

# Environmental drivers of beluga whale *Delphinapterus leucas* habitat use in the Mackenzie Estuary, Northwest Territories, Canada

K. Scharffenberg<sup>1,\*</sup>, D. Whalen<sup>2</sup>, M. Marcoux<sup>1,3</sup>, J. Iacozza<sup>4</sup>, G. Davoren<sup>1</sup>, L. Loseto<sup>1,4</sup>

<sup>1</sup>Dept of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

<sup>2</sup>Natural Resources Canada, Geological Survey of Canada, Dartmouth, Nova Scotia B2Y 4A2, Canada

<sup>3</sup>Freshwater Institute, Fisheries and Oceans Canada, Winnipeg, Manitoba R3T 2N6, Canada

<sup>4</sup>Dept of Environment & Geography, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

**ABSTRACT:** Understanding drivers of habitat use and selection of mobile species is critical for understanding the impacts of climate change and formulating management plans. Eastern Beaufort Sea beluga whales *Delphinapterus leucas* form large summering aggregations in the warm, fresh waters of the Mackenzie Estuary, Northwest Territories, Canada; however, the environmental factors driving spatial and temporal patterns of habitat use within the estuary are not fully understood. We used passive acoustic monitoring to record beluga presence during their summer aggregation (June–August) at known congregation areas and locations with unique oceanographic features in Kugmallit Bay in the Mackenzie River Estuary, while simultaneously recording environmental and oceanographic data. The effectiveness of hydrophones at determining beluga presence/absence was validated using shore-based observations. Multiple logistic regression was used to assess the influence of environmental conditions on presence/absence of belugas. Results indicate that temporal patterns of habitat use varied by location, and were influenced by environmental conditions such as temperature, salinity, and wind speed. Belugas did not frequent commonly used locations during periods with high-speed winds and moved farther into the estuary during periods of cold oceanic influxes. This study provides support for hypotheses that belugas use the location for moulting or to provide a thermal advantage for young belugas. This information can be used to inform decisions by northern communities and policy makers, thus aiding in management of the Beaufort Sea beluga population.

**KEY WORDS:** Passive acoustic monitoring · Oceanography · Estuarine ecology · Arctic

—Resale or republication not permitted without written consent of the publisher—

## 1. INTRODUCTION

Understanding drivers of habitat use and selection is critical for understanding the impacts of climate change on a species and formulating effective management plans. Habitat selection is often based on maximizing resource energetic payoff but may be influenced by predation risk, competition, and abiotic factors (Cassini 2013), or the need to meet another critical life function. Predator habitat selection is often dictated by prey distribution, which in turn may be

driven by resource or habitat requirements of the prey (Staniland et al. 2004), so it is often difficult to distinguish between biotic and abiotic drivers of predator habitat use. There are cases, however, where abiotic variables can be linked directly to predator distribution patterns and are therefore likely drivers of habitat selection. For instance, juvenile bull sharks *Carcharhinus leucas* in the Florida Everglades (USA) select locations with a high level of dissolved oxygen, irrespective of prey abundance (Heithaus et al. 2009), and cow–calf pairs of southern right whales *Eubalaena*

\*Corresponding author: scharffk@myumanitoba.ca

*aena australis* preferentially select shallow waters with gentle slopes that are protected from swells (Elwen & Best 2004).

Beluga whales *Delphinapterus leucas* are marine predators with a circumpolar distribution throughout Arctic and sub-Arctic waters. Most beluga populations undergo seasonal migrations, and in the summer, many belugas occupy shallow coastal waters and warm estuaries, and may even ascend rivers (Rice 1998). In many locations, belugas enter these waters despite subsistence hunting pressure, suggesting that estuaries serve some important function (Finley 1982). Several hypotheses for estuarine use have been proposed, which often vary by location. Proximity to anadromous fish for feeding has been suggested as a key driver for beluga use of warm coastal waters in some locations in Alaska (USA), including Norton Sound (Frost & Lowry 1990, Huntington 1999) and Cook Inlet (Goetz et al. 2012). In contrast, feeding does not appear to be a driver in the Mackenzie Estuary (Canada), where the majority (>99%) of harvested Eastern Beaufort Sea (EBS) belugas had empty stomachs (Harwood et al. 1996). Belugas have been observed to regurgitate food when being chased (Byers & Roberts 1995), which could result in empty stomachs, although most EBS belugas harvested in other locations had full or partially full stomachs (Quakenbush et al. 2015, Loseto et al. 2018a). Calving has been proposed as the primary reason for aggregation in the Churchill River Estuary, perhaps because the estuary provides a thermal advantage for calf growth (Sergeant 1973), although calving appears to occur prior to the arrival of whales in other locations (Cobb et al. 2008). Alternately, the low salinity and high temperatures in estuaries may contribute to high turnover of epidermal cells, thereby accelerating the whales' seasonal moult (St. Aubin et al. 1990). In support of this hypothesis, whales have been observed rolling against the substrate in the estuary of the Churchill River (Watts et al. 1991, Smith et al. 1992), and they preferentially select tidal flats and sandy coastlines in Cook Inlet (Goetz et al. 2007, 2012).

