Long-distance movements and associated diving behaviour of ringed seals (*Pusa hispida*) in the eastern Canadian Arctic

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Abstract

Animal distribution and movement facilitate energy- and nutrient-transfer within and between regions, thus influencing ecosystem structure and function. Ringed seals (*Pusa hispida*) have been observed making sustained, extensive migrations (> 1000km) in the western Canadian

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Arctic, but observations of their movements from the eastern Canadian Arctic are limited. We equipped 12 ringed seals with satellite telemetry tags in Resolute Bay ($n = 7$; 2012, 2013) and Tremblay Sound ($n = 5$; 2017, 2018), Nunavut, to monitor their movements, behavioural states, and diving behaviour from late summer until their spring moult. Six tags transmitted into winter and recorded long-distance movements to southeastern Baffin Island, with three seals travelling through central Baffin Bay (3608 ± 315 km; maximum 4226 km), while three travelled along the Baffin Island coastline (3674 ± 655 km; maximum 4872 km). Seals that travelled through central Baffin Bay made shallower dives (25.4 ± 1.1 m) than those that travelled near the coast (100.0 ± 4.1 m, respectively). Results provide new information on the variability, scales, and pathways of movement and diving behaviour of eastern Canadian Arctic ringed seals. This new knowledge can be used to inform spatial conservation and management priorities of this ecologically- and culturally-important species.

Key words: animal movements, biotelemetry, foraging, marine mammal, state-space model

Introduction

Quantifying animal movement is essential to understand the dynamic structure of ecosystems (Nathan et al. 2008; Wilmers et al. 2015). Marine environments consist of a heterogeneous distribution of resources shaped by spatiotemporal variation in oceanographic conditions that ultimately influence the abundance, movement, and behaviour of species. As animals move, they facilitate the transport of nutrients within and across ecosystems (Doughty et al. 2016). For example, anadromous fishes transport marine nutrients to riverine and terrestrial systems (Darimont et al. 2003; Hanson et al. 2010), whales transport nutrients from deep ocean basins to surface waters (Roman and McCarthy 2010), while reef sharks transfer resources from pelagic to reef systems (McCauley et al. 2012). These connections, however, are particularly difficult to observe in the marine environment due to the great depth, remoteness, expanse, and opacity of ocean ecosystems. Satellite telemetry provides a key tool to overcome these difficulties in understanding basic natural history, allowing monitoring of individuals and indirect observation of animal movement and behavior in relation to environmental conditions across marine environments (Cooke et al. 2004; Hussey et al. 2015).

Given their often-large spatial ranges, marine mammals integrate broad biophysical processes across systems into interpretable metrics; therefore, some species can act as sentinels of environmental change in marine ecosystems (Moore 2008; Hazen et al. 2019; Moore and Kuletz 2019). Arctic marine mammals have adapted to extreme intra-annual fluctuations in environmental conditions, such as seasonal ice-cover and daylight – key features that affect their movement ecology (Moore 2008). For example, narwhal (*Monodon monoceros*) exhibit annual migrations between the winter pack ice in northern Baffin Bay and the open-water fjords and bays between Lancaster Sound and Peel Sound (Heide-Jørgensen et al. 2003). As climate change has modified oceanographic processes in the Arctic at an accelerating pace, including

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dramatically reduced summer sea ice, increased freshwater inputs, surface-layer warming, and altered sedimentation (Wassmann et al. 2011; IPCC 2014), significant trophodynamic shifts have occurred, including alterations to zooplankton communities and changing interactions due to northward range expansions of Subarctic species (Blanchard 2015; Kortsch et al. 2015; Pecl et al. 2017; Yurkowski et al. 2018). It is, therefore, important to establish reference information on movements and dive behaviour of Arctic marine mammals relative to the environment to determine key areas of habitat use, nutrient transfer, and connectivity between populations and systems, as well as the potential for overlap with predators, competitors, conspecifics, and human influences.

The pagophilic ringed seal (*Pusa hispida*) is widely distributed, highly abundant, and occupies a diversity of habitats, ranging from shallow coastal zones to deeper ocean basins during the open water period and land-fast ice to moving pack-ice during the ice-covered period (Smith 1987). As a result of their dependence on sea ice and their sensitivity to changes in snow and ice conditions (McLaren 1958; Smith 1987; Chambellant et al. 2012; Iacozza and Ferguson 2014; Reimer et al. 2019), ringed seals act as an indicator species of environmental change in Arctic ecosystems (Laidre et al. 2008). After the energetically-expensive spring breeding and moulting periods, when energy reserves are expended and blubber is thinnest (Young and Ferguson 2013), ringed seals move among prey patches during the open-water season in summer and fall (Yurkowski et al. 2016), foraging intensively to rebuild energy stores (Smith 1987; Freitas et al. 2008). Throughout the open-water period, both adult and subadult seals make extensive movements into open water, presumably to forage (e.g. Teilmann et al. 1999, Gjertz et al. 2000, Kelly et al. 2010, Crawford et al. 2012, Harwood et al. 2012, Hamilton et al. 2015). During the winter, their movements are more variable, with seals establishing territories and

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maintaining breathing holes in the shore-fast ice, moving throughout the pack ice, or moving into open water (McLaren 1958; Kelly et al. 2010; Crawford et al. 2012; Harwood et al. 2015).

Here, we describe the movements and dive behaviour of ringed seals in the less-studied Eastern Canadian Arctic. With the aid of Inuit partners, ringed seals were equipped with satellite telemetry tags during summer in the Tallurutiup Imanga National Marine Conservation Area (Lancaster Sound), Nunavut, Canada and were tracked to southeast Baffin Island. We fit a two-state switching Bayesian state-space model (BSSM) to satellite-telemetry-derived location data for 12 ringed seals to examine their movements and identify periods of area-restricted movement in addition to investigating diving parameters. Specifically, we compared individual movements, movement paths, and behavioral states, as well as mean daily dive depth and duration and mean daily surface duration. Results will improve our understanding of Eastern Canadian Arctic ringed seal movement ecology and connectivity within and between high- and low-Arctic areas and act as a foundation for future comparative research.

