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Conservation biology

The endangered Spitsbergen bowhead whales' secrets revealed after hundreds of years in hiding

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Spitsbergen's bowhead whales (*Balaena mysticetus*) were hunted to near extinction in the world's first commercial whaling enterprise; this population clearly remains threatened, but nothing is known about its distribution, making assessment unfeasible. In this study, we document range, movement patterns and habitat preferences of this population, based on tagging done from an icebreaker-based helicopter. Despite their reduced abundance, Spitsbergen's bowhead whales occupy much of their historical range, stretching across the northern Barents Region from East Greenland eastward to Franz Josef Land. Unlike larger bowhead populations to the west, they do not migrate in a classical sense, but rather disperse from wintering grounds in the northernmost parts of their range during spring, returning northward again in autumn, a pattern opposite in terms of directionality compared to other Arctic bowhead whale populations. The extreme affiliation of this population with cold, ice-filled waters is a concern given ongoing climate warming and concomitant rapid sea ice habitat loss.

1. Introduction

The Spitsbergen stock of bowhead whales(*Balaena mysticetus*) were hunted to the brink of extinction during the first commercial whaling enterprise, which started in the early 1600s in the Svalbard Archipelago. In the early 1990s, this population was estimated to number in the few tens [1] and its classification remains Endangered on the IUCN Red List today [2]. However, acoustic monitoring in the Fram Strait, between Svalbard and Greenland, demonstrated a year-round presence of bowhead whales in the region, with elaborate and abundant singing taking place 24 h per day in the winter months, suggesting that this drift-ice area in the midst of the southward flowing Arctic Water of the East Greenland Current is a mating ground for this population [3,4]. However, ship-based surveys and a marine mammal sightings database for Svalbard have reported only a few bowheads [5,6]. The track from a single whale tagged in Fram Strait during a bowhead expedition in 2010 reinforced the suggestions by early whalers regarding a very unusual movement pattern in this population: this whale wintered deep in the ice west of Svalbard and went south in the summer, which is opposite to the normal—north in summer and south in winter—seasonal patterns of baleen whales, including bowhead whales, in the Arctic [7]. In late summer 2015, we conducted an aerial survey into the polar ice north of Svalbard using helicopters based on ships, to estimate bowhead whale numbers. Fifteen sightings, involving 27 bowhead whales in the study area, suggested that the Spitsbergen bowhead whale population likely numbers in the low hundreds [8]. This survey further reinforced the strong affiliation this population has with sea ice. The relatively high densities observed suggested the possibility of working more intensively with individuals in this population within their sea ice habitat. Thus, this study was designed to tag bowheads in the Spitsbergen population to determine year-round movement patterns and fine-scale habitat use to address conservation needs and to design future surveys to determine abundance across the range of this endangered population.

2. Material and methods

Because Spitsbergen bowhead whales are highly ice affiliated, the novel use of a helicopter tagging platform (based on a ship) was the only logistically functional option. We used an Écureuil Eurocoper AS350 to search for and approach the whales in the drifting sea ice of the western Fram Strait in late May–early June 2017. Sixteen Spot 5 satellite transmitters (https://wildlifecomputers.com/) were deployed using an ARTS (Aerial Rocket Transmitter System) [9] air gun (12–14 bar pressure) from a distance of approximately 10 m. The custom-designed darts were 30 cm in length, and thus penetrated only the skin and blubber layer (i.e. did not reach the muscle). Generalized additive mixed effect models (GAMMs) were used to study movement and space use (via calculating time spent in area (TSA)) relative to environmental conditions within seasons. Details regarding the sampling regime, data filtering, extraction and calculation of environmental variables and statistical analyses can be found in the electronic supplementary material.

3. Results

Thirteen of the tagged bowhead whales provided location information; mean record length was 181 ± 199 days (range 4–709 days). Following our application of a speed, distance, angle filter and selection of a one-year study period (see electronic supplementary material, table S1), we retained 12 201 locations (electronic supplementary material, figure S1). Subsequent to creating 1 h interpolations within the identified track segments (defined as sections of tracks where there were no gaps in transmission greater than 24 h; see electronic supplementary material, figure S2), 22 489 location estimates were obtained, 22 268 of which were retained for habitat assessment because they could be associated with oceanographic parameters (figure 1*a*). During the study period, the animals were exposed to highly variable environmental conditions ranging from shallow, coastal areas to deep (max. 5018 m) offshore (max. 411 km) areas. The whales traversed areas with sea surface temperatures ranging from −1.8°C to 4.34°C (mean = 0.29 ± 1.52°C), with sea ice concentrations ranging from open water to 100% coverage. We tagged all of the animals in a restricted area in central Fram Strait (close to 78°N, 0°), but they did not migrate directionally in any classical sense; they simply dispersed north and south, east and west (figures 1*a* and 2*a*,*b*), at relatively high swimming speeds (1–2 km h^{-1}) over the summer period (figure 2*c*). Eleven of the whales stayed west of Svalbard, while the other two moved eastward to Franz Josef Land and somewhat beyond (figure 1*a* and electronic supplementary material, figure S3). During the autumn, movements were more homogeneously northward, and speed of travel was reduced (figure 2*a*,*c* and electronic supplementary material, figure S4). All of the whales spent the winter in relatively small areas in waters off Northeast Greenland or Franz Josef Land (electronic supplementary material, figure S4). Toward the end of winter and during the spring, the whales started moving more quickly once again, generally in a southward direction (figure 2*a*,*c*).

We explored movement patterns and habitat use throughout the year using GAMMs (details regarding model selection, model diagnostics and model outputs can be found in the electronic supplementary material, tables S2, S3, figures S5 and S6). The GAMMs showed that during summer, the whales occupied the marginal ice zone (MIZ, the edge of which is defined as the extent of at least 15% ice cover) in deep, offshore areas over the continental slope, where relatively high ice concentrations prevailed, with sea surface temperatures (SST) averaging 2°C (figures 1*b* and 2*d*–*f*; electronic supplementary material figure S7). In autumn, the whales moved into shallower areas, closer to coastlines and spent more time in lighter ice concentrations or open water areas, but SSTs were progressively colder, reaching below zero by October (figures 1*b* and 2*e*–*f*; electronic supplementary material, figure S7). As winter approached the animals returned to deeper, offshore areas where they occupied areas with high sea ice concentrations, often exceeding 90%, with SSTs below zero (figures 1*b* and 2*d*–*f*; electronic supplementary material, figure S7). In spring, few tags were still providing locations, but the whales for which we have data occupied areas with progressively declining ice concentrations and progressively higher SST values (temperatures became positive), although they remained offshore in deep, relatively cold areas (figure 2*e* and electronic supplementary material, figure S7). In all seasons, the whales spent most of their time inside the margins of the drifting ice, though during late summer and early autumn they made forays into open water (figure 1*b*).

GAMMs investigating TSA relative to environmental conditions within seasons suggested that depth was important in summer, autumn and winter, but the whales changed preference according to season, particularly spending more time in shallow areas in the autumn (electronic supplementary material, figure S8; also see electronic supplementary material figure S4). Proximity to coastlines also appeared to be an important variable influencing TSA; the whales were closest to the coast in autumn and furthest from the coast in winter (electronic supplementary material, figure S8). TSA was impacted by distance to the ice edge, particularly in the winter when the whales spent most of their time deep inside the ice, far from the edges (electronic supplementary material, figure S8). SST was also an important variable with regard to TSA; the whales spent most of their time in cold water, even during summer (SST < −1°C), and maintained this general cold water preference through autumn and winter, when they stayed longer periods of time in water with SSTs between −1°C and +1°C (electronic supplementary material, figure S8). TSA models' output summaries can be found in electronic supplementary material, table S4.