The estimated ~40 000 individuals of the EBS beluga population (Hill & Demaster 1999) migrate from their overwintering location in the Bering Sea to the Beaufort Sea in the spring (Hauser et al. 2014, Muto et al. 2016) and form large summering aggregations in the Mackenzie Estuary (Harwood et al. 1996). Indigenous Peoples have been hunting belugas in the Mackenzie Estuary for centuries (Fraker et al. 1979), and the hunt remains important, as it contributes to food security and has cultural significance (Usher

2002, Hoover et al. 2016). The importance of beluga whales to the local communities resulted in a long-term conservation effort with the creation of Canada's first Arctic marine protected area, the Tarrum Nirjutait Marine Protected Area (TNMPA) in 2010 (Fisheries Joint Management Committee 2013). The TNMPA was established to protect belugas while maintaining subsistence hunting traditions. In recent years, researchers have further defined the spatial and temporal patterns of habitat use within the Mackenzie Estuary. Examples include the development of a pilot passive acoustic monitoring project (Simard et al. 2014) and the analysis of past aerial survey data to identify 'hot spots' where belugas are more likely to gather year after year (Harwood et al. 2014).

Beluga whales are a vocal species, making a variety of calls, generally categorized into whistles, pulsed tones, echolocation clicks, and combined calls (Sjare & Smith 1986). Whistles have a narrow bandwidth between a frequency of 200 Hz and 20 kHz, with continuous waveform and a definable contour (e.g. flat, wavy, ascending, descending; Belikov & Bel'kovich 2006), while pulsed tones are broadband signals with few measurable characteristics (Sjare & Smith 1986, Belikov & Bel'kovich 2008). Both whistles and pulsed calls are thought to be communicative in belugas (Belikov & Bel'kovich 2008, Panova et al. 2012), and there is evidence that specific broadband pulsed trains act as signature calls used to maintain contact with other group members (Vergara et al. 2010, Morisaka et al. 2013). Echolocation clicks are broadband, covering a spectrum of 100 Hz to 120 kHz, with peak frequency between 40 and 120 kHz (Ford 1977, Au et al. 1985). Combined calls are combinations of the calls described above (Belikov & Bel'kovich 2006).

Passive acoustic monitoring (PAM), including the use of autonomous hydrophones, has emerged as a valuable marine mammal monitoring technique, especially in highly vocal species like beluga whales (Simard et al. 2010, Castellote et al. 2013, 2015, 2016). In the Mackenzie Estuary, Simard et al. (2014) used PAM to clearly document the timing of belugas entering the estuary (immediately after ice-break up) and detected a semi-diurnal pattern, with presence around high tide and absence around low tide. Simard et al. (2014) also hypothesized that there could be linkages between beluga habitat use and environmental variables, including air temperature, water temperature, wind speed, and wind direction, but more information over larger spatial and temporal scales, coupled with visual observations, would be required to test this.

In this paper, we build on the research by Harwood et al. (2014) and Simard et al. (2014) by using an expanded PAM array to identify spatial and temporal patterns of beluga habitat use from June to August 2017 in the Mackenzie Estuary. Secondly, we compare acoustic data with visual observations to validate PAM in determining beluga presence in the estuary. Finally, we test the hypothesis that habitat use patterns are influenced by local environmental conditions like water temperature, water depth, salinity, wind speed, and wind direction. By including the presence of watercraft in our models, we also control for anthropogenic influences on beluga habitat use patterns. Understanding how these variables influence beluga movement is crucial for predicting how belugas will be impacted by the climate-driven changes that are rapidly affecting the Arctic (Stroeve et al. 2012).

## 2. MATERIALS AND METHODS

### 2.1. Study area

The Mackenzie River estuary is 80 km across and is comprised of low-lying alluvial islands with 3 main channels: East Channel, Peel Channel, and Middle Channel (Fig. 1a). Peak flow occurs during spring due to snowmelt and breakup of river ice, but summer flows remain high due to contributions from rainfall (Yang et al. 2015). The estuary is covered in ice from early October until about mid-June (Galley et al. 2008). The Mackenzie River is the most sediment-rich river in the Arctic, with a substrate comprised mostly of clay and silt (Carmack & Macdonald 2002), resulting in high turbidity. Discharge from the river forms warm freshwater plumes that tend to flow eastward along the Tuktoyaktuk Peninsula, although this is heavily influenced by winds. Easterly winds typically cause upwelling and can push plume waters several hundred kilometers offshore, while westerly winds force plume waters against the coast, enhancing flow along the Tuktoyaktuk Peninsula (Carmack & Macdonald 2002). Sea surface temperatures in the estuary are generally 5–10°C warmer than in the offshore waters (Fraker et al. 1979).