Materials and Methods

Tagging

A total of 12 ringed seals were captured using 12"-stretched monofilament nets set perpendicular to shore. In 2012 and 2013, 7 ringed seals were tagged in Resolute Bay (74.6973° N, 94.8297° W), Nunavut, Canada, and, in 2017 and 2018, 5 ringed seals were tagged in Tremblay Sound (72.4548° N, 80.8886° W), Nunavut, Canada. Nets were set in relatively shallow water (~6 m depth) and were monitored continuously. Upon capture, nets were pulled in by hand and seals were restrained for subsequent processing. Morphometric information was recorded, including approximate standard length (measured dorsally from nose to tip of tail), axillary girth, and body weight (Committee on Marine Mammals 1967). Claw growth annuli

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were counted to estimate age (McLaren 1958). A satellite telemetry transmitter (STT; SRDL-9000x Sea Mammal Research Unit, St. Andrews, Scotland) was attached to the fur dorsally between the scapulae, using five-minute epoxy glue after rinsing the area with acetone. Time-depth recordings, such as dive depth (registered at depths > 4 m) and dive duration, were sampled every 4 s. Surface duration was classified as the length of time the individual was between 0 – 4 m before the next dive or haul-out. Tags transmitted to satellites when ringed seals were at the surface and the tag's saltwater switch was dry. Tags were programmed to transmit up to 225 times per day, and locations were estimated via the Argos satellite system.

Data Analysis

Ringed seal telemetry tracks were analysed using Bayesian state-space modelling (BSSM) in the package *bsam* v 1.2.2 (Jonsen et al. 2005, 2013; Jonsen 2016) in R v 3.6.1 (R Core Team 2019). Markov chain Monte Carlo (MCMC) sampling methods using Just Another Gibbs Sampler (JAGS) were performed to estimate movement parameters and behavioral state (area-restricted movement vs. transiting) for each ringed seal based on turning angles (Jonsen et al. 2013). Seal tracks with high turning angles between locations were classified as area-restricted movement behaviour, whereas low turning angles between locations were classified as transiting behaviour. Analysis was performed at a time-step of 12 h, an approach common in ice-covered environments (Bestley et al. 2013). Two MCMC chains were run for 30,000 iterations, with a burn-in of 20,000, and every 10th sample from the remaining 10,000 used for parameter estimation. Chain convergence and autocorrelation were assessed visually via trace and autocorrelation plots, and chain convergence for each parameter was estimated by Gelman and Rubin's potential scale reduction factor, which was < 1.1 for all parameters (Gelman et al. 1992; Brooks and Gelman 1998). The BSSM calculates a continuous probability behavioral state value

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between 0 (travelling) and 1 (area-restricted movement), where a value ≥ 0.5 is presumed to be lingering in the area, either resting or actively foraging.

Behavioural state maps for each ringed seal were examined in ArcGIS Pro (v 2.4.2) to determine the date and timing of long-distance movements southward. The starting-date of these long-distance movements was chosen as the first day that each individual (i.e., individuals that made southward movements to southern Baffin Island, hereafter termed long-ranging individuals) began moving southward or eastward into central Baffin Bay after a period of area-restricted movement (i.e., behavioural state ≥ 0.5 for one or more consecutive days). Seals whose tags ceased transmitting in October were excluded from this portion of the analysis and are hereafter termed short-duration individuals. Tracks were then overlaid onto sea ice maps to determine local sea ice concentration at the start of these long-distance movements. For individuals that appeared to reach a destination, exhibiting area-restricted movement behaviour for an extended period of time following long-distance movements, we calculated the mean local sea-ice concentration during this period by extracting sea-ice concentration in each sea-ice grid cell of the area of residency once per week for the duration of the resident period. Sea ice data for 2012-2014 were obtained from the National Snow and Ice Data Centre (NSIDC; www.nsidc.org) and for 2017-2019 were obtained from EUMETSAT Ocean and Sea Ice Satellite Application Facility (OSI SAF; www.osi-saf.org). All sea ice data were acquired from satellites via Special Sensor Microwave Imager (SSM/I). Spatial resolution for 2012-2014 was 25 km and for 2017-2019 was 10 km.

Distances travelled (calculated as the sum of Euclidean distances between successive locations for each track), movement rates, and percentage of time spent in an area-restricted movement state were calculated using estimated locations from state-space models. Ringed seal

diving data were compiled for each day of the tagging period. Mean daily dive depth (m), mean daily dive duration (s), and mean daily surface duration (s) were examined. Dive and movement data were checked for normality and homoscedasticity using Shapiro-Wilk tests of normality and Levene's test for homogeneity of variance, and an ordered quantile normalization transformation (Peterson and Cavanaugh 2019) was applied to movement rates and all dive parameters prior to statistical tests. T-tests and linear mixed-effects models, with seal ID as a random effect, were used to compare distances travelled, movement rates, percentage of time spent conducting area-restricted movements, and dive parameters between long-ranging and short-duration ringed seals, as well as between long-ranging ringed seals before, during, and after their travel southward to southeast Baffin Island. Results are reported as mean ± standard error (SE) of non-transformed data throughout. Analyses were performed using R v 3.6.1 (R Core Team 2019).

Results

Twelve ringed seals were captured and tagged, of which 10 were subadults (8 male and 2 female) and 2 were adults (1 male and 1 female). Deployment durations for tagged ringed seals ranged from 19 to 248 days and averaged 96.3 ± 21.9 days (Table 1). Excluding days where no transmissions were received, total tracked days ranged from 19 to 205 days and averaged 81.6 ± 17.1 days (Table 1). All ringed seals were tagged in August or September, with the two longest-transmitting tags providing data until May of the following year. Total distances travelled by all ringed seals throughout the tagging period averaged 2171 ± 481 km (range: 166 – 4872 km; Table 2).

Transmissions for the short-duration individuals (1 adult and 5 subadults) ceased in October (16 October ± 3.5 d; range: 4 October – 26 October) while in Parry Channel and nearby areas, having moved relatively short distances prior to transmission termination (Table 1, 2, Fig.

