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Abundance and species diversity hotspots of tracked marine predators across the North American Arctic

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Abstract

Aim: Climate change is altering marine ecosystems worldwide and is most pronounced in the Arctic. Economic development is increasing leading to more disturbances and

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pressures on Arctic wildlife. Identifying areas that support higher levels of predator abundance and biodiversity is important for the implementation of targeted conservation measures across the Arctic.

Location: Primarily Canadian Arctic marine waters but also parts of the United States, Greenland and Russia.

Methods: We compiled the largest data set of existing telemetry data for marine predators in the North American Arctic consisting of 1,283 individuals from 21 species. Data were arranged into four species groups: (a) cetaceans and pinnipeds, (b) polar bears *Ursus maritimus* (c) seabirds, and (d) fishes to address the following objectives: (a) to identify abundance hotspots for each species group in the summer–autumn and winter–spring; (b) to identify species diversity hotspots across all species groups and extent of overlap with exclusive economic zones; and (c) to perform a gap analysis that assesses amount of overlap between species diversity hotspots with existing protected areas.

Results: Abundance and species diversity hotspots during summer–autumn and winter–spring were identified in Baffin Bay, Davis Strait, Hudson Bay, Hudson Strait, Amundsen Gulf, and the Beaufort, Chukchi and Bering seas both within and across species groups. Abundance and species diversity hotspots occurred within the continental slope in summer–autumn and offshore in areas of moving pack ice in winter–spring. Gap analysis revealed that the current level of conservation protection that overlaps species diversity hotspots is low covering only 5% (77,498 km²) in summer–autumn and 7% (83,202 km²) in winter–spring.

Main conclusions: We identified several areas of potential importance for Arctic marine predators that could provide policymakers with a starting point for conservation measures given the multitude of threats facing the Arctic. These results are relevant to multilevel and multinational governance to protect this vulnerable ecosystem in our rapidly changing world.

KEYWORDS

animal movement, biologging, climate change, conservation, fishes, marine mammals, protected areas, seabirds

1 | INTRODUCTION

The distribution, abundance and diversity of predators highlight the ecological structuring and functioning of ecosystems (Hairston, Smith, & Slobodkin, 1960). Quantifying these biogeographic features has important implications for understanding how a complex network of interspecific interactions shape communities, resiliency of communities to perturbations, as well as for developing management plans to conserve biodiversity (Estes et al., 2011). Highly mobile marine predators (e.g., marine mammals, seabirds and large fishes) integrate resources at several spatial and temporal scales, and thus act as sentinel species for productivity and changes to ecological dynamics within ecosystems (Costa, Huckstadt, et al., 2010; Moore & Huntington, 2008).

Climate change and anthropogenic stressors, such as overfishing and pollution, are causing deleterious effects on marine habitats and ecosystem functioning (Hoegh-Guldberg & Bruno, 2010). Climate change is most pronounced in the Arctic and is affecting snow depth and water temperature, and, most conspicuously, is causing a reduction in the distribution and thickness of sea ice, as well as changes in its annual phenology, with associated ecological consequences (Post et al., 2013; Stroeve et al., 2012). In addition, economic development in the Arctic is growing rapidly with interest in petroleum exploration, mining, fisheries and the expansion of tourism and shipping activity leading to increased disturbances and pressures on Arctic wildlife (Fort et al., 2013; Gauthier et al., 2009; Pizzolato, Howell, Derksen, Dawson, & Copland, 2014). Given these cumulative stressors, identifying important areas that

sustain higher levels of abundance and biodiversity of Arctic marine predators is important for the implementation of conservation and management measures across the Arctic.

Establishing marine protected areas (MPAs) is one step in maintaining and conserving areas of biological importance; however, only 3.8% of the global ocean is currently protected (7.2% if including currently proposed networks; MPAtlas, 2018). This level of protection is well below the goal of reaching the Aichi Target 11 of 10% by 2020 (Convention of Biological Diversity, 2010). Presently, MPAs are severely lacking in polar seas (Brooks et al., 2016; Hussey, Harcourt, & Auger-Méthé, 2016), though large areas are currently being designated for some level of protection in the Ross Sea in Antarctica and in Tallurutiup Imanga/Lancaster Sound in the Arctic (MPAtlas, 2018). In addition, the International Union for Conservation of Nature has identified areas like the North Water Polynya and Disko Bay in West Greenland as important and could qualify for World Heritage status and protection through The United Nations Educational, Scientific and Cultural Organization (Speer et al., 2017).

Given the logistical challenges of observing animals within the dynamic nature of polar environments, the application of animal telemetry devices has revolutionized our understanding of the movement ecology of marine species (Hussey et al., 2015). Telemetry data have provided novel insights into complex, previously unknown behaviours, including predator–prey interactions (Breed et al., 2017), fishing fleet interactions with fishes and seabirds (Queiroz et al., 2016; Rolland, Barbraud, & Weimerskirch, 2008; Tuck, Polacheck, Croxall, & Weimerskirch, 2001), environmental drivers of habitat use (Amélineau et al., 2018; Block et al., 2011; Raymond et al., 2015), species diversity hotspots (Grecian et al., 2016) and identifying critical conservation areas (Dias et al., 2017; Lascelles et al., 2016; Ramos et al., 2017). Traditionally, telemetry studies on Arctic marine predators have focused on single or a few species. However, the amount of telemetry data currently available for Arctic marine predators now provides ample opportunity to amalgamate data sets from species across several classes to quantify abundance and species diversity hotspots, and to infer specific areas of higher biological importance. Altogether, this approach allows a high return on investment for using animal telemetry data for conservation decision-making (McGowan et al., 2017).

In the current study, we compiled existing animal tracking data collected between 1989 and 2016 during summer–autumn and winter–spring for 21 Arctic marine species across cetacean, pinniped, polar bear (*Ursus maritimus*), seabird and fish species groups. This unique data set is unprecedented for the Arctic, allowing the opportunity to identify spatio-temporal hotspots across a significant portion of the Arctic, from eastern Russia to West Greenland, although mainly focussed on Canadian waters. There is a myriad of ecological, conservational and socio-political questions that can be addressed with such a large data set. However, given the current low level of conservation protection across the Arctic and sovereignty disputes between nations, the immediate priority is to examine the spatio-temporal overlap of species diversity hotspots relative to protected areas and exclusive economic zones (EEZs).

Our objectives were threefold. First, we identified abundance hotspots for three (i.e., cetaceans and pinnipeds, polar bears and seabirds) of the four species groups by season. Each of these species groupings represents a different method of movement, either swimming, walking or flying. Space-use and abundance hotspots could not be identified for fish as a species group separately due to their low sample size ($n = 55$; see Methods). Second, we mapped the seasonal distribution of all species groups, including fishes, to identify species diversity hotspots across the Arctic. Given increased economic development across the Arctic, we also assessed the spatial extent of species diversity hotspots within EEZs of Canada, United States of America, Russia and offshore waters of Greenland by season. Third, given the current low-level of conservation protection across the Arctic, we performed a gap analysis by calculating the amount of spatial overlap between species diversity hotspots and existing protected areas by season. This fills a critical gap in identifying biologically important areas that are unprotected and provides policymakers with a starting point for expanding conservation protection measures across the North American Arctic. As such, we provide shapefiles of all associated abundance and species diversity densities and hotspots in Yurkowski et al. (2018).

2 | METHODS

2.1 | Study area

We compiled telemetry data from 21 Arctic species ranging longitudinally from eastern Russia in the Bering and Chukchi Seas (166°E) to West Greenland (43°W) and latitudinally from southern Hudson Bay (52°N) to Kane Basin (77°N). We subdivided the North American Arctic into three regions modified slightly from the Conservation of Arctic Flora and Fauna Circumpolar Biodiversity Monitoring Plan (CAFF, 2011): (a) Bering, Chukchi and Beaufort seas, Amundsen Gulf and Viscount Melville Sound (~3,357,500 km²); (b) Jones and Lancaster Sound, Baffin Bay, Davis Strait and Labrador Sea (~2,475,000 km²); and (c) Hudson Bay, Foxe Basin and Hudson Strait (~1,602,500 km²; Figure 1; hereafter referred to West, East and South, respectively). Movements of individuals tagged at locations outside delineated study regions (i.e., Canadian Arctic Archipelago and East Greenland) occurred in the West and East regions, thus were included in all analyses for that respective study region. We also grouped our data into two time-periods, summer–autumn (June to December) and winter–spring (January to May), based upon sea ice being usually fully consolidated (i.e., at or near 100% sea ice concentration) by January, thereby affecting movement for species across all three geographic areas until June (Laidre et al., 2015).