The East Channel of the Mackenzie River flows into Kugmallit Bay (Fig. 1), located between Richards Island and the Tuktoyaktuk Peninsula. The bay is very shallow, with depths rarely exceeding 2 m, although a narrow channel approximately 5–9 m deep exists along the western shore (Fig. 1b). Aside from the channel, most of the bay consists of a flat,

featureless silty bottom, with a sandy shoal in the centre, a partially scoured seabed area along the western shore, and gravel along the southeast (Loseto et al. 2015). Tides within the bay are semidiurnal and have a maximum amplitude of ~50 cm (Simard et al. 2014). Water levels are often driven by wind direction, where prolonged northerly winds can push water into the bay, increasing water levels during storm surges. In June, ice breakup culminates with the breakup of a landfast ice bridge across the mouth of the bay, after which belugas have access to the bay. Most of the belugas harvested in the Mackenzie Delta are landed in Kugmallit Bay (Harwood et al. 2015) by hunters based in Tuktoyaktuk or the East Whitefish camp (Fig. 1b).

### 2.2. Data collection

We equipped seabed moorings with passive acoustic sensors to measure sound in the water column (i.e. whales, anthropogenic noise, and waves), as well as oceanographic sensors to measure the water properties. These moorings were deployed in Kugmallit Bay immediately prior to the break-up of the ice bridge on 20 June and were retrieved on 21 August 2017 (Fig. 1). We based mooring placement on previously identified beluga hotspots (Harwood et al. 2014), unique seabed features, oceanographic conditions, and traditional ecological knowledge. A maximum listening range for a PAM system in Kugmallit Bay was previously estimated at 5–10 km (Simard et al. 2014), but propagation of beluga sounds is likely much less on many days. Simard et al.'s estimate was based on beluga call spectral source levels, propagation loss approximation based on the shallow water depth, and the levels of calls exceeding ambient noise, but did not consider absorption effects and was not empirically tested.

We equipped each mooring with a Song Meter SM2M or Song Meter SM3M Submersible Marine Recorder (Wildlife Acoustics) with factory-calibrated hydrophones. These hydrophones have a recording sensitivity of approximately  $-165$  dB re 1 V/ $\mu$ Pa with a frequency response between 0.2 and 30 kHz ( $\pm 2$  dB) and  $>30$  kHz ( $\pm 5$  dB). The recorders were equipped with either a standard or an ultrasonic hydrophone which determined sample rate (96 or 384 kHz, respectively; Table 1). A 96 kHz sample rate provided a recording bandwidth of 2 Hz to 48 kHz, sufficient to capture beluga social calls, broadband calls, and low-frequency echolocation clicks (Belikov & Bel'kovich 2006), while the 384 kHz sample rate provided record-

