4 species for winter/spring analyses) for (a,c,e) individual hotspots and (b,d,f) location hotspots over (a,b) the entire year, (c,d) during the summer/autumn and (e,f) during the winter/spring

of the tagged animals. Location hotspots also covered a smaller geographic area than individual hotspots for many species, meaning that areas heavily used (i.e. location hotspots) in total covered a smaller geographic area than regions visited by the majority of tagged animals (i.e. individual hotspots).

Both individual and location hotspot results are highly relevant for the development of conservation and management plans. In addition to areas important for the majority of the population (i.e. individual hotspots), conservation and management plans also need to target areas important for small segments of the population (i.e. location hotspots), particularly for rare species. Identifying the environmental features underlying important foraging or denning areas will allow plans to be expanded to additional foraging and denning areas that were likely used by untagged members of the population. Such measures will be important for species that forage over large areas either as single animals or in small groups. Denning areas of polar bears may only be used by small segments of the population, but it is important to manage disturbance risks in order to maximize survival of female bears with cubs of the year.

Species richness values overlapped significantly with high individual hotspot levels. This overlap was generally higher around the Svalbard Archipelago than in coastal areas of Northeast Greenland. A few coastal hotspots in Northeast Greenland resulted from heavy use by a few marine mammal species. Expanded biotelemetry data collection in Northeast Greenland, especially on species where biotelemetry data are currently lacking (e.g. bearded seals), would likely increase the overlap between high species richness and hotspot levels in this region. Overlap between high values of species richness and hotspot levels was also higher for individual hotspots than for location hotspots. Regions important for the majority of a tagged population are more likely to also be important regions for additional species, in contrast to areas heavily used by smaller segments of a population.

Similarities and differences among identified hotspot areas for individual species highlight the ecological niches they each occupy. Bearded seals and walruses are both benthic foragers that feed in shallow, coastal regions (Lowther et al. 2015, Hamilton et al. 2018, 2019b), and thus they would be expected to have similar hotspots in regions where both species are found. Similarities would also be expected among species with tight coastal distributions (e.g. ringed seals and white whales *Delphinapterus leucas* in Svalbard; Hamilton et al. 2016, Vacquié-Garcia et al. 2018); species that are heavily dependent on sea ice (e.g. ringed seals and polar bears in the MIZ; Lone et al. 2018, 2019); and species that dive to intermediate depths in open ocean areas (e.g. harp seals and hooded seals; Folkow et al. 2004, Vacquié-Garcia et al. 2017a). However, it is important to note that species can have quite different habitat and movement patterns in different areas of their range, which could impact the breadth and location of hotspots.

Fjords and coastal areas around the Svalbard Archipelago were identified as hotspots for the majority of the marine mammals included in these analyses, and as areas of high species richness in the Northeast Atlantic Arctic, confirming work done on individual species and small species groups (e.g. Blanchet et al. 2014, Hamilton et al. 2017, 2018, Vacquié-Garcia et al. 2018). Fjords and coastal areas of Northeast Greenland were also identified as marine mammal hotspots that were used heavily by a variety of marine mammal species (e.g. Dietz et al. 1994, Boertmann & Mosbech 2012, present study). Rapid changes are occurring in these important coastal hotspot areas. Large decreases in land-fast ice extent and duration have occurred in coastal regions of Svalbard over recent decades (Meredith et al. 2019, Pavlova et al. 2019). Additionally, the number of tidewater glacier fronts, which are important hotspots for many Arctic marine mammals, have also decreased in Svalbard (Błaszczyk et al. 2009). Retreat of tidewater glaciers onto land will likely reduce the amount of upwelling-derived nutrients, and advection towards inner fjords of production arising elsewhere, leading to decreases in productivity and accessibility of concentrated food supplies to higher trophic levels in these regions (Meredith et al. 2019). Numerous changes have already occurred in the distribution, behaviour, predator–prey relationships and breeding ecology of Arctic marine mammal species in relation to these changes in their habitat (e.g. Hamilton et al. 2016, 2017, 2019a, Vacquié-Garcia et al. 2018, Kovacs et al. 2020b). How hotspot locations may shift in the coming decades and how species will ultimately fare as the climate continues to warm are currently unknown. However, the future breeding success of bearded seals and ringed seals in relation to earlier melting of the sea ice and reduced opportunities for the latter species to build snow lairs are serious concerns for the continued existence of these Arctic seals.