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1). These individuals travelled an average distance of 702 ± 465 km (range: 166 –1574 km; Table 2). The dates on which long-ranging seals initiated their travel southward ranged from 19 September to 25 November (14 October ± 9.6 d; Table 2). Local ice concentration at the start of these movements was highly variable, ranging from 0 to 75+ % (29.2 ± 14.5 %; Fig. 2). Long-ranging ringed seals travelled, on average, 1209 ± 252 km (range: 649 – 2021 km; Table 2) before moving southward. During their southward movement, distance travelled averaged 2023 ± 175 km (range: 1637 – 2577 km; Table 2), while, after reaching southeastern Baffin Island, seals moved much less (614 ± 339 km; range: 143 – 1587 km; Table 2).

Ringed seals varied markedly in their movement paths, with three of the six long-ranging individuals moving south along the coast of Baffin Island (107840, 159284, 159289), while the other three moved into the open water of Baffin Bay (107832, 107836, 107839), one of which reached the coast of Disko Island, Greenland (107839; 69.8319° N, 53.9962° W; Fig. 1). Long-ranging ringed seals moved along a similar eastward path into central Baffin Bay but diverged as they moved south (Fig. 1), with most having different final destinations. One subadult (est. age 0; 107832) reached Angijak Island (65.6729° N, 62.3339° W) on 2012-11-25 (36 d of long-distance travel) and remained there for ~4 months (mean local sea-ice concentration: 90.4 ± 4.5 %), with tag transmissions terminating on 2013-03-27. For two individuals, 107836 (subadult, est. age 0) and 159284 (subadult, est. age 3), tags stopped transmitting near Brevoort Island (63.4626° N, 64.2982° W) on 2013-12-01 (58 d of long-distance travel) and 2017-12-31 (36 d of long-distance travel), respectively, with 107836 having inhabited this area for ~2 weeks (mean local sea-ice concentration: 7.3 ± 6.7 %). Seal 107839's (subadult, est. age 1) tag stopped transmitting east of Resolution Island (61.5087° N, 64.9475° W) on 2013-11-09 (44 d of long-distance travel) while still in transit. Two long-ranging ringed seals reached and spent a

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significant amount of time overwintering in Cumberland Sound: one (107840; adult, est. age 7) entered Cumberland Sound on 2014-01-02 (78 d of long-distance travel) and inhabited the moving ice areas of Cumberland Sound for ~3 months (mean local sea-ice concentration: 88.1 ± 2.5 %) before moving northward on 2014-04-08, with transmissions ceasing on 2014-05-06 near Qikiqtarjuaq (67.5556° N, 64.0257° W); the second individual (159289; subadult, est. age 4-5) entered Cumberland Sound on 2018-12-13 (62 d of long-distance travel) and stayed near its mouth, around Abraham Bay (65.1394° N, 64.3613° W), for ~5.5 months (mean local sea-ice concentration: 83.9 ± 2.2 %) before the tag ceased transmitting on 2019-05-25.

Distance travelled was not biased by tag duration, as there was no significant difference in distance travelled between short-duration ringed seals (702 ± 214 km) and long-ranging ringed seals prior to their travels southward (1209 ± 252 km; $t = 1.5$, df $= 9.7$, $p = 0.16$). Daily movement rate, however, differed between short-duration ringed seals (16.6 ± 1.3 km/d) and long-ranging ringed seals before their travels southward (23.7 ± 1.1 km/d; $t = 7.2$, df $= 430.9$, $p < 0.0001$). While the three long-ranging ringed seals that moved into central Baffin Bay and then southward (107832, 107836, 107839) made relatively fast, directed movements, the other three that travelled southward along Baffin Island (107840, 159284, 159289) made more gradual and meandering movements, with multiple periods of area-restricted movement both in and outside of fjords.

Movement rates for long-ranging seals varied significantly by travel period ($F_{2,847.0} = 159.3$, $p < 0.001$), with individuals moving fastest during their travel southward (39.8 ± 1.3 km/d) compared to before and after (23.7 ± 1.1 km/d and 9.7 ± 0.7 km/d, respectively). Post-hoc analysis identified significant differences in movement rates between all pairwise time-period comparisons ($p < 0.0001$). Time spent exhibiting area-restricted movements also differed

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between travel periods for long-ranging ringed seals ($F_{2,8.6} = 10.3$, $p < 0.01$). Post-hoc analysis revealed that this difference was significant between the during (31.1 ± 10.4 %) and after (88.5 ± 6.2 %) periods ($p < 0.01$). In addition, although coastal-travelling long-ranging seals appeared to spend more time exhibiting area-restricted movement during long-distance movements (49.1 ± 7.7%) than those that travelled through central Baffin Bay (13.2 ± 12.5 %), this difference was not statistically significant ($t = -2.5$, df = 3.3, $p = 0.08$), likely as a result of the low statistical power resulting from a low sample size.

In total 78,751 dives were recorded by ringed seals during the study period. Individual seals made, on average, a minimum of 6560 ± 1380 dives throughout their respective tagging period (range: 2257 – 17,115; Table 2). Dive depth was plotted against dive duration, and 28 unrealistic dive outliers (e.g., 782 m in 8 s, 750 m in 240 s) were identified and removed from the dataset. From the remaining data ($n = 78,723$), the maximum dive depth was 558 m in 1020 s (17 min) by an adult male ringed seal (Table 2). Maximum depth reached by each seal averaged 294 m $\pm$ 38 m. Overall, 70.5% of all recorded dives were shallower than 50 m depth, 82.9 % were shallower than 100 m, 93.6 % were shallower than 200 m, and 98.7 % were shallower than 300 m.

Similar to distance travelled, mean daily surface duration did not appear to be biased by tag duration, with short-duration seals spending similar amounts of time at the surface between dives (77.0 ± 1.8 s) compared to long-ranging seals before their travel southward (83.4 ± 4.1 s; $t = 1.1$, df = 331.2, $p = 0.28$, Fig. 3). Differences in correlated variables of mean daily dive depth and mean daily dive duration (Kendall rank correlation, $z = 35.8$, $\tau = 0.70$, $p < 0.0001$) were observed between short-duration seals (23.2 ± 1.1 m) and long-ranging seals prior to their travel southward (68.3 ± 3.2 m; $t = 13.4$, df = 483.9, $p < 0.0001$; Fig. 3). This difference was primarily

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driven by the three coastal-travelling long-ranging seals (107840, 159284, 159289; Fig. 3) that dived deeper on average prior to their travel southward (100.0 ± 4.1 m) than did long-ranging seals that travelled through central Baffin Bay (25.4 ± 1.1 m; $t = 19.8$, df = 286.5, $p < 0.0001$). Similarly, mean daily dive duration was greater for long-ranging seals prior to their travel southward (228.8 ± 7.2 s) than for seals tagged for a shorter duration (137.7 ± 4.4 s; $t = 10.1$, df = 472.5, $p < 0.0001$; Fig. 3). This, again, was driven by the coastal-travelling long-ranging seals, which made longer dives during this movement period (307.4 ± 8.1 s) than those that travelled through central Baffin Bay (122.5 ± 2.9 s; $t = 20.3$, df = 291.1, $p < 0.0001$).