4. Discussion

In all seasons, the bowheads spent most of their time in cold water and in close association with sea ice. This species is the only baleen whale that resides year-round in the Arctic, and through evolutionary time they have become the most

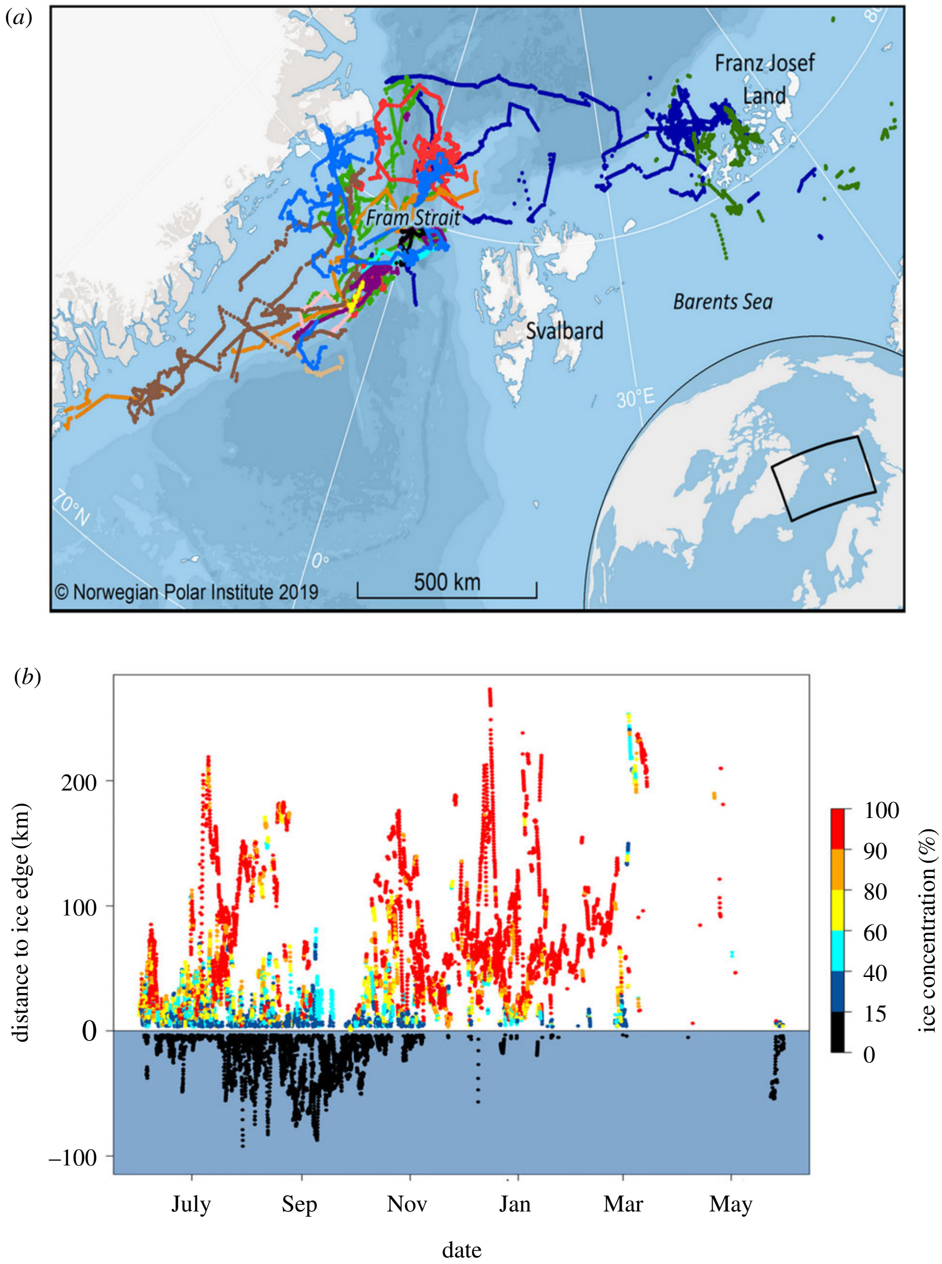

Figure 1. (*a*) Interpolated hourly positions along track segments (1 June 2017–31 May 2018) from 13 bowhead whales tagged in Fram Strait. (*b*) Distance to the ice edge versus date for 13 bowhead whales tagged in Fram Strait. The white background in the top of the figure indicates that the whales are inside the ice edge, whereas a blue background at the bottom of the figure indicates locations in open water. Locations are colour coded according to sea ice concentration.

specialized baleen whale species. Not surprisingly, most of their unique characteristics are associated with their high latitude, cold water, ice-affiliated lifestyle [10]. This includes having no dorsal fin and having a slow, conservative life-history strategy that involves extreme longevity (up to 200 yr), late sexual maturation (20 yr) and a long inter-calf interval (4–7 yr). Additionally, their 4 m long baleen permits ingestion rates during summer and fall that allow for maintenance of a blubber layer that can be up to 50 cm thick. The need to feed heavily on lipid-rich Arctic copepods, euphausiids, amphipods and mysids during the Arctic summer is thought to be the main reason for the northward migration that most bowhead whale populations undertake. Bowhead whales in the Bering–Chukchi–Beaufort and in the Eastern Canada–West Greenland populations move northward in summer along predictable migration corridors [11,12]. Only the Spitsbergen bowhead whale population is known to spend the winter at its northern-most latitudes, moving southward in summer. Although this population occupies the MIZ in the summer and autumn, presumably to take advantage of the production produced by upwelling and ice-melt related phenomena, it does not get pushed south with the ice edge in winter. Instead, individuals move north and remain up to hundreds of kilometres inside the ice edge, in areas classified as having 90–100% ice concentrations. Coastal polynyas in Franz Josef Land in the eastern part of the Spitsbergen bowhead's range and along the North-east coast of Greenland (e.g. North East Water Polynya) and flaw lead systems maintained by the powerful, southward flowing East Greenland Current are likely important determinants of habitat suitability in winter. Occasional incursions of North Atlantic Water in the Fram Strait likely also play a role in keeping enough cracks and leads open in northerly waters of this region, such that they can be winter habitat for bowheads.

The history of human exploitation of this population might play a part in the habitat preference we see in Spitsbergen's