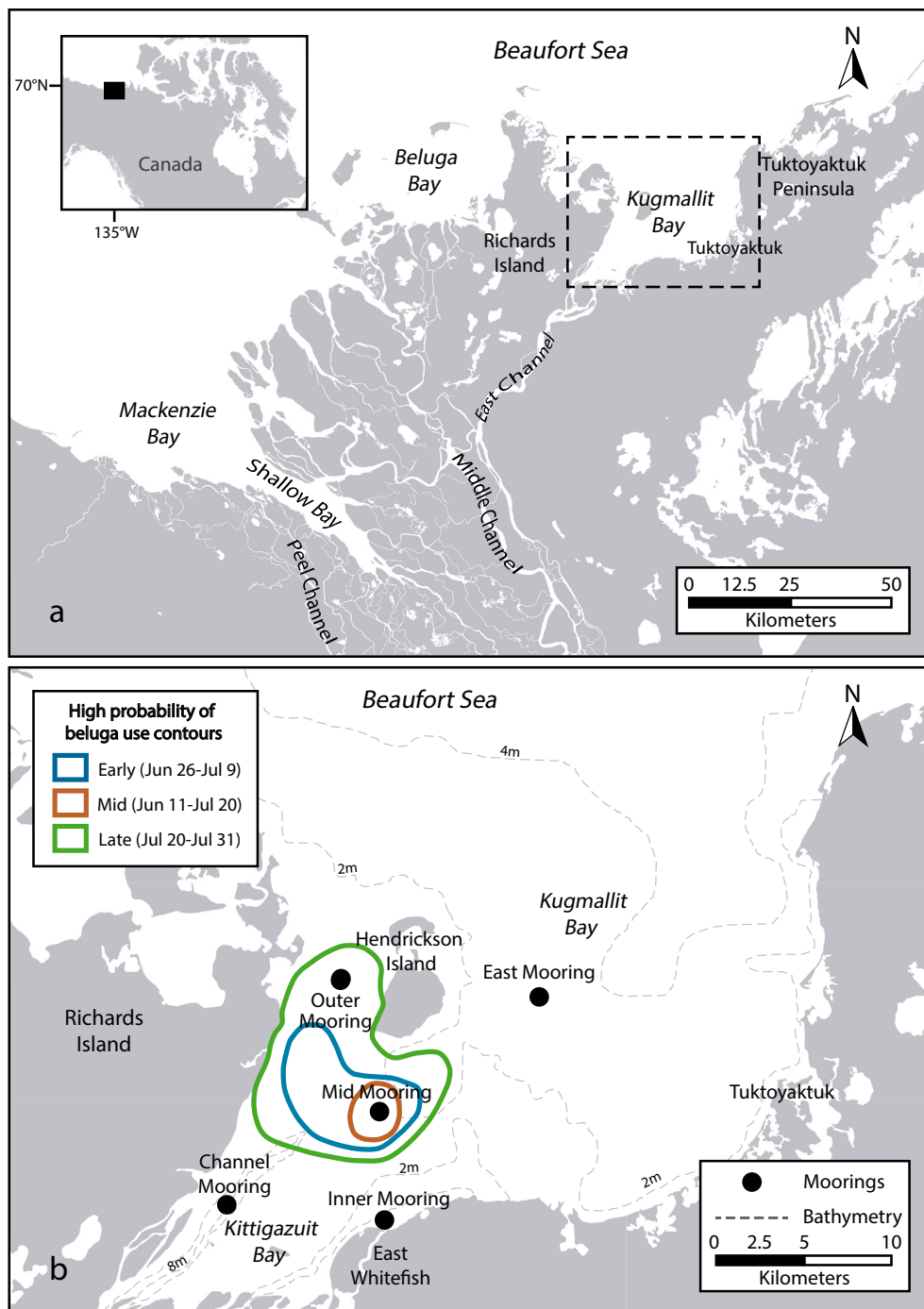


Fig. 1. (a) Mackenzie Delta (Northwest Territories, Canada). The study area is enclosed in the dashed line. (b) Kugmallit Bay, showing the location of the 5 seabed moorings: Outer, Mid, Inner, East, and Channel. Locations of high probability of use, or beluga 'hot spots', are identified as the 50% volume contours of beluga sightings made during aerial surveys in the Mackenzie Estuary during early, mid, and late July during the time periods 1977–1985 and 1992 (data from Harwood et al. 2014). The Channel (bottom left) represents a unique oceanographic feature, and was the location of hydrophone deployment by Simard et al. (2014)

ing bandwidth of 2 Hz to 192 kHz, covering the entire vocal range of belugas, including ultrasonic echolocation clicks (Ford 1977, Au et al. 1985). All recordings were made with a 16-bit sample size and a 25% duty

cycle (15 min on/45 min off). The use of hydrophones with different recording bandwidths represents a shift from the standard hydrophones to ultrasonic in an ongoing, long-term beluga whale monitoring study in

Table 1. Instrumentation of seabed moorings deployed in Kugmallit Bay (Mackenzie River Estuary, Canada) in 2017, with locations indicated in Fig. 1. Hydrophone type is indicated by the sample rate (96 kHz for a standard hydrophone, 384 kHz for an ultra-sonic). Recording start time was defined as the first recording made after deployment of the mooring and end time was the time the battery life of the recorder died. Conductivity-temperature-depth (CTD), temperature-depth (TD), and wave loggers (wave height) ran for the duration of deployment. Bottom depth is the water depth recorded at the time of deployment

Location	Acoustic recorder	Sample rate (kHz)	Recording start (mm/dd; h)	Recording end (mm/dd; h)	Oceanography sensors	Bottom depth (m)
Outer	SM2M	96	06/21; 06:00	08/10; 20:00	CTD, wave logger	1.6
Mid	SM2M	384	06/20; 14:00	08/19; 04:00	CTD	1.6
Inner	SM2M	384	06/20; 21:00	08/19; 04:00	TD	1.1
East	SM3M	384	06/21; 07:00	08/19; 06:00	CTD, wave logger	2.2
Channel	SM2M	96	06/20; 15:00	08/18; 01:00	TD	8.0

Kugmallit Bay. However, during manual analysis for presence/absence, we did not find any sound files where beluga calls were isolated to >48 kHz, so both types are equally adequate in determining presence/absence.

To assess the influence of oceanographic variables on beluga detections, we attached conductivity-temperature-depth recorders (CTDs), temperature-depth recorders (TDs), and wave loggers (to measure wave height; manufactured by RBR) to the moorings (Table 1). In previous years, the Channel and Inner moorings remained fresh throughout the summer, so we did not measure salinity at these sites during this study period (Fisheries and Oceans Canada unpublished data). CTDs and TDs were programmed with a 5 s sampling period, and wave loggers recorded wave bursts of 512 samples every 5 min at a 6 Hz sampling rate. We set up a shore-based weather station (manufactured and monitored by Campbell Scientific) at the East Whitefish hunting camp, near the Inner mooring, to collect weather data. Every 10 min, the station recorded wind speed, wind direction, and air temperature, and averages were transmitted hourly to a publicly accessible website.