2.2 | Species and data types

We used existing telemetry data collected from 1989 to 2016 from 1,283 individuals across four species groups (Table 1): (a) cetaceans and pinnipeds (belugas *Delphinapterus leucas*, narwhals *Monodon monoceros*, bowhead whales *Balaena mysticetus*, ringed

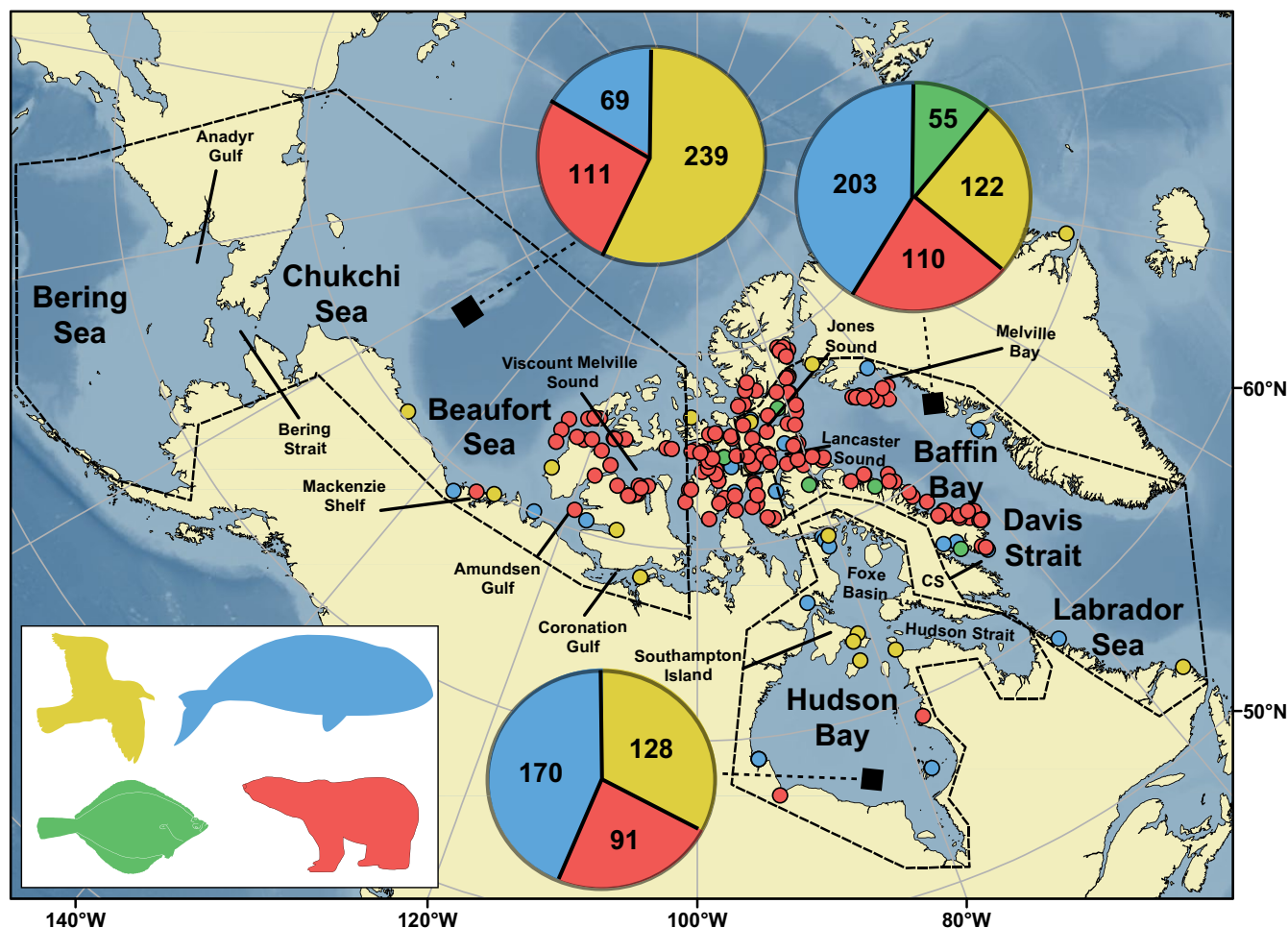


FIGURE 1 Map of the entire study area with the three delineated study regions, West, East and South. Coloured points highlight capture and tagging areas of all species. Movements of individuals tagged at areas outside delineated study regions (i.e., Canadian Arctic Archipelago and East Greenland) occurred in the West and East regions, thus were included in all analyses for that respective study region. Number of tagged individuals within each species group (cetaceans and pinnipeds—blue, polar bears—red, seabirds—yellow, and fishes—green) observed in each region is provided in pie charts. CS: Cumberland Sound

seals *Pusa hispida*, harbour seals *Phoca vitulina* and Atlantic walrus *Odobenus rosmarus rosmarus*); (b) polar bears; (c) seabirds (common eiders *Somateria mollissima*, king eiders *Somateria spectabilis*, ivory gulls *Pagophila eburnea*, long-tailed ducks *Clangula hyemalis*, dove-kies *Alle alle*, northern fulmars *Fulmarus glacialis*, parasitic jaegers *Stercorarius parasitica*, Ross's gulls *Rhodostethia rosea*, thick-billed murre *Uria lomvia*, Sabine's gulls *Xema sabini* and herring gulls *Larus argentatus*); and (d) fishes (Greenland halibut *Reinhardtius hippoglossoides*, Greenland sharks *Somniosus microcephalus* and Arctic skates *Amblyraja hyperborea*; see Table 1). These individuals were captured and instrumented as part of other studies that are described by Orr, Joe, and Evic (2001), Mallory and Gilbert (2008), Dietz et al. (2008, 2014), Ferguson, Dueck, Loseto, and Luque (2010), Gaston et al. (2011), Fisk, Lydersen, and Kovacs (2012), Peklova, Hussey, Hedges, Treble, and Fisk (2012), Spencer, Gilchrist, and Mallory (2014), Harwood, Smith, Auld, Melling, and Yurkowski (2015), Maftei, Davis, and Mallory (2015), Davis, Maftei, and Mallory (2016), Auger-Méthé, Lewis, and Derocher (2016), Lunn et al. (2016) and Bartzen, Dickson, and Bowman (2017).

Depending on species and study, three different types of geolocation systems were used: ARGOS, global positioning system (GPS) and global location sensor (GLS)-type loggers (Table 1). All loggers were programmed to record at least one location per day; however, some were duty cycled every 2 days (ringed seals $n = 9$; narwhal $n = 4$; belugas $n = 4$), 3 days (long-tailed ducks $n = 36$; common eiders $n = 22$; narwhal $n = 34$; belugas $n = 3$), 4 days (belugas $n = 7$; narwhal $n = 20$; polar bears $n = 39$), 5 days (polar bears $n = 110$) and 6 days (belugas $n = 5$). Duty cycling for beluga and narwhal transmitters described above began on October 1. Pop-off ARGOS satellite-linked archival transmitters (PSATs) were deployed on all fishes, and only capture and pop-off locations were used for further analysis. We used data for individual track lengths of ≥ 28 days for further data filtering and processing similar to Le Corre et al. (2012).