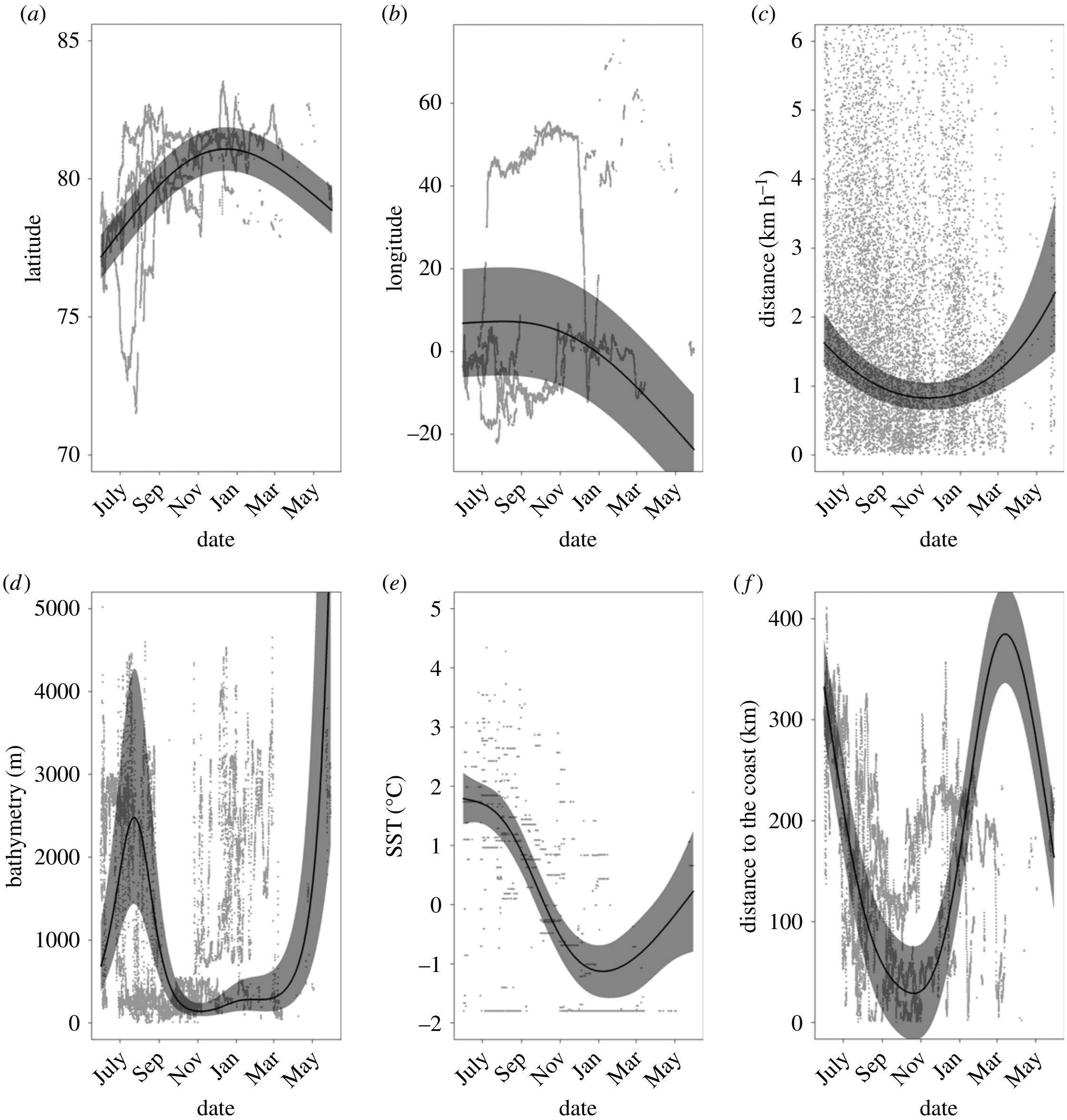

Figure 2. GAMM model outputs comparing (*a*) latitude, (*b*) longitude and (*c*) distance travelled/hour, (*d*) bathymetry (*e*) sea surface temperature and (*f*) distance to the coast versus date for 13 bowhead whales tagged in Fram Strait. Fitted estimates from models (solid curves) are represented along with the 95% CIs (polygons).

bowhead whales in modern times. Coastal and pelagically inclined bowhead whales in the Spitsbergen population were likely extirpated, leaving only individuals that tended to reside in ice protected refugia [13]. Mammal populations that have been reduced to tiny fractions of their former population sizes usually occupy only an edge of their former range [14]. However, we show in this study that this is not the case for Spitsbergen bowhead whales. These whales spread across most of the northern Barents Sea despite their low population numbers, although they remain rare in the Svalbard Archipelago, which was core habitat in the past [5,6]. The minimal cost of transport in the marine environment and the bowhead whale's ability to communicate across distances of many tens of kilometres, potentially up to hundreds of kilometres [15], might facilitate the broad geographic spread we see in this small population.

Bowhead whales are shallow divers that feed on a variety of Arctic crustaceans, primarily in the top 200 m, although they can dive deeper than 500 m [16]. Although we know nothing specific about the diet or seasonal feeding patterns of Spitsbergen bowheads, it is reasonable to assume that they feed primarily during the daylight period, when zooplankton ascend in the water column and when this and other bowhead populations tend to be in shallower areas up on coastal shelves [17]. However, several recent studies suggest that bowhead whales might feed year-round [18,19] and the fact that some calanoid copepod stages occupy intermediate depths in under-ice environments in winter could facilitate winter feeding [20].

Both the Bering–Chukchi–Beaufort and the Eastern Canada West Greenland bowhead populations are recovering from historical overexploitation, and there are a growing number of promising signs for the Spitsbergen population [8,13,21–23], though data is not yet available over time frames meaningful for trend assessment in the latter area. Decreased sea ice owing to global warming will likely promote greater mixing between bowhead whale populations across areas previously covered by continuous ice [24], as this sort of connectivity in the past has been suggested by genetics studies [25]. Narrow ranges of preferred, cold SSTs have been noted for other bowhead whale populations [26,27] and seem to be the case for Spitsbergen bowhead whales according to our SST and TSA analyses. This creates a serious concern that ongoing increases in water temperatures in the Greenland and Barents Seas and concomitant sea ice losses [28,29] might become critical in terms of habitat loss and thermal stress. Reduced ice cover also creates the potential for increased mortality owing to killer whale predation, which is already a serious issue for the Sea of Okhotsk population [30]. Disease exposure, food web changes that result in less food availability (especially fat-rich calanoid copepods) and increased human traffic in the Arctic are also concerns [31]. If Spitsbergen bowhead whales retain their strong preference for cold, ice-covered waters, which we have demonstrated herein, their distribution will retract north to offshore, deep water areas in the future, where they would be forced to rely on pelagic zooplankton production; such a situation is likely to prevent recovery of the population.

Ethics. Animals were tagged according to community standards. Permits for animal handling were given from the Norwegian Animal Research Authority (FOTS ID: 11821) and the Governor of Svalbard (Sysselmannen, permit ID: 16/01600-6).

Data accessibility. Data are available at the National Polar Data Centre for Norway https://doi.org/10.21334/npolar.2020.395011fc.

Authors' contributions. The study was conceived by K.M.K., C.L. and M.P.H.-J. K.M.K., C.L. and O.S. took part in tagging operation in the field. J.V.-G., C.L. and K.M.K. analysed the data; J.V.-G. did the R programming. K.M.K., C.L., J.V.-G., M.P.H.-J., O.S. and D.G. took part in interpretation of the results, writing and editing the manuscript. All authors have approved the final contents of the manuscript and agree to be held accountable for its contents.

Competing interests. We declare we have no competing interests.

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Supplementary material

Methodology

The satellite transmitters deployed on the bowhead whales were housed in stainless-steel cylinders that were attached to the whales dorsally (approximately half way between the head and the tail) with a four-bladed point attached to a 30 cm long rod, which was held in place in the tissue with 4 sets of barbs and 6 backward-facing petals. Tags were surgically sterilized, and the anchoring system was coated with Gentamicyn sulfate antibiotic prior to implantation. The tags were programmed to start searching for satellites at 06:00 hrs daily, and to try up to 200 times. They then closed operations until the next day. All data processing and analyses were done using the R statistical framework (R 3.6.0). Satellite derived locations were filtered using a speed, distance and angle filter (SDA filter; [1,2] using the R package 'argosfilter' (http://cran.r-project.org)). This filter removes all low precision (LC Z) points as well as those requiring unrealistic swimming speeds or unlikely turning angles; the swimming speed threshold was set at 3 m/s and all spikes with angles smaller than 15 or 25 degrees were removed if their lengths were greater than 2.5 or 5 km, respectively [3,4].

Filtered tracks were divided into segments if we did not have a location within a 24 h period, because the bowhead tracks were quite patchy due to their use of ice-filled waters and their ability to breathe through cracks with only their elevated nostrils exposed (and not the tag). A total of 75 segments from the 13 animal's tracking records were identified in the one year study period selected for analyses (01 June 2017 – 31 May 2018). Filtered locations were subsequently interpolated within segments at 1 h intervals along the trip-line to avoid transmission biases. Locations estimated to occur on land were removed using the 1:10 m - file.