### 2.3. Presence/absence validation

To validate that acoustic data are an accurate representation of beluga presence/absence, we conducted shore-based visual surveys from the weather station at East Whitefish, with 3 surveys d<sup>-1</sup> from 9–16 July 2017. Surveys were conducted opportunistically, and logistical challenges resulted in back-to-back surveys on 4 occasions. The weather station was located on top of a cliff (~7 m above sea level) located 400 m from the Inner mooring. We restricted analysis to only the observations near the Inner mooring. Each survey consisted of 3 observers working

together to watch for beluga presence with binoculars for 15 min at the start of the hour to coincide with the hydrophone recording. When belugas were sighted, the observers recorded group size and estimated distance from the hydrophone based on the known distance from the weather station to landmarks around the bay, like Hendrickson Island, Richards Island, and the channel (Fig. 1). Thirteen additional shore-based surveys were carried out opportunistically from Hendrickson Island, with 1 observer looking towards the Mid or Outer mooring. The same protocol was followed (aside from the number of observers), although surveys were less accurate, as establishing the precise location of these moorings from the island was difficult. We supplemented surveys from East Whitefish with unmanned aerial vehicle (UAV) surveys when weather permitted (wind speed <25 km h<sup>-1</sup>, no rain) and when their use would not interfere with nearby subsistence beluga hunts. During UAV surveys, we used a DJI Phantom 4 Pro programmed to photograph a 750 × 500 m grid over the hydrophone at an altitude of 70 m, with a 70 % frontal overlap and 0 % side overlap. Grids were followed by manual searches until battery life was depleted. Due to variability in battery life with wind conditions, manual search time varied greatly (3–15 min).

### 2.4. Sound analysis

We used a combination of automated detection and manual analysis to parse sound files for beluga presence/absence. We first determined beluga presence in each sound file by counting echolocation clicks and broadband pulse calls using a custom MATLAB® (The MathWorks) script, which bases detection on a Teager-Kaiser amplitude detection threshold and click train characteristics, including click duration and inter-click interval (Roy et al.



2010). This automated detector has been used to detect clicks for both narwhals (Marcoux et al. 2017) and belugas (Roy et al. 2010). Aside from belugas, odontocetes are extremely rare in the Mackenzie Estuary (Fraker et al. 1979), so it was assumed that any click trains characteristic of odontocetes were from belugas. Sound files were passed through a 20 kHz high-pass filter to limit the number of false positives due to wind and waves.

We verified positive results from the click detector by visually scanning long-term spectral average (LTSA) plots. These were created using the MATLAB script 'Triton' (Scripps Whale Acoustic Lab) by averaging acoustic energy over 5 s intervals into 100 Hz frequency bins (Fig. 2). Potential false positives and negative results were visually and aurally scanned for whistles and clicks using spectrograms created in Raven (version 1.5; Cornell Lab of Ornithology) and corrected. We also identified sounds from watercraft (broadband signals with low fundamental frequency lasting for several minutes) while scanning the LTSA plots and verified these aurally and visually using spectrograms in 'Triton'.

## 2.5. Data analysis

We first calculated summary statistics regarding spatial and temporal trends of beluga presence. To determine preference for particular locations, we calculated the percentage of recordings where belugas were present for each mooring. We also calculated the duration of presence bouts (defined as consecutive hours of presence without absence) as a metric of preference. To examine temporal trends at each mooring, we calculated the number of detection hours per day (DHPD; the number of hours with positive beluga presence) and plotted this over time. To visualize diel or tidal patterns, we calculated the percentage of positive detections for each hour of the day over the whole season (e.g. the number of days belugas were present at 10:00 h over the total number of days).

We averaged oceanographic data collected at each mooring over each hour to match with hydrophone recordings. We paired each hydrophone recording with the oceanographic data for the hour leading up to the recording, as these would have been the conditions influencing presence/absence at that time. We used time-series plots and correlation matrices (Pearson's  $r$ ) for environmental variables at each mooring to explore relationships among the environmental variables. We

tested differences in environmental variables among moorings using Wilcoxon rank sum and Kruskal-Wallis tests. We used Wilcoxon rank sum and the Rayleigh test for uniformity to test environmental and time of day influences on the detection of watercraft. Pearson's  $r$ , Wilcoxon rank sum, and Kruskal-Wallis tests were performed in the R package 'stats' (version 3.4.3), and the Rayleigh test was performed in the R package 'circular' (version 0.4-93).