2.3 | Data filtering and processing

The three geolocation types had different sampling rates, and ARGOS and GLS data have much higher spatial error ranging from

TABLE 1 Summary of tracking metadata of all species with respect to tagging location

Species	N individuals	Device	N days	Date range	Tracking period
West					
Beluga (<i>Delphinapterus leucas</i>)	41	PTT-ARGOS	2,175	4 July to 3 July	1993, 1995, 1997, 2004–2006
Ringed seal (<i>Pusa hispida</i>)	27	PTT-ARGOS	2,749	25 June to 23 February	1999, 2000, 2001, 2010
Polar bear (<i>Ursus maritimus</i>)	111	PTT-GPS and ARGOS	30,054	13 April to 12 April	1989–1993, 2007–2014
Common eider (<i>Somateria mollissima</i>)	68	PTT-ARGOS	7,702	12 June to 11 June	2001–2004, 2006–2009
King eider (<i>Somateria spectabilis</i>)	94	PTT-ARGOS	7,173	6 June to 5 June	1997–2001, 2003–2005, 2008–2009
Ivory gull (<i>Pagophila eburnea</i>)	12	PTT-ARGOS	4,739	7 June to 6 June	2010
Sabine's gull (<i>Xema sabini</i>)	26	GLS	6,959	1 August to 31 July	2008–2012
Long-tailed duck (<i>Clangula hyemalis</i>)	39	PTT-ARGOS and GLS	1,656	4 August to 3 August	2003–2004, 2009–2011
East					
Beluga (<i>Delphinapterus leucas</i>)	42	PTT-ARGOS	2,826	12 July to 26 May	1998–2000, 2006–2009
Bowhead (<i>Balaena mysticetus</i>)	14	PTT-ARGOS	1,606	11 July to 10 July	2006–2007, 2012–2014
Ringed seal (<i>Pusa hispida</i>)	30	PTT-ARGOS	3,856	8 August to 15 July	2008–2013
Narwhal (<i>Monodon monoceros</i>)	76	PTT-ARGOS	5,363	9 August to 8 August	1997–2000, 2003–2012
Atlantic walrus (<i>Odobenus rosmarus rosmarus</i>)	27	PTT-ARGOS	1,073	19 March to 25 November	1993, 1998–1999, 2001, 2003–2008
Polar bear (<i>Ursus maritimus</i>)	110	PTT-ARGOS	10,610	2 April to 1 April	1991–2001
Dovekie (<i>Alle alle</i>)	78	GLS	16,455	5 August to 22 May	2009–2011
Northern fulmar (<i>Fulmarus glacialis</i>)	5	PTT-ARGOS	852	10 June to 7 March	2004–2006
Parasitic jaeger (<i>Stercorarius parasitica</i>)	3	GLS	757	14 July to 11 June	2010–2012
Long-tailed duck (<i>Clangula hyemalis</i>)	2	GLS	402	20 July to 19 July	2010–2011
Ross's gull (<i>Rhodostethia rosea</i>)	2	PTT-ARGOS and GLS	735	9 June to 8 June	2012–2013
Thick-billed murre (<i>Uria lomvia</i>)	32	GLS	6,233	20 August to 30 May	2007–2010
Greenland shark (<i>Somniosus microcephalus</i>)	45	Pop-off-ARGOS	164	27 July to 26 July	2007–2011, 2012–2016
Greenland halibut (<i>Reinhardtius hippoglossoides</i>)	7	Pop-off-ARGOS	14	17 August to 14 June	2010–2011
Arctic skate (<i>Amblyraja hyperborea</i>)	3	Pop-off-ARGOS	6	1 August to 27 October	2010–2011
South					
Beluga (<i>Delphinapterus leucas</i>)	32	PTT-ARGOS	3,285	3 July to 31 May	1992–1993, 2002–2005, 2012–2013, 2015
Bowhead (<i>Balaena mysticetus</i>)	26	PTT-ARGOS	5,544	30 Jun to 29 June	2006–2007, 2011–2015
Ringed seal (<i>Pusa hispida</i>)	73	PTT-ARGOS	9,923	20 June to 19 June	2006–2012
Harbour seal (<i>Phoca vitulina</i>)	19	PTT-ARGOS	4,084	22 August to 28 June	2001–2002
Narwhal (<i>Monodon monoceros</i>)	9	PTT-ARGOS	742	8 August to 3 June	2006–2007
Atlantic walrus (<i>Odobenus rosmarus rosmarus</i>)	11	PTT-ARGOS	417	3 September to 31 December	2010
Polar bear (<i>Ursus maritimus</i>)	91	PTT-GPS	24,539	31 August to 30 August	2004–2015
Common eider (<i>Somateria mollissima</i>)	66	PTT-ARGOS	9,070	18 June to 17 June	2003–2004, 2012–2015

(Continues)

TABLE 1 (Continued)

Species	N individuals	Device	N days	Date range	Tracking period
Herring gull (<i>Larus argentatus</i>)	28	PTT-ARGOS and GLS	4,913	25 June to 13 June	2007–2011, 2013–2015
Long-tailed duck (<i>Clangula hyemalis</i>)	3	PTT-ARGOS	142	6 June to 28 October	2003–2004
Thick-billed murre (<i>Uria lomvia</i>)	31	GLS	8,861	9 August to 4 June	2007–2010

Note. N days is the sum of all 1-day location estimates from GPS data, state-space model, Douglas filter or best ARGOS location estimates per day for each species. East refers to the Lancaster Sound, Jones Sound, Baffin Bay, Davis Strait and Labrador Sea area, West the Bering, Chukchi and Beaufort Seas, Amundsen Gulf and Viscount Melville Sound area and South the Hudson Bay, Hudson Strait and Foxe Basin area.

0.3 km to 36 km and up to 184 km, respectively (Costa, Robinson, et al., 2010; Phillips, Silk, Croxall, Afansyev, & Briggs, 2004), compared to GPS data. Therefore, telemetry data were filtered using different methodologies across geolocator types and taxa to standardize data sets by obtaining one location estimate per day or every duty cycled day. All data sets from GLS loggers on seabirds, except those that used additional sea surface temperature data, were first filtered by removing locations 1 week on each side of the equinoxes. In addition, based on the behaviour and latitudinal range of the species, and the data quality, GLS data sets were also filtered to remove the nesting period, 1 week on each side of the summer solstice, and extreme geographic outliers. For the duty cycled long-tailed ducks, common eiders and king eiders, the Douglas ARGOS filter, which improves location accuracy by 50%–90%, was applied to obtain one location estimate per duty cycled day (Douglas et al., 2012). For the ARGOS polar bear data, only the most precise location qualities (location classes 1, 2 or 3; i.e., spatial errors ≤ 1.2 km; Costa, Robinson, et al., 2010) were retained per duty cycled day (see Ferguson, Taylor, & Messier, 2000). Data from GPS transmitters deployed on polar bears were not filtered due to their high spatial accuracy (Costa, Robinson, et al., 2010). GPS locations were collected every 4 hr; thus, to obtain a daily location, we only used the time of day with most location estimates (13:00 UTC) for Beaufort Sea and Hudson Bay polar bears. For the remaining ARGOS- and GLS-type tags, we used a discrete-time correlated random walk in the form of hierarchical state-space models (SSM; Jonsen, Mills Flemming, & Myers, 2005; Jonsen, 2016) to reduce location error and produce a single location estimate per day evenly spaced in time (i.e., 1 day time step). For duty cycled transmitters, the time step corresponded with its respective duty cycle interval. Hierarchical state-space models were grouped by species, and individual tracks with data gaps ≥ 7 days were split into segments before interpolation. Because of large data sets for each species with ARGOS data and computational limitations restricting the fit of one large hierarchical SSM per species, we grouped ~ 20 individuals per species per model run. Models were run in R v. 3.3.2 (R Development Core Team, 2016) and JAGS v 4.2.0 (Plummer, 2003) using *bsam* v. 1.1.1 (Jonsen, 2016) for ARGOS data and in *TMB* v. 1.7.4 (Kristensen, Nielsen, Berg, Skaug, & Bell, 2016) for GLS data using modified code (Auger-Méthé et al., 2017). In *bsam*, two Markov chain Monte Carlo chains were run for 40,000 iterations with a 20,000-sample burn-in and thinned every 20

samples. Temporal autocorrelation was assessed visually via trace and autocorrelation plots, and chain convergence was estimated by Gelman and Rubin's potential scale reduction factor, which was < 1.1 for all parameters. Despite differing filtering and processing techniques of different subsets of the data, the spatial error in all locations was much lower than the $50 \text{ km} \times 50 \text{ km}$ spatial resolution of the hotspot analysis described below.