Longitude (LON) and latitude (LAT) of retained interpolated locations, as well as respective distance between them within each segment (DIST, km), were extracted. Each filtered, interpolated location was assigned to a season - locations occurring June-August were assigned to Summer, September-November were assigned to Autumn, December-February were assigned to Winter and March-May were assigned to Spring.

<u>Extraction and calculation of the environmental variables</u>

Five environmental variables, bathymetry (DEP, m), sea ice concentration (ICE, %), distance to the ice edge (ICE EDGE, km), sea surface temperature (SST, °C), and distance to the nearest coast (COAST, km), were calculated for each interpolated location based on their locations and time-stamps. DEP was extracted from the 500 m grid resolution International Bathymetric Chart of the Arctic Ocean Version 3.0 (IBCAO; [5]. ICE was extracted from the daily 6.25 km grid resolution AMSR-E ice remote sensing system [6]. ICE EDGE was calculated from ICE using Qgis (the ice edge was set at 15 % ice concentration). Positive values of ICE EDGE mean that locations were inside the ice while negative values for ICE EDGE reflect open ocean locations (until the 15 % concentration limit). SST was extracted from the monthly 2° grid resolution from the Extended Reconstructed Sea Surface Temperature (ERSST) v5 [7]. Finally, COAST was calculated using the same land file described previously (1:10 m-www.naturalearthdata.com). Interpolated locations with unavailable environmental variables were removed.

Time spent in area

The intermittent nature of location transmissions negated the use of classical methods used to quantify space use, such as First Passage Time [8,9] or State Space Models [10-12], so we calculated time spent in area manually (TSA; [13]. Time spent (h) within a 5 x 5 km grid-square was calculated monthly for each individual as the sum of the interpolated hourly locations within each grid cell. Environmental variables previously described (DEP, ICE, ICE EDGE, SST and COAST) were extracted for each cell as the mean of environmental values corresponding to the interpolated locations occurring within the cells for each individual.

Modelling approach

To explore seasonality, the three movement metrics (LON, LAT, DIST) as well as the five environmental metrics (DEP, ICE, ICE EDGE, SST, COAST) were investigated separately in relation to the day of the year (the number of days since the 1st of June (i.e. the first day of the selected one-year period – day hereafter)). Generalized additive mixed models (GAMM; `uGamm' function in the R package `MuMIn' that called 'gamm' function in the R package `mgcv) were used to study relationships; day of the year was included as a smooth term (k was set at 3 or 6 for the models involving the movement and environmental variables, respectively). Individual ID was included as both a random effect and as a grouping factor in the temporal autocorrelation structure of the order one (corAR1) term. We used a Gaussian family distribution to fit models; DIST, DEP and ICE were log transformed to attempt to meet model assumptions of homoscedasticity and normality of residuals (log(variable+1) for ICE since 0 values were present). We did model selection according to the Akaike's information criterion, AIC [14]. Diagnostics of the selected models as well as temporal and spatial autocorrelation assessment plots were used to validate final models [14, 15].

To quantify space use relative to environmental conditions within seasons, monthly TSA was modelled using generalized additive mixed models (GAMM; ‘gamm’ function in the R package `mgcv) in relation to DEP, ICE EDGE, SST and COAST as well as Season. We did not include ICE in the models since it was highly correlated with ICE EDGE (Pearson correlation 73%). Positive values of TSA were retained for analysis since a value of 0 in a cell does not necessarily mean that the cell was not used by animals. Environmental variables were included as smooth terms (k was set at 4 for those) while Season was included as a “by-variable” (i.e. environmental variables smooth curves were made for each Season). Before we ran models, explanatory variables were standardized - to have a mean of 0 and a standard deviation of 1 - and models were fitted with a Negative binomial family distribution (theta was fixed at 1.602) since TSA was over-dispersed, count data. Individual IDs were included in the models as both a random effect and as a grouping factor in the temporal autocorrelation structure of the order one (corAR1) term. We conducted model selection and model validation using the confidence intervals of the corresponding smooth curves, as recommended by [14].

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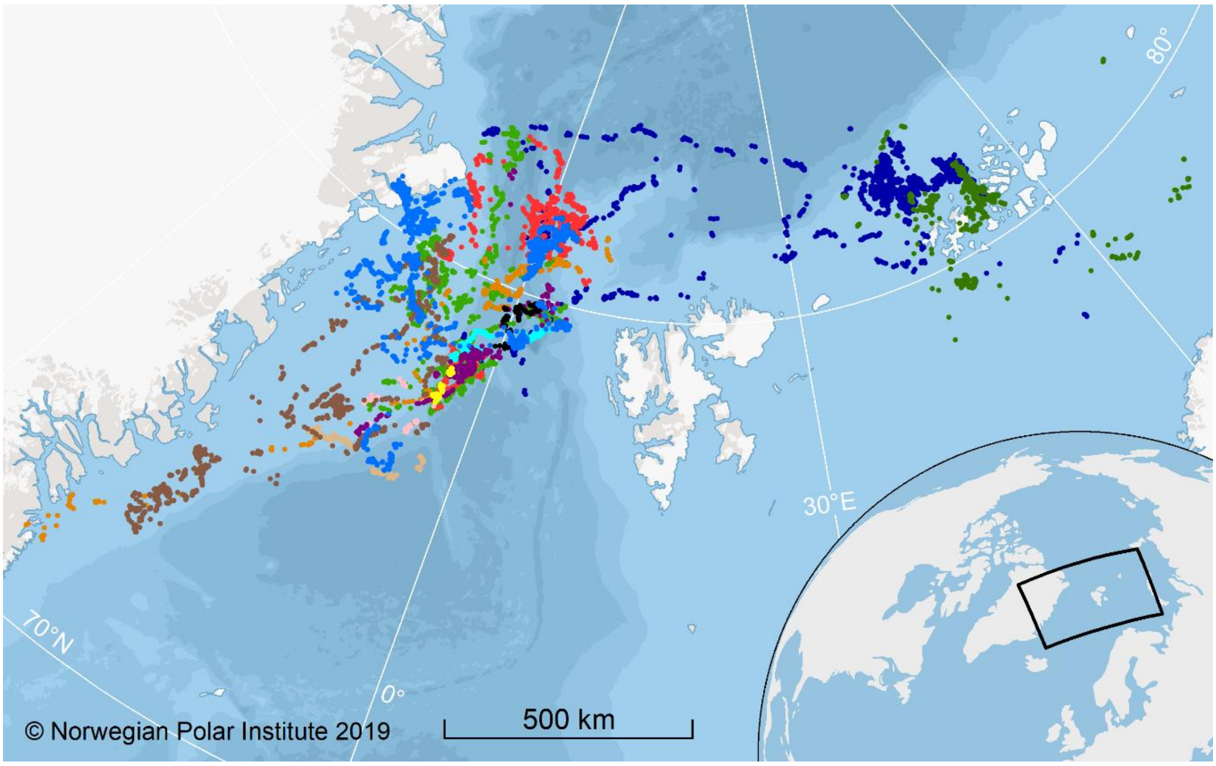

Figure S1. SDA filtered locations (01 June 2017 – 31 May 2018) for 13 bowhead whales tagged in Fram Strait in June 2017. Colors indicate individual animals.