Long-ranging ringed seals differed in mean daily dive depth throughout their travel southward ($F_{2,957.8} = 140.1$, $p < 0.0001$), with mean daily dive depths of 68.3 ± 3.2 m, 78.5 ± 3.2 m, and 46.9 ± 2.4 before, during, and after, respectively (Fig. 3). Post-hoc analysis showed significant differences between the before and after periods ($p < 0.0001$) and between the during and after ($p < 0.0001$) periods. There were also significant differences in mean daily dive duration for long-ranging seals throughout their travel southward ($F_{2,\,957.6} = 43.3$, $p < 0.0001$), with mean daily dive durations of 228.8 ± 7.2 s, 278.8 ± 8.9 s, and 221.6 ± 7.1 s before, during, and after, respectively (Fig. 3). Post-hoc analysis revealed that mean daily dive duration after southward travel was significantly lower than mean daily dive duration before ($p < 0.0001$) and during ($p < 0.0001$). Mean daily surface duration varied by travel period as well ($F_{2,959.6} = 109.4$, $p < 0.0001$), with seals spending 77.0 ± 1.8 s, 77.8 ± 1.9 s, and 139.2 ± 4.1 s at the surface between dives before, during, and after their travel southward, respectively (Fig. 3). This was driven by mean daily surface duration in the after period, as values in this period were significantly greater than both the before ($p < 0.0001$) and during ($p < 0.0001$) periods.

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Discussion

Understanding how animals move through time and space is an important requirement of their successful management and conservation. In the present study, we examined the movements and dive behaviour of 12 ringed seals tagged in the Canadian high Arctic near Resolute Bay and Tremblay Sound, Nunavut to improve understanding of travel pathways, scales of movements, and the level of inter- and intra-individual variation in movement dynamics. Half of the tags (6/12) transmitted for only 1-2 months, at which point the seals were still in high-Arctic areas of Parry Channel and Barrow Strait. Tags on the remaining individuals (6/12) recorded data for much longer and captured long-distance movements to southern Baffin Island, with different final locations recorded. Notably, three of these long-ranging ringed seals travelled into central Baffin Bay and southward, while the other three travelled southward along the coast of Baffin Island. The three seals that travelled through central Baffin Bay made shallower and shorter dives than those that travelled southward along the Baffin Island coast. Distances travelled and the dates of their travel southward relative to sea ice concentration were also variable. Possible reasons for these differences in movement are numerous and likely include a combination of both abiotic and biotic drivers. Results indicate that while many ringed seals may exhibit long-distance movements southward from the high Arctic, individuals vary in their movement strategies and do not appear to follow a singular route, as was observed in the western Canadian Arctic (Harwood et al. 2012), or reach a similar southern destination.

Long-distance movements by ringed seals have been documented in other Arctic regions, including the Beaufort and Chukchi Seas (subadults: 2793 km, adults: ~1500 km, Harwood et al. 2012; adults: ~1700 km, Kelly et al. 2010), Northern Baffin Bay (subadults: ~2500 km, Teilmann et al. 1999), the Bering and Chukchi Seas (subadults: ~1000 km, Crawford et al.

2012), and Svalbard (subadult: 5393 km, Hamilton et al. 2015; adult: ~1500 km, Gjertz et al. 2000), though, in most instances, recorded movements are typically < 500 km (Heide-Jørgensen et al. 1992; Gjertz et al. 2000; Freitas et al. 2008). Ringed seals tagged at higher Arctic latitudes travelled longer distances and have higher movement rates than those tagged at lower Arctic latitudes (Yurkowski et al. 2016; Ferguson et al. 2019). In the present study, ringed seals made one-way long-distance movements of approximately 1769 – 3518 km, some of the longest recorded distances observed for both subadults and adults. Most notably, an adult male ringed seal travelled from Resolute Bay to Cumberland Sound, which, excluding foraging stops in bays and fjords along Baffin Island, represents a distance of approximately 2200 km. To our knowledge, this is one of the longest recorded one-way movements by an adult male ringed seal. In contrast to adult ringed seals, subadults commonly travel long distances (Teilmann et al. 1999; Crawford et al. 2012; Harwood et al. 2012; Hamilton et al. 2015), as they do not need to establish territories for mating and are competitively excluded from land-fast ice areas by adult seals during winter (Smith et al. 1991). Although the greatest distance travelled in the present study was by an adult seal, low sample sizes did not allow for statistical comparison between adult and subadult age-classes.

The adult male that travelled the greatest distance also undertook the deepest dive, reaching a depth of 558 m. Dives of this depth are relatively uncommon for this species and are likely near the limit of ringed seals' diving capabilities (Hammill 2018). While a few studies have documented maximal depths similar to this (e.g., 500+ m, Born et al. 2004; 542 m, Harwood et al. 2015), the vast majority of recorded dives are below 100 m, with occasional dives deeper than 300 m (Gjertz et al. 2000; Born et al. 2004; Benoit et al. 2010; Harwood et al. 2012; Hamilton et al. 2016; Crawford et al. 2019). This trend was confirmed by the data in this study.

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As an adult male, its large body size likely allowed it to reach these depths, as larger seals are typically able to dive deeper due to increased physiological capabilities compared to smaller seals (Lydersen et al. 1992; Kelly and Wartzok 1996).