We used multiple logistic regression to test the hypothesis that local environmental conditions influence beluga presence/absence. Logistic regression models were created in the R package 'stats' (version 3.4.3) to generate a response curve describing the probability of occurrence as a function of one or more environmental variables. We used the likelihood ratio test to determine the significance of each parameter's contribution to the model and compared the deviance of a model with only the intercept to the deviance of each fitted model (Hosmer et al. 2013). We considered the inclusion of a parameter significant if it resulted in a reduction in deviance larger than the critical value of chi-squared at the 95 % level for  $n$  degrees of freedom ( $n$  = number of additional parameters). We used the reduction in deviance ( $R$ ) to assess the contribution of each variable to the explanation of variance in data points:

$$R = (1 - D_1/D_0) \times 100 \% \quad (1)$$

where  $R$  is the reduction in deviance,  $D_0$  is the deviance of the model without explanatory variables, and  $D_1$  is the deviance of the model with explanatory variables. The variables salinity, temperature, wind speed, wind direction, water depth, date, time of day, and presence of watercraft were considered. We isolated tide from seasonal and wind-generated fluctuations in water depth by subtracting a 13 h centred moving average from water depth to create a tidal variable. This was tested as a covariate as well. We converted each circular variable (i.e. wind direction, time of day) to an angle ( $\theta$ ) and added them to the model as 2 variables ( $\sin \theta$  and  $\cos \theta$ ). In cases where only 1 component was significant, the other was excluded from the model. The presence of watercraft had the potential to influence belugas not only at the time of detection, but for several hours after passing (Caron & Smith 1990), so we tested different blocks of time following the passage of watercraft as predictors (i.e. watercraft detected within the last hour, within the last 2 h etc.,

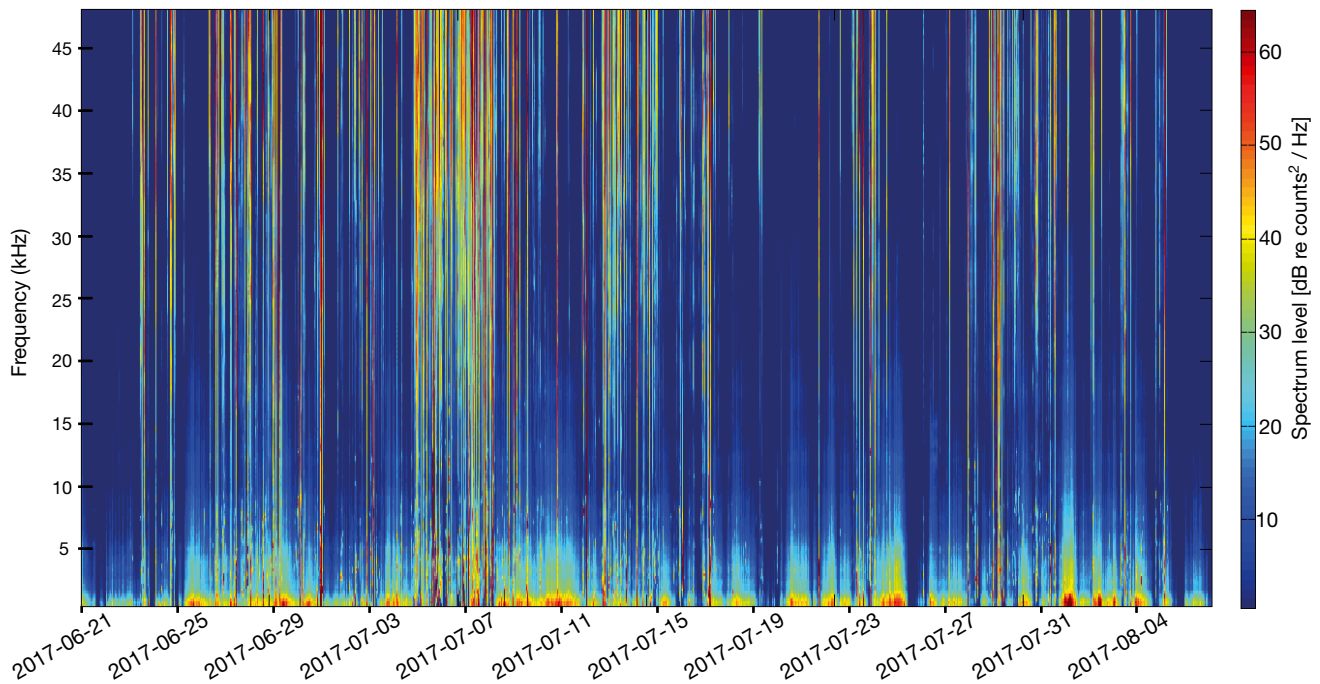


Fig. 2. Long-term spectral average plot with 100 Hz frequency bins averaged over 5 s time intervals for the Mid mooring (see Fig. 1) from 21 June to 7 August 2017. Periods of high beluga presence appear as broadband streaks extending to the top of the plot. Wind and wave activity appear primarily below 7 kHz, decreasing in power at higher frequencies.

to a maximum of 12 h). We included the block with the greatest reduction in deviance as a covariate in the final model.