2.4 | Hotspot analysis

Space-use and abundance hotspots were identified by species groups during summer–autumn and winter–spring. We constructed spatial density maps by summing the number of unique individuals (i.e., abundance) for each species group excluding fishes within $50 \text{ km} \times 50 \text{ km}$ grid cells in each geographic region using ArcGIS 10.5 (ESRI Inc., USA). We used the same binning approach across all species groups including fishes to estimate abundance and species diversity (i.e., unique number of species) per $50 \text{ km} \times 50 \text{ km}$ grid cell. All data were projected to a Lambert azimuthal equal-area projection before analysis. We then performed a spatial hotspot analysis in the form of Getis-Ord G_i^* statistic (Getis & Ord, 1992) in ArcGIS to quantify specific areas of high spatial clustering and significance for abundance and species diversity. This analysis determines the spatial clustering of grid cell values that are higher (hotspot) or lower (coldspot) than is expected by a random distribution. Significance tests were performed between nearby grid cells (i.e., both unique number of individuals and species per grid cell) in the surrounding neighbourhood area using a z-score (Getis & Ord, 1992). To conceptualize the spatial relationship, we used the recommended fixed distance band to ensure each feature has a neighbour within a specified distance that was objectively calculated within ArcGIS, an approach similar to Queiroz et al. (2016). A z-score between -1.96 and -1.15 (light blue), and 1.15 and 1.96 (orange) signifies significance at the $\alpha = 0.10$ level, whereas a z-score above 1.96 (red) or below -1.96 (dark blue) is significant at the $\alpha = 0.05$ level and, throughout this study, indicates a hotspot and coldspot for that weighting variable, respectively. In the East, grid cells along the West Greenland continental shelf were removed due to lower confidence in our results owing to a lower amount of tagging areas ($n = 14$) compared to Canada ($n = 187$). Results from hotspot analysis that included and removed the West Greenland continental shelf

prior to analysis revealed similar results for abundance and species diversity hotspots both within and across species groups, respectively (see Section 12 and Supporting Information Figures S1–S3 in Appendix S1).

The sampling of taxa and locations was not random or uniform across the entire study area; therefore, we verified whether our hotspots overlapped with areas expected to be highly used based on a space-use model that accounted for this heterogeneity of sampling effort. We used a modified version of the null usage equation developed by Grecian et al. (2016; see Supporting Information Appendix S1 for equation and a description of parameters). Null usage represents the intensity with which the cell is expected to be used at a given point in time based on proximity to tagging locations and average speed of species tagged (see Supporting Information Figure S4 in Appendix S1 for null usage map). To test whether null usage explained species diversity in each region, we then performed a generalized least squares model with an exponential spatial correlation structure between unique number of species and null usage per region using *nlme* v 3.1-131 (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) in R.

We obtained shapefiles for existing protected areas across the study area from the World Database on Protected Areas (www.protectedplanet.net), MPAtlas (Marine Conservation Institute, MPAtlas, 2018), Fisheries and Oceans Canada (Ottawa, Canada) and Parks Canada Agency (Gatineau, Quebec). Protected areas defined in our study afford at least some level of protection and include Bottom-Contact Fishery Closures, National Parks, National Wildlife Areas, Migratory Bird Sanctuaries, National Marine Conservation Areas, Territorial Parks and Marine Protected Areas (see Figure 2). Shapefiles for EEZs of Canada, United States of America, Russia and Greenland were obtained from marine regions (www.marineregions.org). As a gap analysis, we calculated the spatial and percentage overlap (km² and % area, respectively) of species diversity hotspots within protected areas and EEZs using the union and intersect geoprocessing tools in ArcGIS.

3 | RESULTS

We obtained 186,786 daily location estimates after data filtering and processing. For each defined geographic region, there was a total of 37,188 locations (summer–autumn locations = 23,979) in the East region, 52,014 locations (37,054) in the West region and 57,482 locations (38,367) in the South region (Table 1). In the East, there were a total of 30,408 locations (summer–autumn = 20,272) following location removal along the West Greenland continental shelf. During summer–autumn, and with some individuals travelling across the geographic region boundaries, the total number of unique individuals and unique number of species was highest in the East region (530 and 19, respectively—500 and 19 following location removal from West Greenland), followed by the South region (436 and 16, respectively) and West region (389 and 10, respectively). Similarly, throughout the winter–spring, the East had the highest number of

tracked individuals and species (310 and 16, respectively—281 and 16 following location removal from West Greenland) compared to the South region (271 and 13, respectively) and West region (240 and 8, respectively). The hotspot analysis in all three geographic regions identified key space-use and abundance hotspots for cetaceans and pinnipeds, polar bears and seabirds, and species diversity hotspots across all four species groups. Null usage did not explain unique number of species per grid cell in the East ($t_{915} = 1.03$, p -value = 0.30) and South ($t_{591} = 1.71$, p -value = 0.09) but did in the West ($t_{1283} = 2.62$, p -value = 0.01; see Supporting Information Table S1 in Appendix S1 for model results). Species diversity was related to null usage in the West likely because this region has less telemetry data than the other regions and the vast majority of tagging locations occurred in the Central Arctic Archipelago and eastwards with little sampling effort in Russia and Alaska. Supporting Information Appendix S1 contains figures of location and abundance densities within and across each species group by geographic area, as well as species diversity densities by geographic area (Supporting Information Figures S5–S11).

3.1 | Abundance hotspots by species group and season

During summer–autumn (June to December), hotspots for cetaceans and pinnipeds occurred in areas of south-western and south-eastern Hudson Bay and north-west and southern Foxe Basin in the South; Cumberland Sound, western Davis Strait near the Cumberland Peninsula, Lancaster Sound and Jones Sound in the East; and Amundsen Gulf, Viscount Melville Sound and southern Beaufort Sea near the Mackenzie Shelf in the West (Figure 3a,c). Polar bear hotspots occurred in south-western Hudson Bay, western Baffin Bay/Davis Strait and southern Beaufort Sea (Figure 3a,c). For seabirds, hotspots were identified in southern Foxe Basin, offshore waters in Hudson Bay ranging from the Southampton Island coast to 150 km offshore from south Hudson Bay shoreline in the South, offshore waters of Baffin Bay, Davis Strait and eastern Labrador Sea in the East, and in the Amundsen Gulf, Dolphin and Union Strait, southern Beaufort Sea near the Mackenzie Shelf, Anadyr Gulf, Bering Strait and Chukchi Sea in the West (Figure 3e).

Throughout winter–spring (January to May), locations of hotspots for cetaceans and pinnipeds were generally similar to the summer–autumn hotspots, albeit with a more restricted size and also included Hudson Strait—an area of moving pack ice (Figure 3b). We could not calculate hotspots in the West for the cetacean and pinniped species group due to low numbers of individuals (6) and locations (134). For polar bears, winter–spring hotspots occurred in western and central Hudson Bay in the South, western Davis Strait and Labrador Sea, offshore areas of northern Baffin Bay extending into Lancaster Sound and Jones Sound in the East, and southern Beaufort Sea near the Mackenzie Shelf in the West (Figure 3d). For seabirds, Hudson Strait is a key wintering hotspot along with offshore pack ice areas of Davis Strait, Labrador Sea, Anadyr Gulf and Bering Strait (Figure 3f).