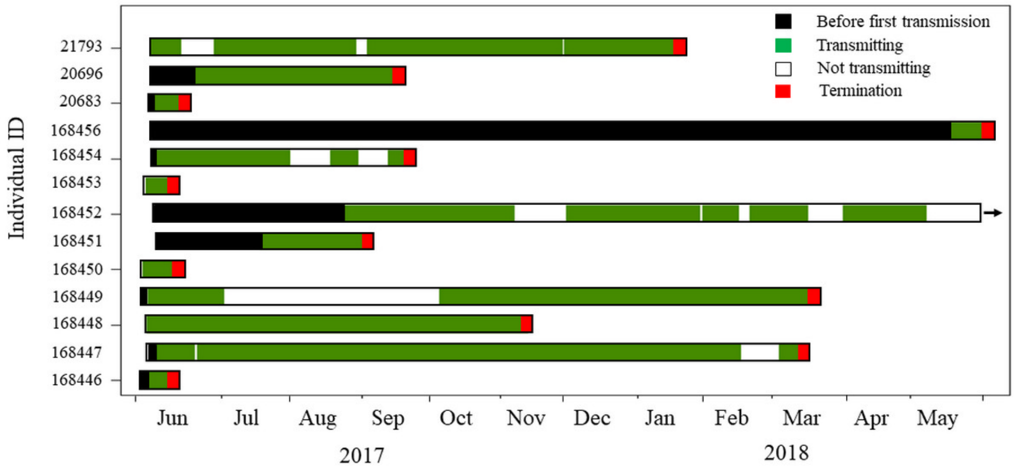

Figure S2. Location transmission records for 13 bowhead whales tagged in Fram Strait from in late May and early June 2017 – for the period 01 June 2017 until 31 May 2018. (The complete record for animal no. 168452, which extended into May 2019, is depicted in detail in Fig. S3).

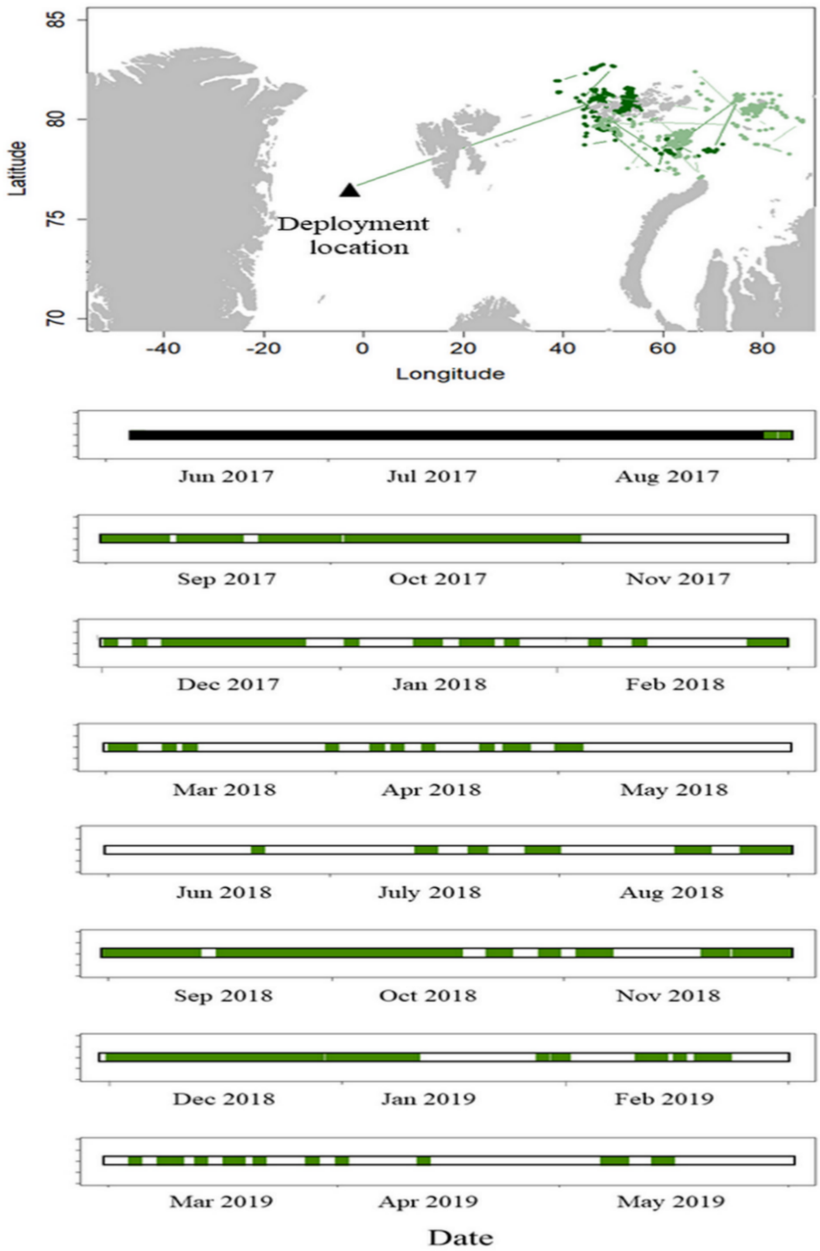

Figure S3. Entire track for bowhead whale no ID-168452, tagged in Fram Strait in June 2017. The tag sent the first location in August 2017 at which time the whale had moved to Franz Josef Land in Russia. The triangle on the map indicates where this whale was tagged. The dark green dots are locations used in this study and the light green dots go beyond the study period (until May 2019). The bar chart under the map depicts - the period between tagging and the first location (black), days with transmission of locations (green) and gaps in the record of more than 24 hours (white).