We first analysed each variable independently using univariate logistic regression and added to the model in a stepwise manner, beginning with the variable which resulted in the greatest reduction in deviance. Prior to its inclusion in the model, we centred each variable on its mean (by subtracting the mean from each observation) to ease the interpretability of regression coefficients (Dalal & Zickar 2012). To determine the most parsimonious model, we excluded variables if they did not result in a significant reduction in deviance or did not reduce the model's Bayesian information criterion score, which penalizes complex models (Schwarz 1978). We also excluded variables if their significance in the model was due to correlation with more relevant variables. Interactions between and among variables were not included to ease model interpretation. To test for autocorrelation in beluga detections, we performed the runs test for randomness in the R package 'tseries' (version 0.10-44). We used the Rayleigh test for uniformity to test if beluga detections were concentrated during high tide at the Channel. This was done in place of a logistic regression model because the overall detection rate was low.

### 3. RESULTS

#### 3.1. Visual surveys

At the East Whitefish weather station, belugas were sighted at distances ranging from 100 m to 2 km from the Inner mooring during 8 of 22 shore-based surveys. The number of belugas in these sightings ranged from 1 to >20, and they were always detected on the hydrophone. There was also 1 visual observation of 6 belugas at least 5 km from the mooring, and 2 visual observations of large groups of belugas approximately 10 km from the mooring; during these sightings, belugas were not detected on the hydrophone. Additionally, there was 1 instance where belugas were detected on the hydrophone but were not visually observed.

At Hendrickson Island, belugas were sighted during 7 of 13 shore-based surveys. There were no instances where belugas were visually observed and not heard on the hydrophone; however, there were 4 instances where belugas were detected on the hydrophone but not visually observed. Group size and distance from the hydrophone were not recorded at Hendrickson Island. The UAV did not improve the ability of the observers to determine presence/absence, because when whale presence

was documented with the UAV, whale presence was always first observed by the observers with binoculars.

### 3.2. Spatial and temporal patterns of habitat use

The first beluga detection was made early on 22 June, 2 d after deployment, with the last detection made on 18 August, 3 d prior to retrieval. The Outer mooring stopped recording on 10 August, but beluga vocalizations occurred in the last recording, suggesting that there was undetected activity at that location afterwards. All other recorders stopped on 18 or 19 August (see Table 1), so there may have been undetected beluga activity afterwards at these locations as well, although detection rate had declined substantially prior to this date. At each mooring, more than 95 % of positive detections contained high-frequency calls (>20 kHz). Overall detection rate was highest at the Outer and Mid moorings, with detections in 62.4 and 62.9 % of recordings, respectively, followed by

the Inner mooring (39.4 %), East mooring (22.8 %), and the Channel (4.6 %). Following the first detection, DHPD were low for 2 d but increased afterwards. Patterns in DHPD were similar at the Outer and Mid moorings, where detection rate was high until mid-July and fluctuated thereafter (Fig. 3). The Outer and Mid moorings have similar water depths and seabed conditions (D. Whalen et al. unpubl.), and both experience warm fresh waters for most of the summer. The sites only differed during NW wind events when the Outer mooring was inundated with cold saline water that did not reach the Mid mooring. At the Inner mooring, DHPD began to decline in early July, but a second peak occurred towards the end of July (Fig. 3). Overall, DHPD at the Mid, Inner, and Channel moorings decreased significantly as the season progressed (Mann-Kendall tau = -0.326,  $p < 0.01$ ; tau = -0.313,  $p < 0.01$ ; tau = -0.276,  $p < 0.01$ ). The runs test for randomness showed a non-random distribution in detections ( $p < 0.001$  for all moorings). This was emphasized by continuous periods of presence at the Outer and Mid sites, up to 128 and 112 h,