Ringed seals that travelled southward took different routes, displaying either a coastal movement behaviour along Baffin Island or an offshore movement behaviour through central Baffin Bay. The reasons for these two distinct movement behaviours are unclear, but possible explanations include surface currents, competition, predator avoidance, ice conditions, and foraging strategies. Based on the present data, however, there is insufficient information to further test these hypotheses and whether individual or interacting factors drive observed movements. Sea surface current directions in Baffin Bay do not overlap with the directionality of ringed seal movements to a large extent, particularly for those that travelled through open water (Fig. 1; Aksenov et al. 2010; Hamilton and Wu 2013), and few studies have documented current-following in pinnipeds (e.g., northern fur seal, *Callorhinus ursinus*; Ream et al. 2005). There is also insufficient evidence to support competitive exclusion of subadults by territorial adult seals (Krafft et al. 2007) driving open-water movements; ringed seals that travelled offshore did not appear to make initial attempts to travel along the coast. Crawford et al. (2012) similarly found that territoriality by adult ringed seals did not adequately explain long-distance movements by subadults in the Bering and Chukchi Seas. Based on the time of year and associated ice conditions when individuals initiated their travel southward, it seems unlikely that predator avoidance could explain these open-water paths. Polar bears (*Ursus maritimus*), the main predators of ringed seals, hunt on the sea ice most intensely from May to July (Hammill and Smith 1991; Smith and Lydersen 1991; Messier et al. 1992; Galicia et al. 2015). Ringed seals began their movements before ice had formed in the area, suggesting that predation risk was low

during their travel south. Furthermore, ice conditions at the initiation of their travel southward varied considerably between individuals, suggesting that ringed seals do not conform to a single strategy of ice association and instead exhibit individual variation in their movement and behaviour. We accept, however, that the low number of tags that transmitted long enough to capture long-distance movements may be too low to identify a pattern. To our knowledge, no other study has assessed sea-ice concentration as a trigger for long-distance movements in ringed seals, although it has been examined in belugas (Bailleul et al. 2012; Hauser et al. 2017), and further study is needed. Increased foraging opportunities could explain this movement, and, although we do not have the data to determine this with certainty, patterns of dive behaviour and behavioural state results support this as a potential explanatory factor, both for routes taken and final destinations.

In summer and early fall, ringed seals spent more than half of their time exhibiting area-restricted movement behavior, with intermediate daily movement rates, behavioural states, and diving parameters compared to other time periods. At this time, seals were likely foraging intensively to rebuild fat stores following the spring fasting season, which occurs primarily from April to June (McLaren 1958; Welch et al. 1992; Quakenbush et al. 2011; Young and Ferguson 2013).

During fall and early winter, daily movement rates of long-ranging seals were at their highest, and, correspondingly, time in area-restricted movement behaviour was at its lowest. For open-water seals, dives were shorter and shallower than those of coastal-travelling seals. Ringed seals are known to switch from deeper, benthic feeding to pelagic feeding depending on their local environment and prey availability (McLaren 1958). The observed patterns in diving suggest that open-water seals might be foraging on pelagic prey, such as amphipods, requiring shallower

dives (McLaren 1958; Auel and Werner 2003; Ogloff et al. 2019). In support, one of the main amphipod prey species (Siegstad et al. 1998; Wathne et al. 2000; Holst et al. 2001; Labansen et al. 2011; Ogloff et al. 2019) of ringed seals, *Themisto libellula*, is common in the upper 25 m of the pelagic environment (Wathne et al. 2000; Auel and Werner 2003; Havermans et al. 2019), which overlaps with the mean daily dive depth (25.4 m) of ringed seals that travelled through central Baffin Bay. In contrast, the coastal-travelling seals, which more-often occupied shallower water over the shelf and in bays and fjords along Baffin Island, were able to dive to the sea floor and access benthic prey fish, such as *Boreogadus saida* and sculpin (McLaren 1958; Wathne et al. 2000; Labansen et al. 2011; Ogloff et al. 2019). Similar findings were documented for ringed seals in the North Water Polynya (Born et al. 2004). Importantly, however, vertical overlap with prey does not confirm with certainty that ringed seals forage extensively during this time, as ringed seals are known to make travel dives, defined by their directionality and relatively shallow depth (Kelly and Wartzok 1996; Simpkins et al. 2001). The short surface duration during long-distance movements, in addition to relatively shallow diving and seals being predominantly in a travelling behavioral state (~69% of time), may provide evidence for this type of movement.

During the winter and early spring, the four tags that were still transmitting recorded extended periods of residency of 2 weeks up to ~5.5 months in an area. Surface duration and time exhibiting area-restricted movement behaviour were at their highest, while daily movement rate, distance travelled, mean daily dive depth, and mean daily dive duration were at their lowest. Given that these periods of residency occurred primarily in winter, with high sea-ice concentrations, it is possible that individuals were spending more time hauled out, maintaining breathing holes, or moving throughout the pack ice (McLaren 1958). Specifically, seal 107832, an immature individual, spent ~ 4 months at Angijak Island before tag transmissions stopped in

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late March. Based on timing, this individual was likely foraging and building fat reserves in preparation for the spring moult, which takes place from mid-May to mid-July (McLaren 1958). Seal 107836 remained near Brevoort Island for ~2 weeks in late November, perhaps foraging in the mostly-open water in preparation for winter (McLaren 1958). Two ringed seals (159289 and 107840) resided in Cumberland Sound for a large portion of the winter (~5.5 and ~3 months, respectively). A mature male, 107840, moved clockwise around Cumberland Sound over the winter before exiting and travelling northward and residing near Qikiqtarjuaq for a short time before tag transmissions stopped. As this ringed seal was mature, it is likely that this extensive residency in Cumberland Sound served to build energy reserves in preparation for spring breeding, which may have occurred while still in Cumberland Sound, and the following moult, which may have occurred near Qikiqtarjuaq. In contrast, the subadult, 159289, stayed in a small area near the mouth of Cumberland Sound for almost 6 months in the land-fast ice, most likely maintaining a breathing hole and foraging, before transmissions stopped in late May, perhaps during moulting (McLaren 1958). As noted previously, subadult ringed seals are often excluded from prime mating and feeding territory by larger, aggressive conspecifics as early as ice-formation in the fall, resulting in subadults being relegated to peripheral habitats with less-stable sea ice (McLaren 1958; Smith 1987; Smith and Lydersen 1991; Krafft et al. 2007; Kelly et al. 2010; Crawford et al. 2012). This could explain why subadults tended to occupy peripheral areas throughout the study area, while the adult male moved deep into Cumberland Sound. Both adult and subadult ringed seals can also occupy the pack-ice during the breeding season (Finley et al. 1983), so it is possible that seal 159289 was a young adult employing this strategy.