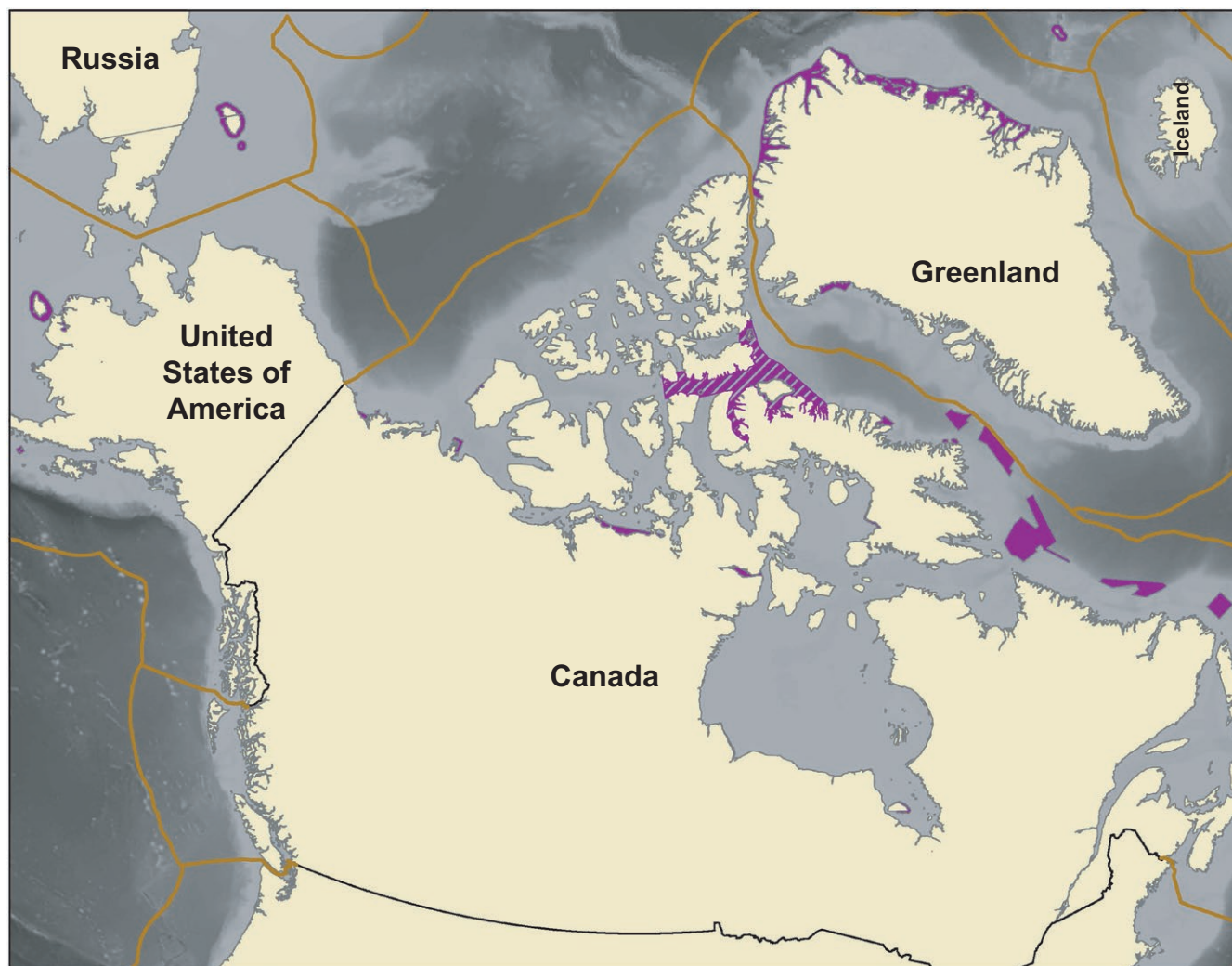


FIGURE 2 Map of the study area highlighting protected areas (purple) and exclusive economic zones (EEZs; brown) of Canada, Greenland, United States of America and Russia. Note that the Tallurutiup Imanga/Lancaster Sound National Marine Conservation Area (dashed) is proposed and is currently in the process of implementation

3.2 | Species diversity hotspots by season

In summer–autumn, species diversity hotspots in the West were identified from Bering Strait and Chukchi Sea to the Coronation Gulf and also included Viscount Melville Sound (860,139 km²; Figure 4a). In the South, species diversity was higher around Southampton Island and eastwards into Hudson Strait (182,852 km²; Figure 4a). Species diversity hotspots in the East encompassed large areas of Lancaster Sound, nearshore and offshore waters of Baffin Bay, Cumberland Sound and western Davis Strait near south-east Baffin Island (480,217 km²; Figure 4a). There was minimal overlap of species diversity hotspots and existing protected areas during summer, the largest occurring in the East (with and without Tallurutiup Imanga/Lancaster Sound: 71,141 km², 15%, and 9,812 km², 2%, respectively), followed by the West (6,099 km², <1%) and South (258 km², <1%; Table 2; Figure 5a). Across the entire study area, species diversity hotspots primarily occurred within Canadian waters (65.17%; 992,766 km²)

followed by Alaskan waters along the continental shelf (21.81%; 332,251 km²), the Russian Chukchi Shelf (7.08%; 107,809 km²) and offshore Greenland waters of Baffin Bay (5.95%; 90,582 km²; Table 3).

In winter–spring, species diversity hotspots occurred in areas of moving pack ice in all three geographic areas: (a) along the continental shelf from the Mackenzie Shelf westwards to Chukchi Sea and in Bering Strait (336,892 km²), (b) in northern Hudson Bay near Southampton Island and Hudson Strait (267,925 km²) and (c) along the continental shelf of the Labrador Sea northwards to coastal and offshore areas of Davis Strait and southern Baffin Bay (588,340 km²; Figure 4b). Overlap of species diversity hotspots and existing protected areas during winter was 14% in the East (81,327 km²) and <1% in the West (1,615 km²) and South (258 km²; Table 2; Figure 5b). Across the entire study area, species diversity hotspots primarily occurred within Canadian waters (66.92%; 798,429 km²), followed by Alaskan waters along the continental shelf (14.52%; 173,204 km²), Greenlandic waters of Baffin Bay and

Davis Strait (13.73%; 163,811 km²) and the Russian Chukchi Shelf (4.84%; 57,713 km²; Table 3). We provide more detailed information in Supporting Information Figures S2 and S3 in Appendix S1 for species diversity hotspots with and without the West Greenland continental shelf included by geographic area. In the East, species diversity hotspots were nearly identical in Canadian and offshore waters using both approaches (see Figure 4 and Supporting Information Figures S2 and S3).

4 | DISCUSSION

We identified the spatio-temporal distribution of a diverse assemblage of highly mobile Arctic marine predators using telemetry data from tagged species at multiple locations across the study area. While sampling of taxa and locations was not random nor planned for the purpose of this study, the broad diversity of location data provides novel insights into marine predator distribution in the North American Arctic. We delineated key biological hotspots within and across cetacean and pinniped, polar bear, seabird and fish species groups by season in relation to protected areas and political-economic zones over much of the North American Arctic. Hotspots were generally along the continental shelf and slope throughout summer-autumn and were generally offshore in known areas of moving pack ice during winter-spring. These near-apex and apex predators play a crucial role in structuring Arctic food webs through strong top-down trophic control—a key characteristic of cold-water ecosystems (Boyce, Frank, Worm, & Leggett, 2015). Identifying areas where predator densities are highest provides critical information for Arctic conservation and biodiversity to mitigate potential deleterious effects of anthropogenic stressors on the Arctic ecosystem.

4.1 | Spatio-temporal hotspots of Arctic marine predators

Hotspots across species groups were generally within the continental shelf during summer-autumn. In the West, nutrient-rich waters from the Pacific Ocean and Bering Sea flow northwards through the Bering Strait and southern Chukchi Sea leading to enhanced pelagic and benthic faunal biomass (Grebmeier, Cooper, Feder, & Sirenko, 2006). Higher zooplankton biomass occurs along the continental shelf and shelf break to the Mackenzie Delta (Grebmeier et al., 2006) where zooplankton become entrained via mesoscale physical processes (i.e., upwelling and eddies) that attract zooplanktivorous fish such as Arctic cod (*Boreogadus saida*; Logerwell, Rand, & Weingartner, 2011; Majewski et al., 2015)—a key prey item for higher trophic-level Arctic predators (Welch, Crawford, & Hop, 1993). These hotspot areas encompassed marine predator hotspots documented in Citta et al. (2018) and Kuletz et al. (2015). During winter-spring, hotspots occurred in recurring areas of moving ice westwards of the Cape Bathurst Polynya—an important winter habitat for marine mammals and seabirds during spring migration (Citta

et al., 2015; Dickson & Gilchrist, 2002; Harwood & Stirling, 1992; Stirling, Andriashek, & Calvert, 1993).

In the East, many of the fjords along Baffin Island are high energy systems due to increased organic carbon content in the water column via primary productivity (Syvitski, LeBlanc, & Cranston, 1990), and therefore have the ability to support high densities of upper trophic-level predators as observed in our study. Huettmann, Artukhin, Gilg, and Humphries (2011) and Wong, Gjerdum, Morgan, and Mallory (2014) documented seabird hotspots in similar areas using predictive modelling and at-sea observer data, respectively. Combining other data types (i.e., at-sea observation, fisheries independent survey) and telemetry data from other pan-Arctic population/species that overwinter in our study area (i.e., dovekies from Spitsbergen and Bjørnøya; Fort et al., 2013) with our telemetry data will further refine our multispecies hotspots. During winter, species diversity hotspots were concentrated in dense mobile pack ice areas of Baffin Bay and Davis Strait, which have increased foraging opportunities during the phytoplankton bloom during spring (Arrigo & van Dijken, 2011).