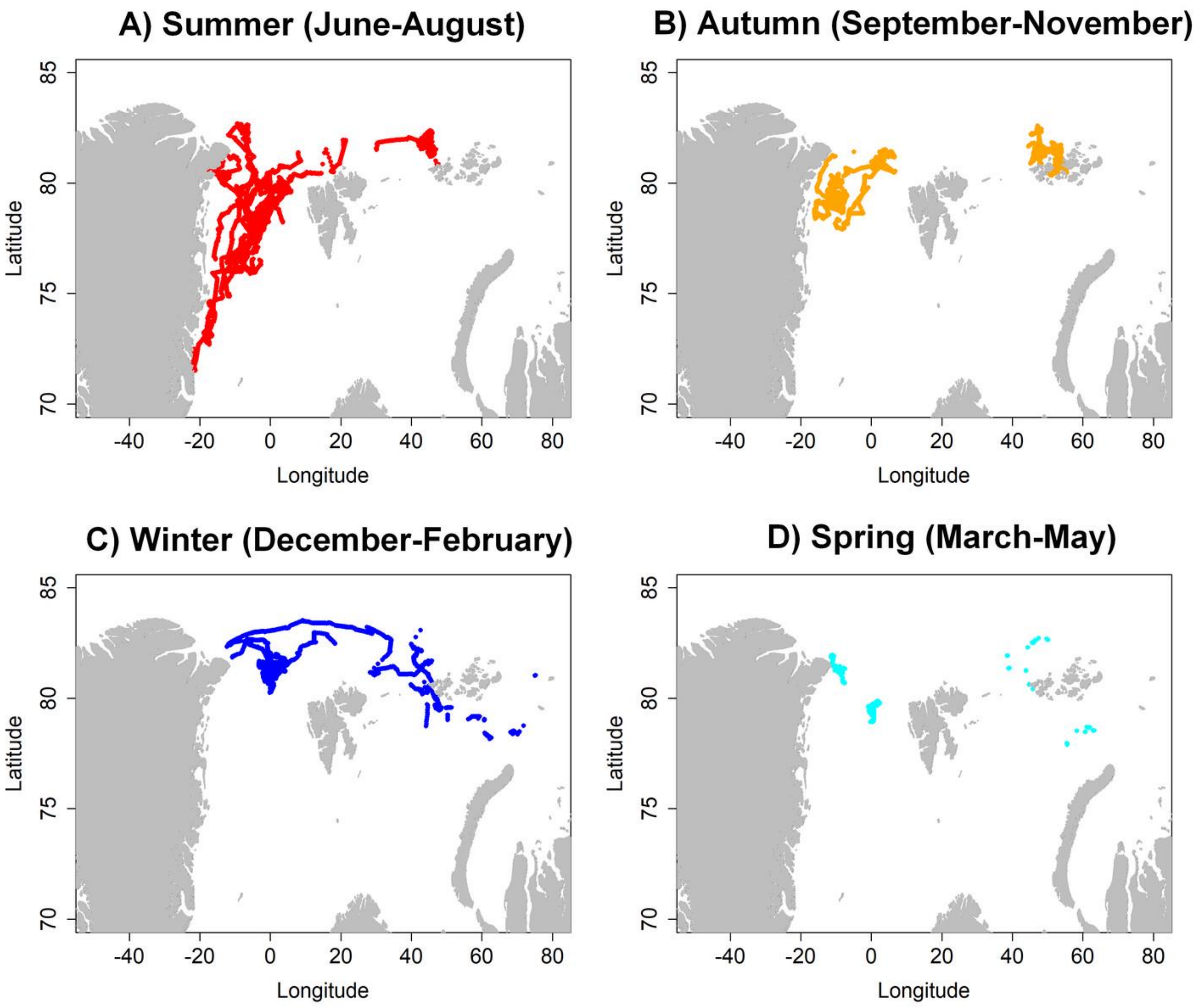

Figure S4. Latitude-longitude of positions interpolated hourly along track segments for 13 bowhead whales tagged in Fram Strait plotted according to season: A) summer; B) autumn; C) winter and; D) spring.

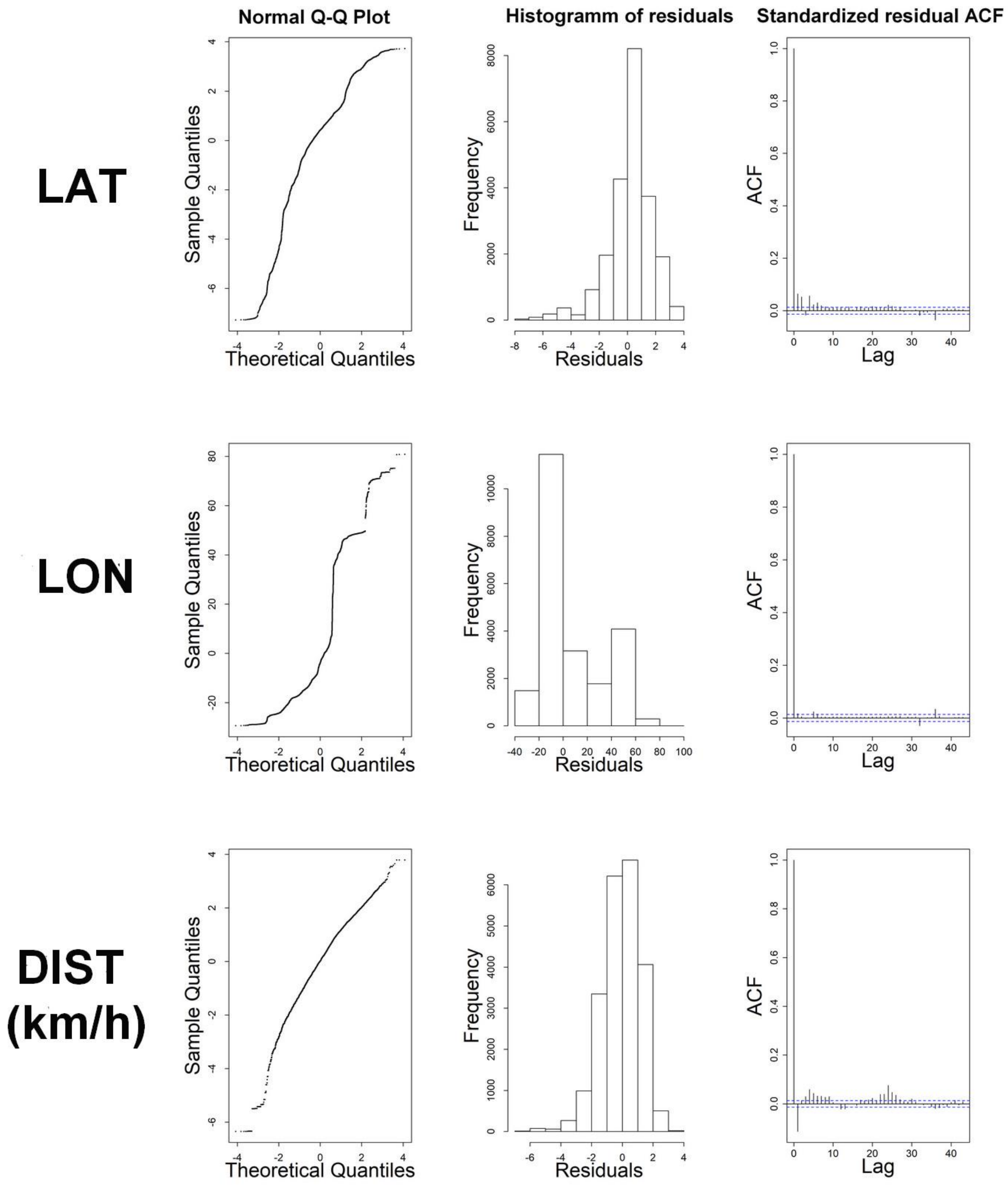

Figure S5. Diagnostic residual plots (Normal Q-Q Plot, Histogram of residuals and Standardized residual ACF) for the selected models investigating movement metrics relative to date.