Long-distance southward movements by ringed seals in the high Arctic facilitate the transfer of nutrients and genes from the high Arctic, where the greatest fat deposition occurs

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during intensive foraging in the open-water season, to lower latitudes, where seals may breed or are more likely to be consumed by predators (Smith and Hammill 1981; Furgal et al. 1996; Young and Ferguson 2013; Pilfold et al. 2014; Galicia et al. 2015). Tags deployed on seals 107839 and 159284 stopped transmitting at Resolution Island and Brevoort Island, respectively, while seals were still in transit, so it is unclear whether they displayed any residency behaviour to these areas or elsewhere. Seal 107839, having reached the southernmost tip of Baffin Island while still in a transiting state when its tag stopped transmitting, may have been travelling into Hudson Strait, Ungava Bay, or the Labrador Sea. This suggests that mixing between high-Arctic and low-Arctic ringed seals may occur; however, this individual was immature and more data for adult individuals would be required to confirm this.

It is not known whether these long-distance travels southward represent seasonal migrations, with seals returning northward and transferring nutrients from the low Arctic to the high Arctic. Inter-annual site fidelity to breeding or foraging areas has been documented for ringed seals in other areas of the Arctic (Smith and Hammill 1981; Krafft et al. 2007; Freitas et al. 2008; Kelly et al. 2010; Harwood et al. 2015), suggesting that some seals do return to the same area across multiple years. It is also unknown how common this long-distance movement strategy is for high-Arctic ringed seals and whether tagging site or year might influence observed patterns. Given that the behaviour of short-duration ringed seals differed little from the behaviour of long-ranging seals prior to their travel southward, and that all tags that transmitted throughout the fall and winter captured a long-distance movement, it is plausible that many of the ringed seals that summer around northern Baffin Island make similar long-distance travels. Increased sample sizes in future studies would be needed to quantify how common this movement strategy is for high-Arctic ringed seals, as some individuals also overwinter in our high-Arctic study area

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(Kelly et al. 2010; Young et al. 2019; Yurkowski et al. 2019), and would allow for comparison among age classes, high-Arctic locations, and years. Given the scale of ringed seal movements, the proximity of Resolute Bay and Tremblay Sound (< 500 km), and the overlap in ringed seals' movement paths around northern Baffin Island during summer and early fall (prior to southward movements), we suspect that tagging location would not be a significant predictor of long-distance southward movements by ringed seals.

These preliminary data suggest flexibility and high variability in ringed seal movement behaviour among individuals, which may allow ringed seals to adjust to changing sea ice conditions during long-distance travels; however, the strong association between ringed seals and sea ice (McLaren 1958; Smith and Stirling 1975) for breeding may concurrently limit their resilience to these changes. Future studies in the high Arctic should aim to increase sample sizes and age and sex representation while incorporating environmental data, prey distribution, and physiology/energetics into analyses. This study provides an improved understanding of the natural history and movements of eastern Canadian Arctic ringed seals, the main prey of polar bears and an important subsistence species for harvesters in Nunavut. An important aspect of this study is the inclusion of local expertise and Indigenous knowledge by working directly with Indigenous partners to capture and tag seals. Understanding the general movement ecology of ringed seals will allow for more well-informed and effective management and conservation of ringed seals given impending ecological challenges, such as increased shipping traffic, oil exploration, development, and climate change.

Acknowledgements

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Tables and Figure Captions

Table 1: Morphometric data and tracking durations of 12 ringed seals tagged (SMRU-SRDL-9000x) in Tremblay Sound ($n = 5$; 2017 and 2018) and Resolute Bay ($n = 7$; 2012 and 2013), Nunavut.

Table 2: Distance travelled, movement rate, time spent exhibiting area-restricted movement (ARM), number of recorded dives, and maximum dive depth for 12 ringed seals tagged (SMRU-SRDL-9000x) in Tremblay Sound ($n = 5$; 2017 and 2018) and Resolute Bay ($n = 7$; 2012 and 2013), Nunavut. Tags were deployed in August or September of the respective year and transmitted from 19 to 243 days. Initiation date of long-distance movements (LDM) correspond to the dotted vertical lines in Figure 2.

Figure 1: Behavioural state and movements of 12 tagged ringed seals tagged in Tremblay Sound ($n = 5$; 2017 and 2018) and Resolute Bay ($n = 7$; 2012 and 2013), Nunavut. Red line segments denote area-restricted movement (ARM) behaviour, whereas blue line segments denote transiting behaviour. Tags (SMRU-SRDL-9000x) were deployed in August or September of the respective year and transmitted from 19 to 243 days. The end point of each track is denoted by a red or green "x" for seals tagged for long or short durations, respectively. Orange (warm) and bright blue (cold) arrows in the inset refer broadly to surface currents, based on Hamilton and Wu (2013). Map was created using R v 3.6.1 (R Core Team 2019) using a base map from the *rnaturalearth* package (South 2017).

Figure 2: Latitude and longitude of 12 tagged ringed seals tagged (SMRU-SRDL-9000x) in Tremblay Sound ($n = 5$; 2017 and 2018) and Resolute Bay ($n = 7$; 2012 and 2013), Nunavut. Latitude and longitude are plotted on separate panels for each year that seals were tracked, and each line in each panel represents a single tagged seal, coded by color. Tags were deployed in August or September of the respective year and transmitted from 19 to 243 days. Dotted vertical lines indicate the date at which long-ranging seals began their long-distance movement, and ice percentage denoted for each refers to the sea ice concentration at each seals' location at that time. Dotted vertical lines are colored to match each seal track ID for clarity.

Figure 3: Mean daily dive depth (a), mean daily dive duration (c), and mean daily surface duration (c) for 12 ringed seals tagged (SMRU-SRDL-9000x) in Tremblay Sound ($n = 5$; 2017 and 2018) and Resolute Bay ($n = 7$; 2012 and 2013), Nunavut. Tags were deployed in August or September of the respective year and transmitted from 19 to 243 days. The black horizontal lines on each boxplot indicate the median, while the red dotted line is the mean. Whiskers denote the highest and lowest points that fall within $1.5 \times$ inter-quartile range; points outside of this are outliers. The lower and upper limits of the boxes represent the first and third quartiles.