Species diversity hotspots coincided with productivity patterns of the Hudson Bay complex: Foxe Basin and Hudson Strait have greater primary and secondary productivity compared to Hudson Bay, while western Hudson Bay has higher productivity compared to eastern Hudson Bay (Harvey, Starr, Theriault, Saucier, & Gosselin, 2006). Hotspots occurred around Southampton Island, an area that includes the core area of Palaeo-Inuit occupation for over 3,500 years, suggesting this area continues to have enhanced and reliable productivity (Hodgetts, 2007). Overwintering hotspots were within the moving pack ice and open water areas of Hudson Strait highlighting the ecological importance of polynyas and pack ice areas to Arctic ecosystem structure and function (Stirling, 1997). For polar bears, abundance hotspots typically occurred in south-western Hudson Bay; however, it is important to note that a dichotomy existed between species diversity and polar bear hotspots. This highlights the importance of examining both within and across species groups for conservation and management as only investigating biodiversity hotspots would have negated the identification of critical polar bear habitat.

4.2 | Conservation implications

The current level of overlap between species diversity hotspots and current conservation areas is low across our study region of the Arctic where a total protected area of 5% (77,498 km²) and 7% (83,202 km²) overlapped in summer-autumn and winter-spring, respectively. Given the multitude of threats facing the Arctic today, such as climate change, offshore oil and gas activities, shipping and fisheries potential (Huntington, 2009), it is important for policy- and decision-makers to inform priority spatial planning and development with ecological data. Although the feasibility of implementing protection across our entire identified hotspot range is likely impossible, we provide a starting point to inform management and conservation decisions. In the Canadian Arctic, currently established

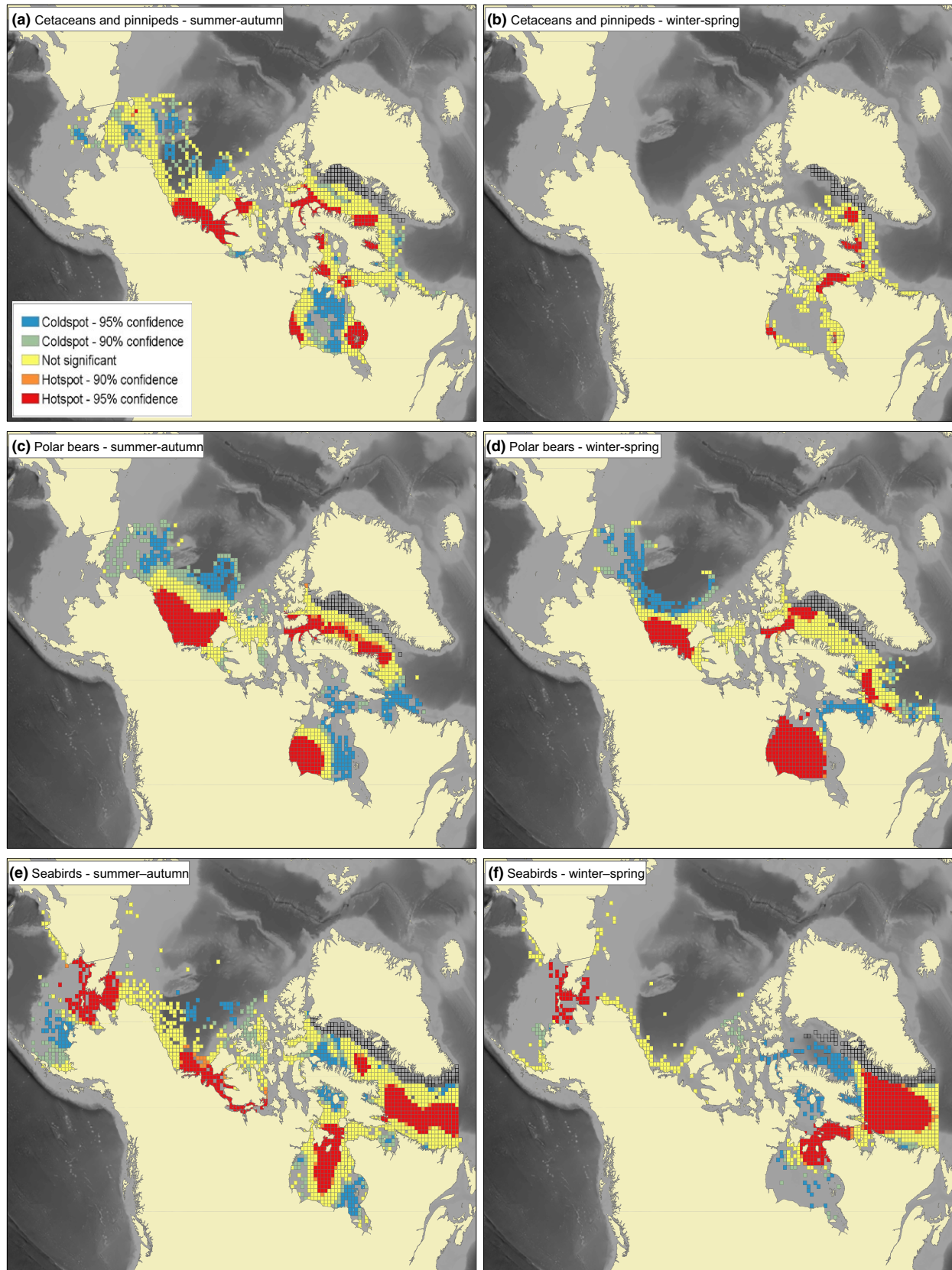


FIGURE 3 Map of calculated high (hotspot: red) and low (coldspot: dark blue) number of unique individuals per 50 km × 50 km grid cell for tracked cetaceans and pinnipeds (a, b), seabirds (c, d) and polar bears (e, f) by summer–autumn (a, c, e,) and winter–spring (b, d, f) across the study area. Note that the significance values for the different geographic regions are based on different numbers of tracked individuals and species. Grid cells along the West Greenland continental shelf have been masked due to a lower number of tagging locations in these areas than in Canadian waters resulting in less confidence in identifying hotspots and coldspots

protected areas are often small and designed to protect single species. For example, in the West, the Tarium Niryutait (1,740 km²) and Anguniaqvia niqiqyuam (2,361 km²) MPAs were established to primarily protect beluga whales (DFO, 2013). While recent progress has led to the designation of a large protected area (Tallurutiup Imanga/Lancaster Sound), and despite protected areas only being one tool for species and habitat conservation, our results further highlight the urgent need to address the limited protection coverage in the Arctic (Hussey et al., 2016).

With prolific interest in economic development in the Arctic at a multinational level, the anthropogenic pressures on Arctic wildlife have never been higher. Summer-autumn (65.17%) and winter-spring (66.92%) species diversity hotspots were mainly found in the EEZ of Canada, a country which has committed to protecting 10% of its marine waters by 2020 (Government of Canada 2018).

However, a relatively large portion of species diversity hotspots also occurred in EEZs of USA (21.81% and 14.52% in summer-autumn and winter-spring, respectively) and offshore waters of Greenland (5.95% in summer-autumn; 13.73% in winter-spring). Therefore, these hotspots are mainly found in national jurisdictions where protection is likely simpler to implement than in international waters. This also highlights the need for multinational collaboration and data sharing from government and non-governmental organizations in implementing effective spatial planning and conservation strategies to protect the Arctic and its wildlife, as advocated for by the Arctic Council (PAME, 2015). A strong first step recently occurred in international waters of the high Central Arctic Ocean where nine nations have placed a 16-year fishing moratorium in these waters allowing data collections and monitoring to take precedent prior to sustainable and well-managed fishing (Hoag, 2017).