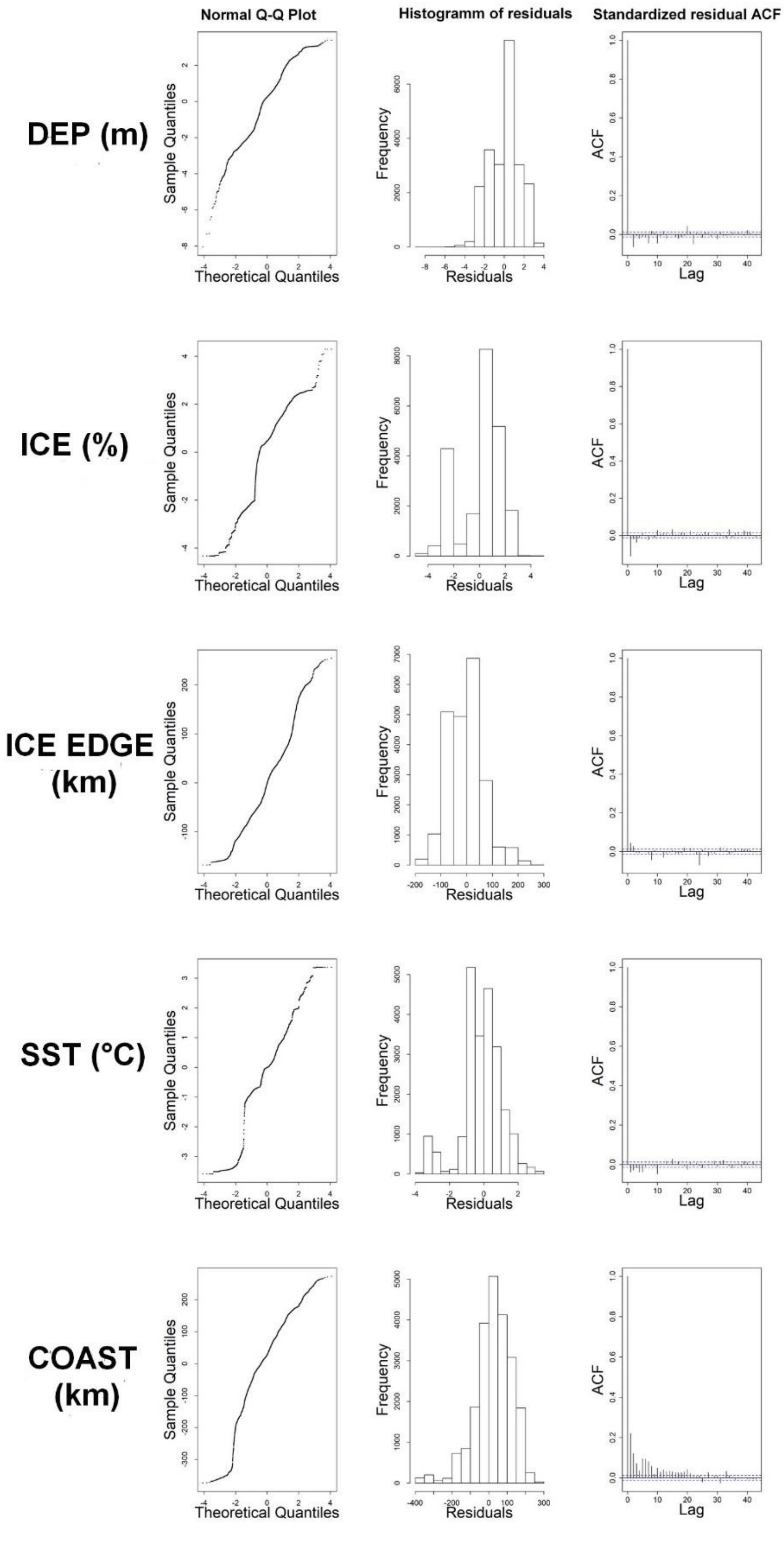

Figure S6. Diagnostic residual plots (Normal Q-Q Plot, Histogram of residuals and Standardized residual ACF) for the selected models that investigate environmental metrics relative to date.

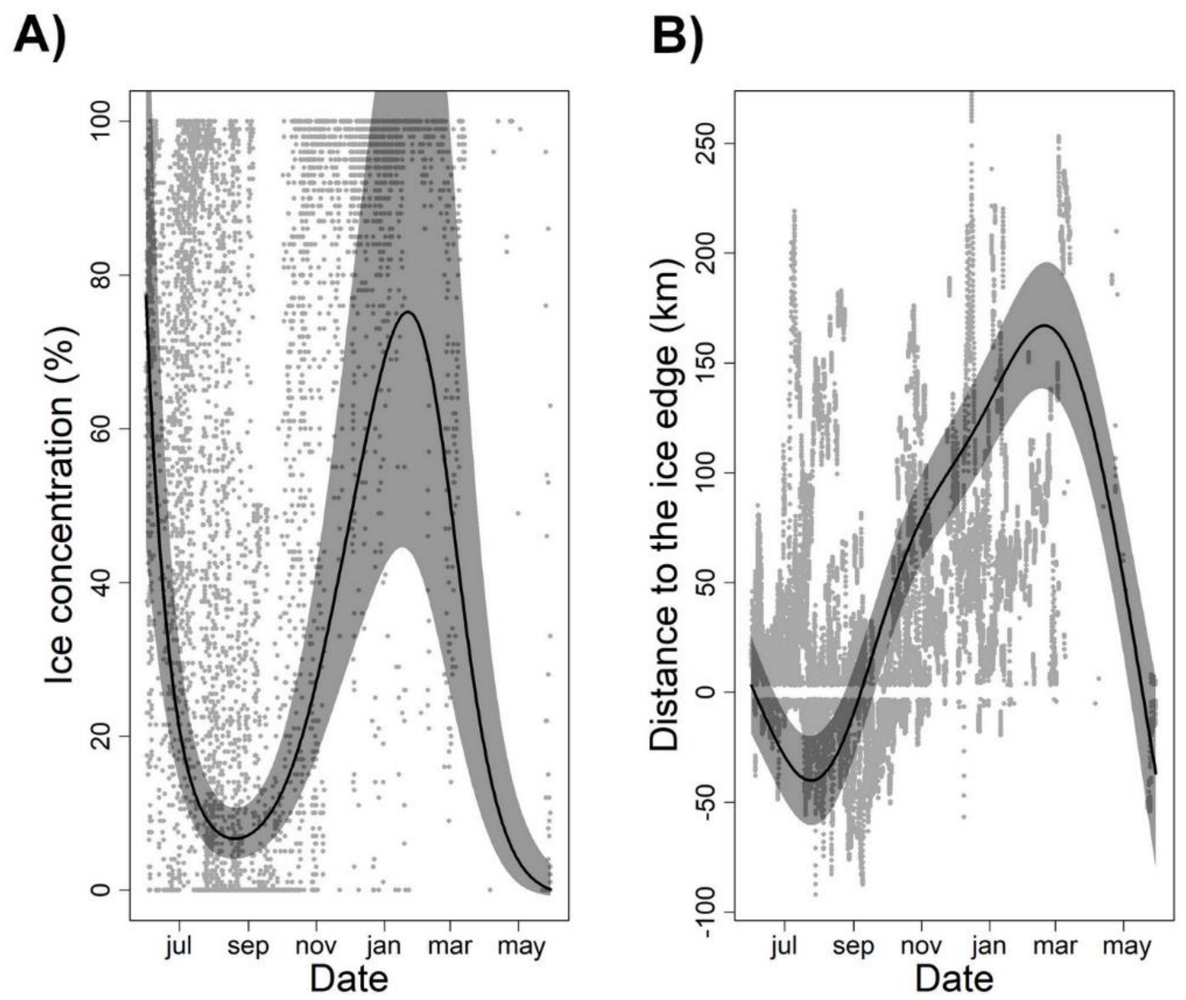

Figure S7. GAMM model outputs comparing A) sea ice concentration and B) distance to the ice edge vs date for 13 bowhead whales tagged in Fram Strait. Fitted estimates from models (solid black curves) are represented along with the 95 % CIs (dark grey polygons). Positive values of distance to the ice edge mean that locations were inside the ice while negative values for ice edge reflect open ocean locations (less than 15% sea ice concentrations)