Tables and Figures

Table 1: Ringed seal morphometrics and tagging duration

Tagging Location	Tag ID	Field Sex	Age Class	Claw Age	Approximate Standard Length (cm)	Axillary Girth[a] (cm)	Body Mass (kg)	Deployment Date (Y-M-D)	Date of Last Location (Y-M-D)	Tracking Duration	Days without Location	Total Days Tracked
Tremblay	159283	M	Subadult	5	112	60*	45	2018-08-15	2018-10-04	49	1.5	47.5
Tremblay	159284	M	Subadult	3	91	93.5	40	2017-08-28	2018-01-11	125	28	97
Tremblay	159285	M	Subadult	2	92	94	35	2017-09-09	2017-10-25	45	5	40
Tremblay	159286	M	Subadult	4-5	111	82*	40	2018-08-12	2018-10-14	63	5	58
Tremblay	159289	F	Subadult	4-5	100	58*	40	2018-08-18	2019-05-25	131	45.5	85.5
Resolute	107832	M	Subadult	0	75	77	25	2012-08-01	2013-03-27	238	49	189
Resolute	107833	F	Adult	6	110	112	55	2013-09-05	2013-10-24	49	2	47
Resolute	107834	M	Subadult	2	117	109	59	2012-09-25	2012-10-23	28	1.5	26.5
Resolute	107836	M	Subadult	0	96	93	35	2013-08-30	2013-12-02	93	1	92
Resolute	107838	M	Subadult	0	109	99	50	2012-09-21	2012-10-11	19	0	19
Resolute	107839	F	Subadult	1	101	88	30	2013-08-28	2013-11-09	73	0	73
Resolute	107840	M	Adult	7	120	111	60	2013-09-05	2014-05-06	243	38.5	204.5

[a]Axillary girth refers to the circumference of the animal measured under the pectoral flippers. Values with an asterisk (*) are measurements made dorsally from flipper to flipper, rather than girth.

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Table 2: Tracking and dive parameters for tagged ringed seals

Tag ID	Total Distance (km)	Prior to Long-Distance Movement			During Long-Distance Movement					After Long-Distance Movement			Number of Dives Recorded	Maximum Depth Recorded (m)
		Distance (km)	Mean (SE) Distance Per Day (km/d)	Time in ARM (%)	Initiation of LDM (Y-M-D)	End of LDM (Y-M-D)	Distance (km)	Mean (SE) Distance Per Day (km/d)	Time in ARM (%)	Distance (km)	Mean (SE) Distance Per Day (km/d)	Time in ARM (%)		
159283	1574.4	1574.4	32.1 (4.1)	63.6	-	-	-	-	-	-	-	-	3406	294
159284	3575.4	1826.5	21.7 (2.0)	73.5	2017-11-25	2017-12-31	1748.8	48.6 (4.1)	46.6	-	-	-	5058	462
159285	458.6	458.6	10.2 (2.9)	90.2	-	-	-	-	-	-	-	-	3766	170
159286	1039.4	1039.4	16.5 (2.1)	79.4	-	-	-	-	-	-	-	-	3560	246
159289	2574.4	706.9	12.9 (1.4)	76.4	2018-10-12	2018-12-13	1710.8	29.5 (3.0)	63.5	156.8	12.1 (2.0)	82.1	9180	422
107832	4225.9	2020.6	25.6 (2.1)	32.9	2012-10-19	2012-11-24	1636.7	44.2 (2.9)	1.4	568.6	4.9 (0.5)	97.9	13982	214
107833	653.1	653.1	13.3 (2.4)	83.7	-	-	-	-	-	-	-	-	3070	186
107834	318.6	318.6	11.4 (2.7)	68.4	-	-	-	-	-	-	-	-	2530	186
107836	3402.6	682.9	34.1 (5.0)	32.5	2013-09-19	2013-11-16	2576.5	43.7 (3.1)	38.1	143.2	10.2 (1.2)	100	6837	374
107838	166.4	166.4	8.8 (3.2)	51.3	-	-	-	-	-	-	-	-	2257	170
107839	3196.1	648.6	22.4 (3.9)	54.4	2013-09-26	2013-11-09	2547.5	57.9 (2.1)	0	-	-	-	7962	246
107840	4872.1	1367.4	35.1 (3.3)	47.4	2013-10-14	2013-12-31	1917.3	27.0 (2.3)	37.3	1587.3	14.4 (1.2)	74.1	17115	558