The MIZ was identified as a marine mammal hotspot and an area of high species richness in the Greenland Sea and northern Barents Sea, confirming results from previous studies (e.g. Boertmann & Mosbech 2012, Laidre et al. 2015b, Vacquié-Garcia et al. 2017b, Lone et al. 2018). The MIZ has long been recognized as a unique and important habitat for many marine mammals (as well as birds and fishes) (e.g. Stirling 1997). The spatial area covered by the MIZ is highly dynamic both intra- and inter-annually (Vinje 2009), which has a large influence on where marine mammal hotspots occur in both space and time. Hotspots for marine mammals found in the MIZ (e.g. polar bears, harp seals and hooded seals) were generally found further north in the summer/autumn than in the winter/spring, reflecting intra-annual variations in sea-ice extent. Polynyas and openings in the sea ice are also extremely important for marine mammals (Stirling 1997). Polynyas situated in the mouths of fjords and adjacent to the coast in Northeast Greenland (e.g. Northeast Water Polynya, polynya outside Scoresby Sound) and adjacent to islands in the northern Barents Sea are important over-wintering areas for many species (Born & Knutsen 1992, Boertmann & Mosbech 2012, Lowther et al. 2015, Kovacs et al. 2020a). These regions were identified as hotspots for bowhead whales *Balaena mys-*

ticetus, walruses and narwhals *Monodon monoceros* in the present study.

Sea ice serves multiple functions for different Arctic marine mammal species. It is a pupping, nursing and resting habitat for Arctic seals; a hunting platform and transport corridor for polar bears; a foraging habitat for the majority of Arctic marine mammal species; and it provides protection for ice-adapted Arctic marine mammals from aquatic predators and storm events (see Kovacs et al. 2011 for details). There is thus a large conservation concern for marine mammals given the ongoing declines in sea-ice extent and volume. The extent to which Arctic marine mammals can simply shift their ranges north is currently unknown, as this would involve shifting their distributions from over the productive Arctic continental shelf seas to over the less productive, deep Arctic Ocean Basin for many species. There is considerable uncertainty regarding how the levels of primary and secondary productivity and the presence of fish and invertebrate stocks will change in the Arctic Ocean Basin as sea-ice declines continue (see e.g. Haug et al. 2017, Meredith et al. 2019). However, the northward shift of the MIZ and general decrease in sea-ice extent are already having negative consequences for many marine mammal species, including range shifts, increased foraging costs, changes in habitat use patterns and changes in terrestrial denning locations of polar bears (Derocher et al. 2011, Hamilton et al. 2015, Laidre et al. 2015b, Lone et al. 2018). Ongoing distributional shifts will undoubtedly impact the location of marine mammal hotspots in the coming decades.

Not all marine mammals in the Greenland and the Barents Sea had hotspots solely in the MIZ or coastal regions of Northeast Greenland and Svalbard. Open ocean hotspots were important for some species, especially for harp seals, hooded seals, harbour seals and seasonally resident whales. Harp seals and hooded seals make extensive use of open ocean areas for foraging in the summer and autumn (Folkow et al. 2004, Vacquié-Garcia et al. 2017a), while the shelf edge is important for harbour seals and migratory whales around Svalbard (Blanchet et al. 2014, Storrie et al. 2018). Some species seem to be showing signs of adjusting to making greater use of waters off the immediate coastline in fjords as sea-ice extent declines, including white whales and harbour seals (Vacquié-Garcia et al. 2018, Hamilton et al. 2019a, Norwegian Polar Institute's Marine Mammal Sightings Database, contact K.M.K. for more information). Seasonally resident whales have also expanded their distributional areas in northern

regions following decreases in sea-ice extent (Storrie et al. 2018, Hansen et al. 2019); these 'boreal' species are likely to be climate 'winners' in the coming decades with resultant increases in their numbers and the number of areas that are hotspots for this species group in Arctic areas. However, not all species are adapting to using open ocean areas. Ringed seals continue to use their 'traditional' habitats, and polar bears are dependent on sea ice when in offshore areas as well as when they are moving between areas (transit corridors), particularly when accompanied by young cubs (Hamilton et al. 2015, 2019a, Lone et al. 2018, 2019).

Human activities are increasing in Arctic regions as declines in sea ice make these regions more accessible. These activities pose risks to marine mammals if activities overlap with identified hotspot regions. Oil and gas exploration and production are shifting northward in the study region, and levels of ship traffic are increasing (Reeves et al. 2014). Noise-induced behavioural disturbance and auditory masking from oil and gas exploration and production and boat traffic can potentially occur over large distances (Reeves et al. 2014, Halliday et al. 2017, Bröker 2019). Ships disrupting sea-ice habitat could have serious impacts on breeding and moulting groups of harp seals and hooded seals in the Greenland Sea, as has been demonstrated in the White Sea (Chernook & Boltnev 2008). Tourism is also increasing in the Svalbard Archipelago (www.mosj.no) and in Greenland (www.stat.gl). Tourist activities have the potential to have negative impacts on marine mammals (Rode et al 2018), although appropriate regulations managing tourism activities can help minimize impacts on marine mammals (Øren et al. 2018).