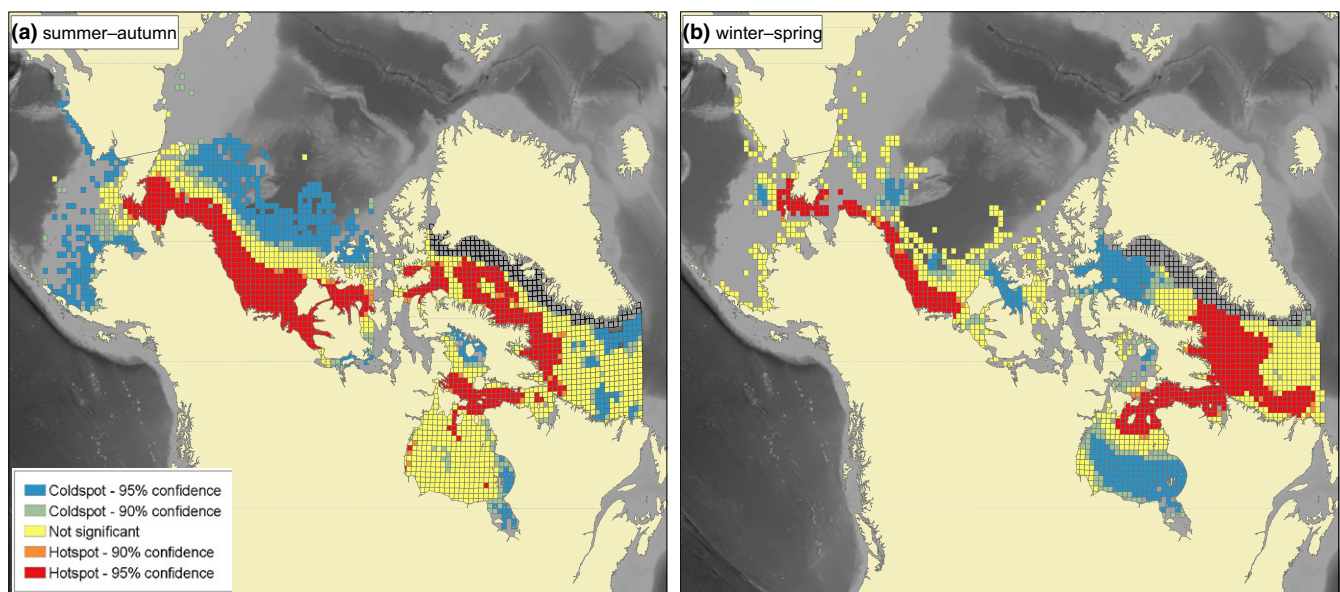


FIGURE 4 Species diversity hotspots (red) and coldspots (dark blue) by summer-autumn (a) and winter-spring (b) of all tracked species groups (cetaceans and pinnipeds, seabirds, polar bears and fishes) per 50 km × 50 km grid cell across the study area. Note that the significance values for the different geographic areas are based on different numbers of tracked individuals and species. Grid cells along the West Greenland continental shelf have been masked due to a lower number of tagging locations in these areas than in Canadian waters resulting in less confidence in identifying hotspots and coldspots

TABLE 2 Spatial overlap (km² and % area) of species diversity hotspots with protected areas within each study region (West, East and South)

Area	Hotspot size (km ²)	Protected area spatial overlap (km ²)	Protected area percentage overlap (% area)
Summer-autumn			
West	860,139	6,099	0.07
East	480,217	71,141 ^a	14.80
South	182,852	258	0.01
Winter-spring			
West	336,892	1,615	0.05
East	588,340	81,329	13.80
South	267,925	258	<0.01

^aWithout Tallurutiup Imanga/Lancaster Sound NMCA = 9,812 km² and 2.0%.

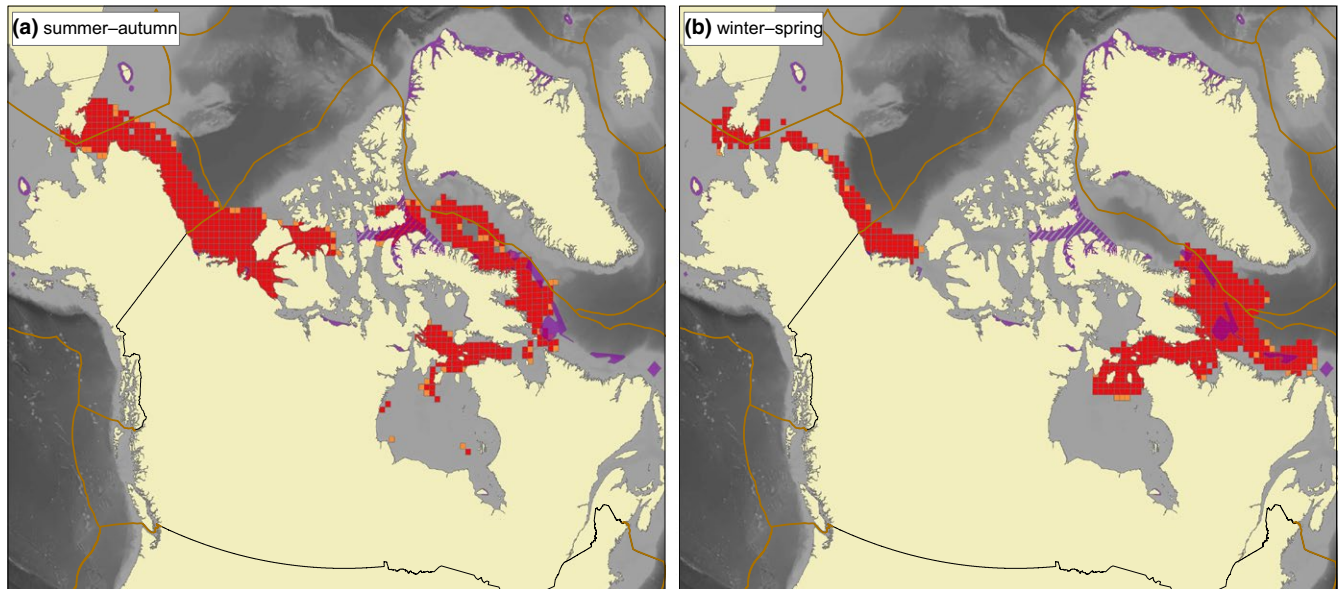


FIGURE 5 Map of species diversity hotspots at $\alpha = 0.10$ (orange) and $\alpha = 0.05$ (red) levels by summer-autumn (a) and winter-spring (b) relative to protected areas (purple) and exclusive economic zones (EEZs; brown) across the entire study region. Note that the Tallurutiup Imanga/Lancaster Sound National Marine Conservation Area (dashed) is proposed and is currently in the process of implementation

The most pervasive threat to the Arctic and its wildlife is climate change, where decreases in the body condition of marine mammals and seabirds (Harwood, Smith, George, et al., 2015; Sciuillo, Thiemann, & Lunn, 2016) have been observed in association with changing sea ice conditions. A warming Arctic is redistributing species with more temperate-associated species expanding their range northwards, which has changed the trophic structure of the Arctic ecosystem (Fossheim et al., 2015; Frainer et al., 2017; Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015; Yurkowski et al., 2017). Furthermore, interest in expanding fisheries exploitation of coastal and offshore waters within EEZs of Arctic nations is high (Christiansen, Mecklenburg, & Karamushko, 2014), which can increase risks of entanglement and bycatch mortality, a global

cumulative threat to marine megafauna (Lewison et al., 2014) that can lead to trophic downgrading (Estes et al., 2011). In Baffin Bay, for example, a long-lived apex predator, the Greenland shark (Nielsen et al., 2016), is a bycatch species in expanding Greenland halibut and northern shrimp (*Pandulus borealis*) fisheries (MacNeil et al., 2012). Seabirds are at similar risk (Hedd et al., 2016).