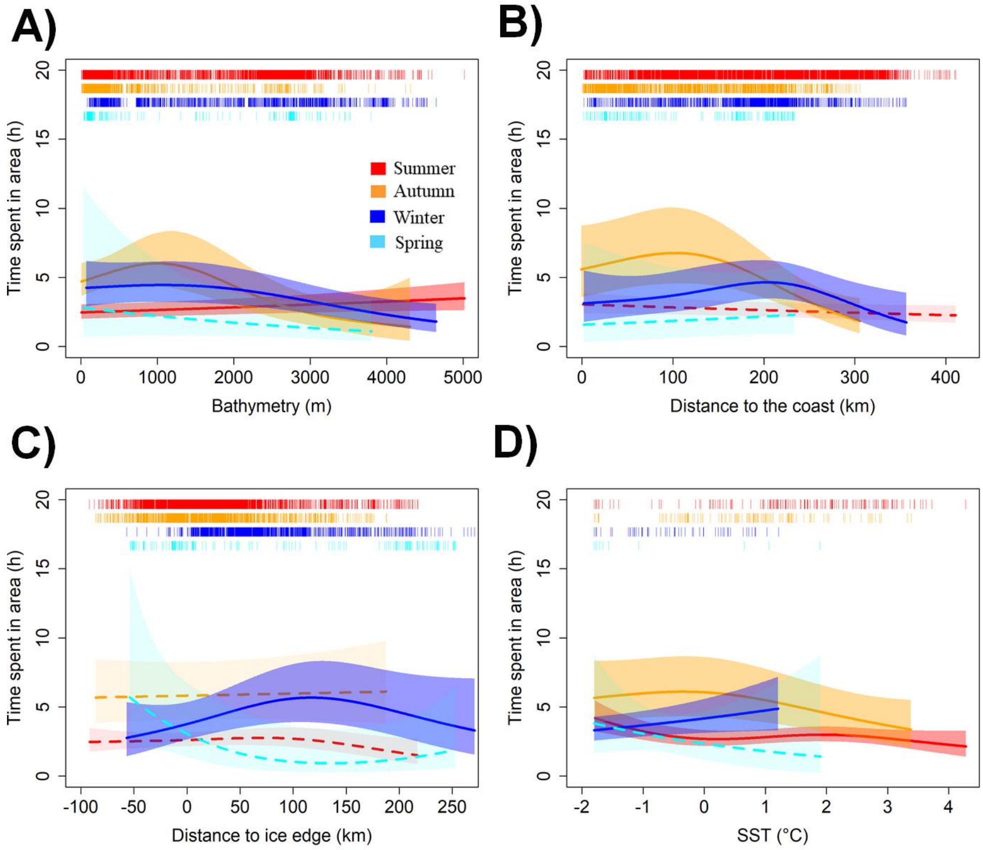

Figure S8. GAMM model outputs comparing TSA for 13 bowhead whales tagging in Fram Strait with respect to A) bathymetry, B) distance to the coast, C) distance to the ice edge, and D) SST. Fitted estimates from model are represented along with the 95 % CIs (polygons). Statistically significant relationships are depicted with solid lines, whereas dotted lines are used for relationships not meeting $p \leq 0.05$. Positive values of distance to the ice edge mean that locations were inside the ice while negative values for ice edge reflect open ocean locations (less than 15 % sea ice concentration). The seasonally colour codes lines at the top of each illustration show the distribution of available data.

Table S1. Details regarding tag deployments and data records (after track filtration and selection of one complete year) for 13 bowhead whales tagged in Fram Strait including ID number, deployment date, deployment location (longitude, latitude), date of first transmission, total duration of data record, number of segments (parts of the total record of individuals without gaps of more than 24 hr), mean segment duration and SD for segment durations.

ID	Deployment date (d/m/y)	Longitude (west of O^{o})	Latitude (^{o}N)	Date of first transmission (d/m/y)	Duration (d)	Number of segments	Mean segment duration (d)	SD segment duration (d)
168446	01/06/2017	4.37	77.32	03/06/2017	2	1	2	NA
168447	03/06/2017	3.91	76.88	07/06/2017	276	11	19	41
168448	03/06/2017	3.82	76.90	03/06/2017	158	5	30	60
168449	01/06/2017	4.38	77.32	03/06/2017	284	16	10	11
168450	30/05/2017	4.73	77.97	30/05/2017	7	1	7	NA
168451	04/06/2017	3.55	76.57	04/06/2017	38	2	17	16
168452	05/06/2017	3.09	76.53	29/08/2017	247	30	3	6
168453	02/06/2017	4.68	77.14	02/06/2017	4	1	4	NA
168454	04/06/2017	4.25	76.68	06/06/2017	103	6	8	13
168456	04/06/2017	4.07	76.06	23/05/2018	7	1	7	NA
20683	04/06/2017	3.06	76.59	05/06/2017	6	1	6	NA
20696	04/06/2017	4.07	76.06	23/06/2017	82	3	27	20
21793	04/06/2017	4.25	76.69	04/06/2017	224	10	15	20

Table S2. Degrees of freedom (df) and AIC values for models investigating movement (LAT, LON, DIST) and environmental (DEP, ICE, ICE EDGE, SST, COAST) metrics relative to date (day).

Movement metrics			
	s(day)	***df***	***AIC***
LAT	+	6	-71672.9
		4	-68005.1
	s(day)	***df***	***AIC***
LON	+	6	9219.9
		4	9928.4
	s(day)	***df***	***AIC***
DIST	+	6	48526.7
		4	48568.0
Environmental metrics			
	s(day)	***df***	***AIC***
DEP	+	6	-25822.2
		4	-25376.8
	s(day)	***df***	***AIC***
ICE	+	6	24633.1
		4	24726.8
	s(day)	***df***	***AIC***
ICE EDGE	+	6	140528.1
		4	140967.5
	s(day)	***df***	***AIC***
SST	+	6	-10770.5
		4	-10564.8
	s(day)	***df***	***AIC***
COAST	+	6	115172.3
		4	121751.4

Table S3. GAMM model output summaries investigating movement (LAT, LON, DIST) and environmental metrics (DEP, ICE, ICE EDGE, SST, COAST) as a function of the date (day). The estimates, *t-values* and *p-values* are shown for the linear predictor variables and the estimated degrees of freedom (edf), F and *p-values* are shown for the predictor variables included in the smooth function in each model. The level of temporal autocorrelation (Phi value) is also given.

Movement metrics									
		estimate	***t-value***	***p-value***		***edf***	***F***	***p-value***	***Phi value***
LAT	Intercept	79.76	203.30	<0.001	s(day)	1.99	2033.00	<0.001	0.99
LON	Intercept	4.39	0.67	0.50	s(day)	1.99	356.50	<0.001	0.99
DIST	Intercept	0.04	0.34	0.74	s(day)	1.98	27.17	<0.001	0.80
Environmental metrics									
		estimate	***t-value***	***p*-value**		edf	F	***p-value***	***Phi value***
DEP	Intercept	6.36	24.82	<0.001	s(day)	4.94	92.48	<0.001	0.99
ICE	Intercept	3.06	17.30	<0.001	s(day)	4.75	27.43	<0.001	0.96
ICE EDGE	Intercept	35.58	3.85	<0.001	s(day)	4.94	93.69	<0.001	0.99
SST	Intercept	0.39	2.58	<0.01	s(day)	4.39	55.22	<0.001	0.98
COAST	Intercept	129.64	5.61	<0.001	s(day)	4.99	1558.00	<0.001	0.99

Table S4. GAMM model output summaries investigating TSA as a function of the environmental conditions within seasons. The estimates, *t-values* and *p-values* are shown for the linear predictor variables and the estimated degrees of freedom (edf), F and *p-values* are shown for the predictor variables included in the smooth function in each model. The level of temporal autocorrelation (phi value) is 0.28.

	Estimate	***t value***	***p-value***
Intercept	1.06	9.36	<0.001
Spring	-0.24	-0.54	0.59
Summer	0.04	0.44	0.66
Winter	0.09	0.60	0.55
	edf	***F***	***p-value***
s(DEP):Autumn	2.25	7.41	0.001
s(DEP):Spring	1	0.91	0.34
s(DEP):Summer	1	5.76	0.02
s(DEP):Winter	1.89	10.78	<0.001
s(COAST):Autumn	2.24	6.62	<0.001
s(COAST):Spring	1	0.26	0.61
s(COAST):Summer	1	3.25	0.07
s(COAST):Winter	2.48	3.15	0.02
s(ICE EDGE):Autumn	1	0.08	0.78
s(ICE EDGE):Spring	2.10	2.42	0.06
s(ICE EDGE):Summer	2.27	1.08	0.20
s(ICE EDGE):Winter	2.00	3.75	0.02
s(SST):Autumn	1.89	4.92	0.03
s(SST):Spring	1	0.66	0.42
s(SST):Summer	2.65	4.56	0.01
s(SST):Winter	1	4.41	0.04