4.1. Biases and research gaps

The hotspot analyses herein identified areas that are important for individual species and species groups within this Arctic region. The strongest bias to the hotspot results is undoubtedly tagging location(s). Areas with less tagging effort are underrepresented in the hotspot analysis. Ideally, tags should be deployed evenly over the total distribution area of each species within the study area (Queiroz et al. 2016). The number of individuals tagged in different locations should also be weighted by the representative population sizes of a species in each area. However, the costs of this research limit the number of tags and locations where deployments take place, and population size information is lacking for most

species. The present study was thus restricted to a simple equal-weighting option. To address this bias, null model hotspots were created for each species to illustrate where hotspots were expected based on the capture locations. The amount of overlap between null model hotspots and marine mammal hotspots varied a lot. In general, overlap was greatest for species that have restricted, local movements around their capture locations (e.g. bearded seals, harbour seals) compared to species that ranged widely throughout the study region (e.g. hooded seals, seasonally resident whales). Interpretation of the hotspot results in light of the null models is also complicated by fieldwork being carried out in areas where each species is known to occur. Harbour seals were tagged at the only known breeding area and main moulting area for this species in Svalbard (Lydersen & Kovacs 2010). Similarly, walruses were tagged at sites known to be used heavily by this species (Kovacs et al. 2014). The overlap of hotspots with null model hotspots is unavoidable in the above examples as these are the main distributional areas for these species.

Discrepancies between marine mammal hotspots and IUCN ranges serve as a useful gap analysis that highlights areas and species where more research is needed. Polar bears with an inshore movement strategy were under-represented in the biotelemetry data from Northeast Greenland because most of the polar bears tagged in East Greenland were caught offshore in the north (Laidre et al. 2015b). Therefore, few coastal hotspots in the northeast and no hotspots in Southeast Greenland were identified, even though polar bears reside in these regions year-round (Boertmann & Mosbech 2012, Laidre et al. 2018). A small number of tagging locations throughout a species' distributional area is exacerbated by localized movement patterns of some species (e.g. bearded seals, ringed seals), leading to large discrepancies between hotspot areal coverage and species' ranges. In the Northeast Atlantic, more marine mammal biotelemetry data are needed in eastern Svalbard, around Nordaustlandet, in East Greenland and particularly around Franz Josef Land. Species for which more research effort is needed include bearded seals, ringed seals, walruses, harp seals and narwhals due to low areal coverage or paucity of current data from one of the sexes or from various age classes. Tagging effort needs to be continued through the coming decades to document shifting hotspot locations as climate change continues.

Sex and age class were not included in the hotspot analyses as the proportion of individuals tagged of different sex and age classes was variable among the tagged species. For example, all of the data for harp seals in this study were from pups, and only male walruses and mostly female polar bears were tagged. The different age classes of some species have similar space-use patterns (e.g. Folkow et al. 2004, 2010, Blanchet et al. 2016, Hamilton et al. 2019b), but differences in space-use patterns between the different sexes, age classes and life history stages have been documented for many species in this region (e.g. Freitas et al. 2012, Kovacs et al. 2014, Hamilton et al. 2015, 2016). Biases may also result if some age classes or one of the sexes have a longer tracking duration than the rest of the population. This is because individuals with longer tracking durations will have a larger impact on the hotspots results than those with shorter tracking durations. The biotelemetry tags deployed on male polar bears (i.e. ear tags) have shorter battery lives than the tags deployed on female polar bears (i.e. collars; Wiig et al. 2017), biasing hotspot results towards areas used by female polar bears, especially during time periods and in regions when only data from female bears exist. Efforts should be made to deploy instruments on both sexes and various age groups of all species in order to identify similarities and differences in movement strategies, behaviour and hotspot location.

4.2. Conclusions

This study consolidated biotelemetry data from marine mammals in the Greenland and northern Barents Seas in order to identify where marine mammal hotspots and areas of high species richness occur. The results clearly show that the MIZ of the Greenland Sea and northern Barents Sea and coastal regions and fjords of Svalbard and Northeast Greenland are marine mammal hotspots and areas of high species richness. Protection in the form of management and conservation plans is needed in these habitats to help guard against a myriad of threats from climate change and expanding human activities. Due to the high inter- and intra-annual variability in the location and extent of the MIZ and the resultant identified shifts in seasonal locations of marine mammal hotspots, conservation and management plans targeting this important marine mammal habitat will need to be flexible in both space and time in order to protect the many species that use this dynamic zone (see e.g. Pressey et al. 2007, Game et al. 2009, D'Aloia et al. 2019). Many seabird and fish species are also found in the MIZ due to its high summer pulse of biological

productivity as well as in coastal regions of Svalbard and East Greenland (e.g. Gulliksen & Lønne 1989, Hunt et al. 1996, Hop & Gjøsæter 2013); conservation measures targeting these regions will positively benefit many groups of Arctic biota.

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