With a rapid decline in multiyear ice, shipping across the Canadian Arctic has increased, raising the risks of ship strikes, oil spills, destruction of habitat through ice-breaking activity and noise pollution (Fox et al., 2016; Huntington, 2009). Also, interest in oil and gas exploration and exploitation is driving increased seismic surveys that can negatively affect the marine environment through zooplankton mortality (McCauley et al., 2017) and potential non-consumptive (i.e., sublethal) effects across all trophic levels (Christiansen et al., 2014; Gordon et al., 2003). Seismic activity was approved by the National Energy Board of Canada in 2014 in Baffin Bay, an area presumed to hold one of the largest undiscovered oil reserves across the globe (McCauley et al., 2017). However, following a lack of required consultation with Inuit communities in the area (e.g., Clyde River, Nunavut) and given concerns for ecosystem disruption, the Supreme Court of Canada overturned this initiative (Tasker, 2017). Oil exploitation will increase infrastructure development, shipping and the potential for oil spills, of which Arctic nations are ill-equipped to respond to with associated effects having extensive and long-lasting ecological impacts (Gulas, Downton, D'Souza, Hayden, & Walker, 2017; Shelton et al., 2017). As such, identifying areas that are important to wildlife and where such activities should be limited is increasingly important.

Anthropogenic stressors are greatest during the open water period and will likely intensify, both in duration and in coverage, with a continued reduction in sea ice extent (e.g., Dawson, Pizzolato,

TABLE 3 Spatial overlap (km² and % area) of species diversity hotspots with the exclusive economic zones (EEZs) of Canada, United States of America (USA), Greenland and Russia

EEZ	Spatial overlap (km ²)	Percentage overlap (% area)
Summer-autumn		
Canada	992,766	65.17
USA	332,251	21.81
Greenland	90,582	5.95
Russia	107,809	7.08
Winter-spring		
Canada	798,429	66.92
USA	173,204	14.52
Greenland	163,811	13.73
Russia	57,713	4.84

Howell, Copland, & Johnston, 2018; PAME, 2009). Though direct impacts of anthropogenic stressors are currently less during the ice-covered period, they would increase with spring ice-breaking activity by mineral, gas and oil extraction and transport leading to sea ice habitat destruction for wildlife and traditional hunting travel routes for Inuit. As well, key overwintering areas (i.e., Cape Bathurst Polynya, North Water Polynya, Baffin Bay/Davis Strait, and Hudson Strait) deserve conservation protection from fisheries and trawling activities during summer–autumn to minimize impacts on, and preserve important food sources and habitat for, many predators during the overwintering period. Given the pervading anthropogenic stressors in the Arctic throughout the year, our shapefiles and analyses provide a foundation for assessing the ecological implications of economic development and resource extraction within these hotspots and for the continued designation of conservation protection in North American Arctic waters. Our results and associated data layers (i.e., shapefiles) can be used to inform ecosystem-based management for developing cumulative effect assessments in a risk management framework that includes risk identification, risk analysis and risk evaluation (Stelzenmüller et al., 2018).

4.3 | Knowledge gaps

Several knowledge gaps could impact our data interpretation. First, tracking marine predators in the Arctic is constrained by logistical challenges, high costs (Mallory et al., 2018) and the highly seasonal environment that results in limited and intermittent access to field sites near Inuit communities typically during summer–autumn. Therefore, much of the available predator telemetry data we used are from tagging locations coincident with established long-term monitoring studies where many of these species are known to aggregate (i.e., cetaceans and seabirds) or are central-place foragers from colonies (i.e., seabirds). Due to this logistical constraint, the sample sizes across species are unequal and species with higher numbers of tracked individuals could have a stronger influence on estimated hotspots. The location of tagging likely influenced our abundance hotspots per species group. However, the sampling distribution of tagging locations only influenced species diversity hotspots in the West. No influence was detected in the East and South, likely given to our broad distribution of tagging locations from north to south and east to west in each of these two geographic regions. The influence of sampling effort in the West is most likely due to the lack of tagging locations from Russia and Alaska. However, despite this limitation, identified hotspots in the West encompassed important areas previously documented in Harwood and Stirling (1992), Dickson and Gilchrist (2002), Grebmeier et al. (2006), Kuletz et al., 2015; Citta et al. (2018), suggesting that our hotspot identification based on tracking data was effectively capturing known key locations. We are also most confident in hotspots identified within and near Canadian waters given higher number of tagging locations compared to West Greenland, Alaska and Russia. We suggest that our species diversity hotspots of these mobile marine predators in North American waters reflect areas of high importance.

Second, additional tracking data could also lead to the refinement of hotspots, investigate long-term changes in their spatial distribution or identify additional areas of significance, such as Prince Regent Inlet, Gulf of Boothia, Store Hellefiskebanke, Disko Bay and North Water Polynya in the East—areas of high biological importance (Andersen et al., 2017; Ferguson et al., 2010; Speer et al., 2017). Our estimated coldspots could also change with the addition of more tracking data. For example, south-eastern Hudson Bay in the South, and Kotzebue Sound and Norton Sound in the West are productive areas where marine megafauna aggregate (Andersen et al., 2017; Citta et al., 2018; Dietz et al., 2014; Gilchrist & Robertson, 2000; Hobson et al., 2002), but were classified as coldspots in our analysis. Moreover, Lancaster Sound is generally considered a seabird hotspot (Mallory & Fontaine, 2004), but relatively limited seabird telemetry from that region may have contributed to its appearance as a coldspot for seabird abundance during the summer–autumn, although overall it was a species diversity hotspot. There is also a dearth of marine predator telemetry data above 75°N compared to lower latitudes; therefore, focused tagging efforts of marine predators at these high latitudes are needed to reveal critical habitat and areas of importance in these typically ice-covered seas.

Third, we recognize that key site identification is an iterative process that is refined with the addition of more data from any single type of approach, and benefits from pooling multiple data approaches. In this context, we offer the analyses here as one layer of data synthesis for top marine predators in North American Arctic waters based on available telemetry data. Compiling individual telemetry data sets with other sources of relevant location data, including at-sea observation data, aerial survey data, passive acoustic monitoring, independent fisheries surveys, primary production, environmental variables and Inuit ecological knowledge, over a large spatial and temporal scale would further refine the distribution patterns of these mobile marine predators, improving our ability to identify abundance and species diversity hotspots (Hays et al., 2016). For example, future studies determining the environmental drivers of these species diversity hotspots are needed to improve Arctic conservation and to predict how hotspots may change in the future. Moreover, there is a large data gap on movement behaviour of marine fishes compared to marine mammals and seabirds in the Arctic. Ongoing studies by The Ocean Tracking Network have provided insight into the movement ecology of key pelagic and deep-water fishes (Hussey et al., 2018; Kessel et al., 2016; Moore et al., 2016) with implications for fisheries and conservation management (Barkley et al., 2018; Hussey et al., 2017). Continued telemetry studies on Arctic fishes along with other marine predators will further expand our knowledge of the mechanisms and processes that affect Arctic ecosystem structure and function and will improve our understanding of important areas for conservation.

4.4 | Future directions

Retrospective analysis of multispecies telemetry data can reveal important areas of predator occurrence, overlap and high ecological diversity, thereby providing one layer of important information for

identifying potential MPAs, ecological and biological significant areas (EBSAs) and important bird and biodiversity areas (IBAs; Delord et al., 2014; Raymond et al., 2015; Lascelles et al., 2016). Currently, this analytical approach is being implemented by several regional research programmes around the globe: (a) Antarctica (Retrospective Analysis of Antarctic Tracking Data (RAATD)), (b) the Pacific Ocean (Global Tagging of Pacific Predators—GTOPP; Block et al., 2011), and (c) Atlantic and Indian Oceans (BirdLife International; Dias et al., 2017). At present, there are no such large-scale, multispecies efforts across the circumpolar Arctic Ocean. While the analysis presented here provides the most comprehensive data on hotspots of abundance and diversity of Arctic marine predators to date, we urge increased international collaborative effort among Arctic nations to share telemetry resources. Integration of pan-Arctic telemetry and additional data sources will allow ongoing refinement of the process to identify priority areas of high biological importance as well as enable more systematic prioritization of conservation exercises to better select protected areas and enhance Arctic conservation. This process will enable the implementation of appropriate multilevel (i.e., territorial and national) and multinational regulations and adaptive conservation strategies to protect the vulnerable Arctic ecosystem in our rapidly changing world (PAME, 2015).

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DATA ACCESSIBILITY

The Getis-Ord G_i^* analysis outputs for abundance densities and hotspots by species group and abundance and species diversity densities and hotspots across species groups by season are deposited as GIS shapefiles (WGS84 projection) at Yurkowski et al. (2018): <https://doi.org/10.6084/m9.figshare.7130402>.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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