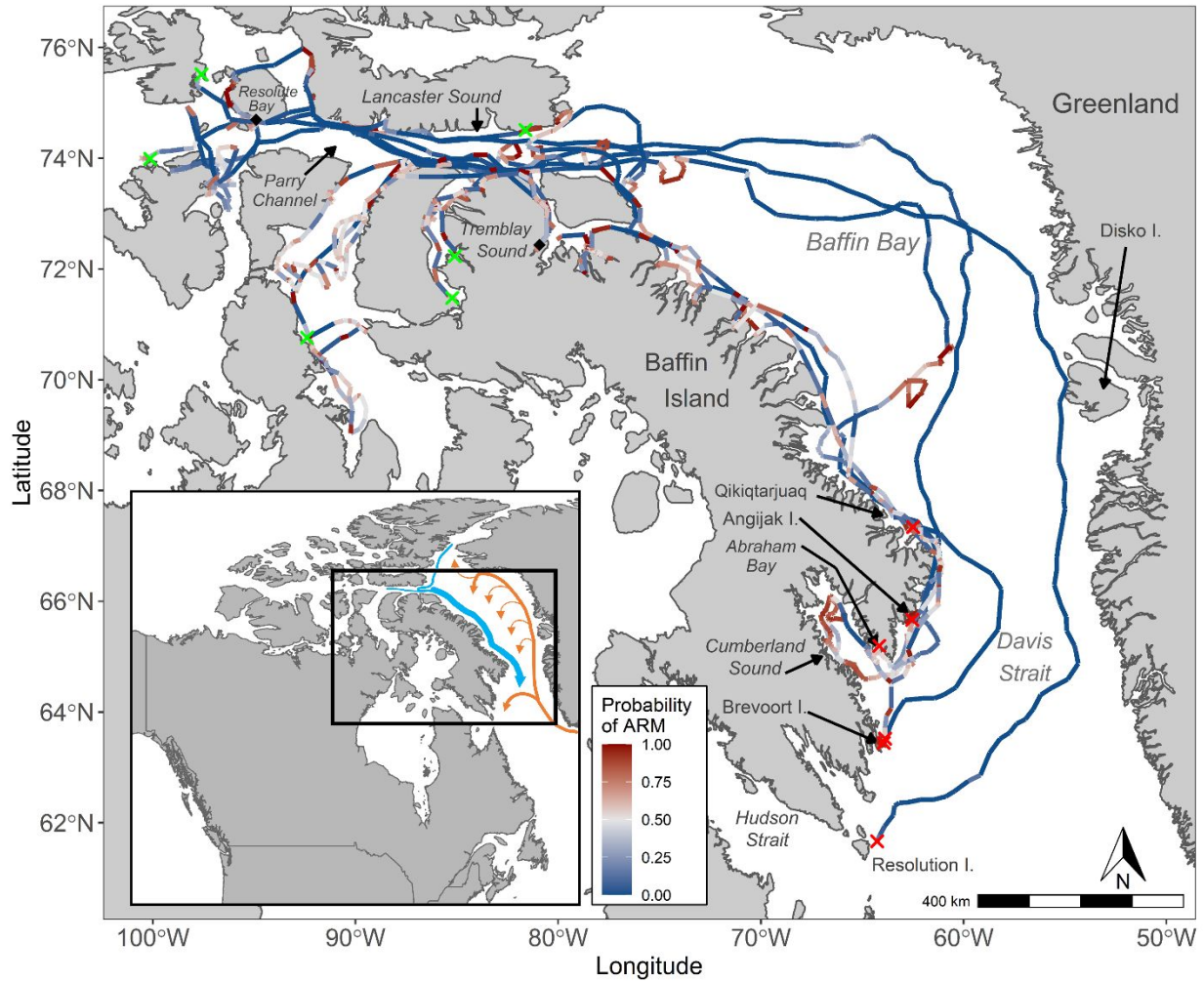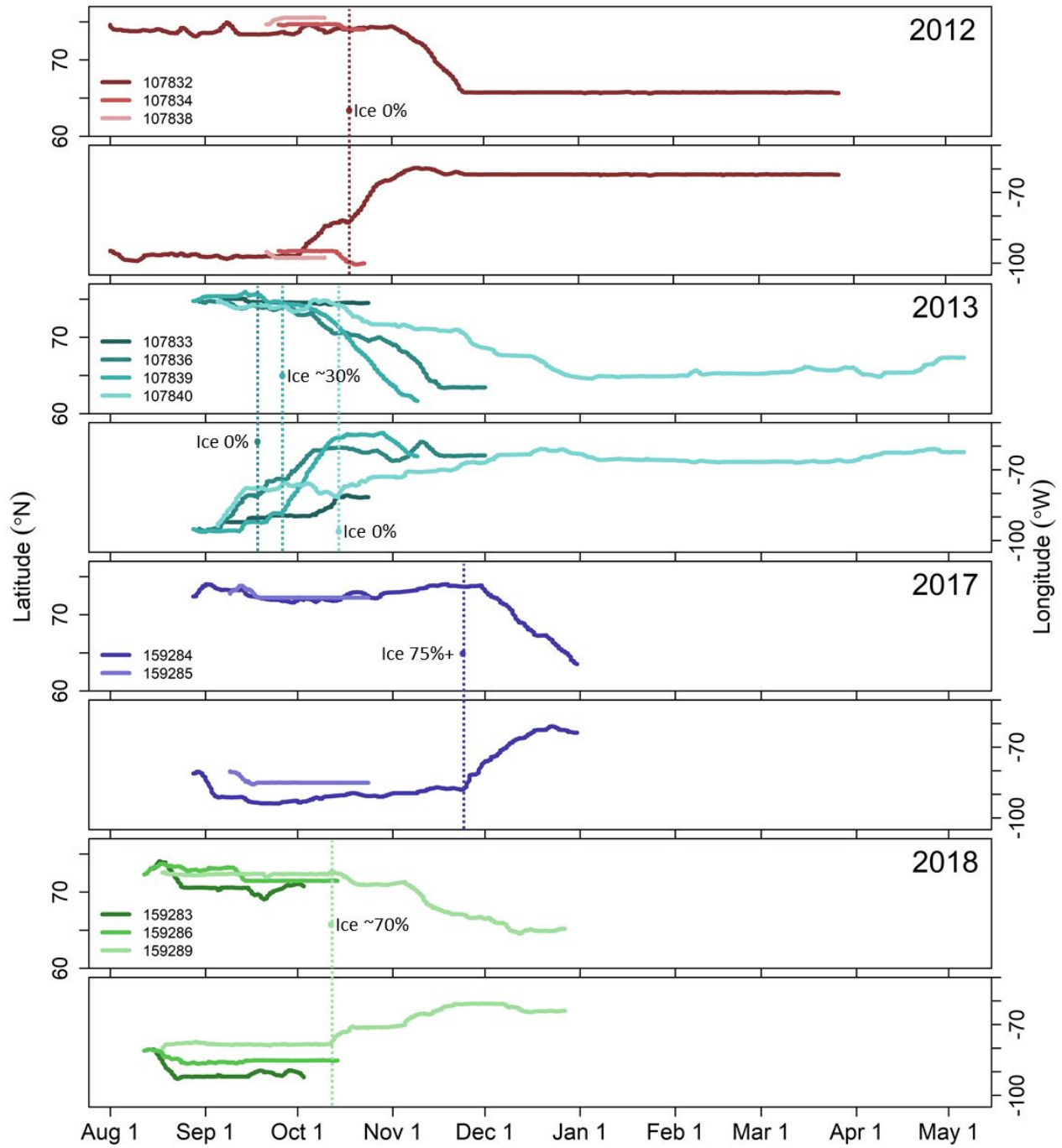Figure 1: Map of ringed seal tracks and important locations

Figure 2: Latitude and longitude of tagged seals

Figure 3: boxplots of dive parameters