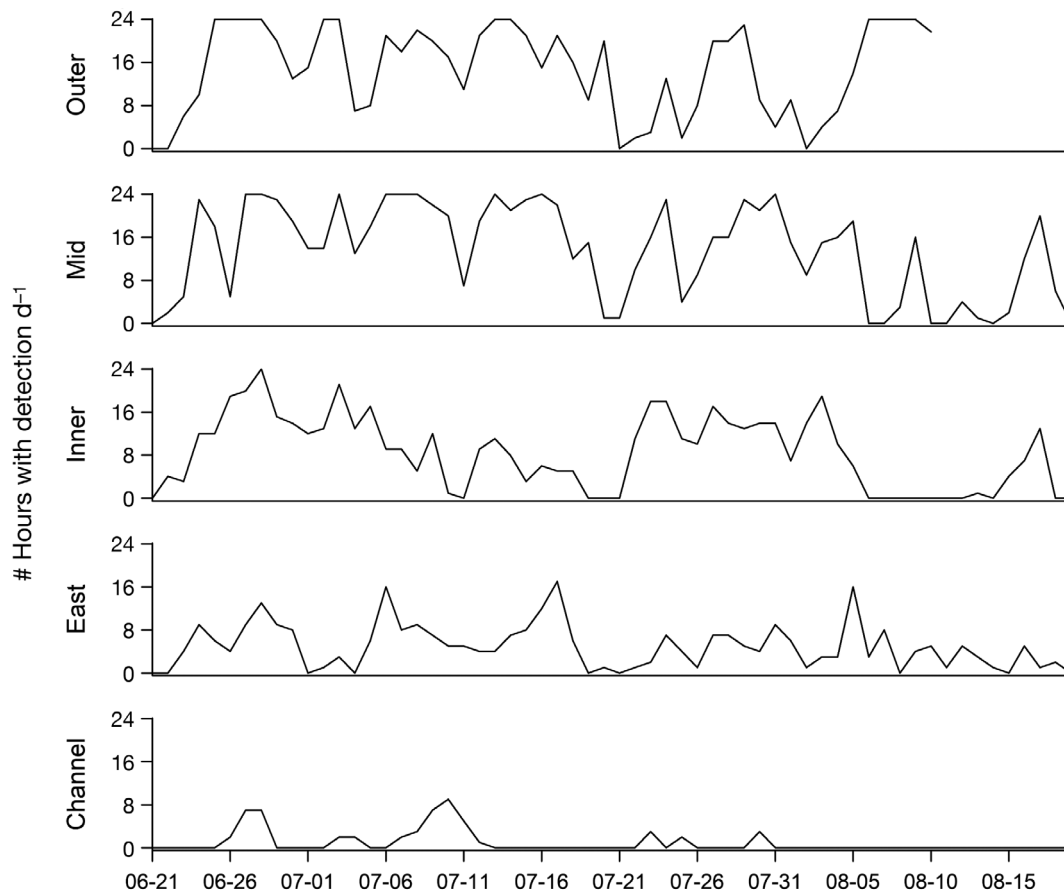


Fig. 3. Beluga detection hours per day at each mooring from 21 June to 19 August 2017. At the Outer mooring, the recorder's battery died on 10 August



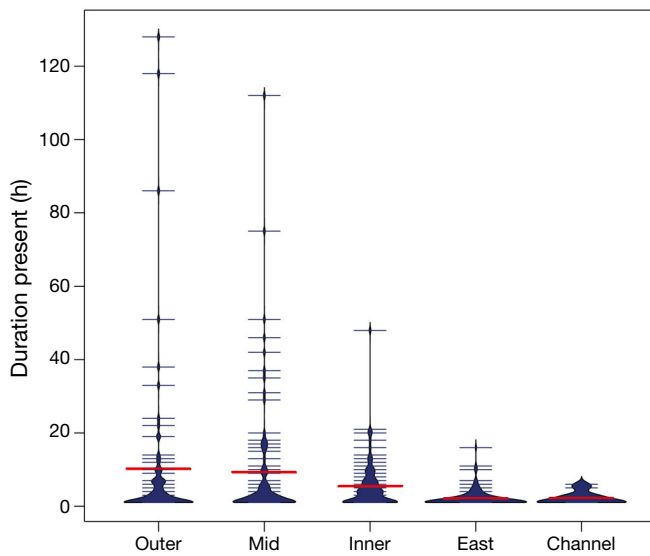


Fig. 4. Bean plot showing duration of bouts at each mooring from 21 June to 10 August 2017. The length of a bout (shown by the blue horizontal lines) was defined as the number of consecutive hours of beluga presence without absence. The width of each bean is determined by the relative abundance of bouts of a given length. The red line is the mean bout duration. Bouts at the Outer and Mid moorings were longest, while the majority of bouts at the East and Channel moorings were short

respectively (Fig. 4). It was assumed that such long periods of presence were due to continuously favourable conditions, rather than the presence of belugas at time  $t - 1$ , so an autocorrelation structure was not incorporated into models of environmental drivers. Despite the low detection rate near the Channel mooring, we noted a semi-diurnal cycle, with most detections occurring during the mornings and evenings (mean detection time: 16.9 h after midnight; circular variance: 0.81; Fig. 5). A diel pattern was also apparent at the Inner mooring, where belugas were more commonly present in the mornings (mean detection time: 6.3 h after midnight; circular variance 0.76; Fig. 5), and the East mooring, with more detections made around mid-day (mean detection time: 10.9 h after midnight; circular variance 0.83). We did not observe strong diel patterns at the Mid or Outer moorings.

### 3.3. Environmental conditions

Environmental conditions in the estuary varied greatly across all 5 moorings and throughout the summer (Fig. 6; see Figs. S1–S3 in the Supplement at [www.int-res.com/articles/suppl/m626p209\\_supp.pdf](http://www.int-res.com/articles/suppl/m626p209_supp.pdf)). To assess the relationship of environmental variables

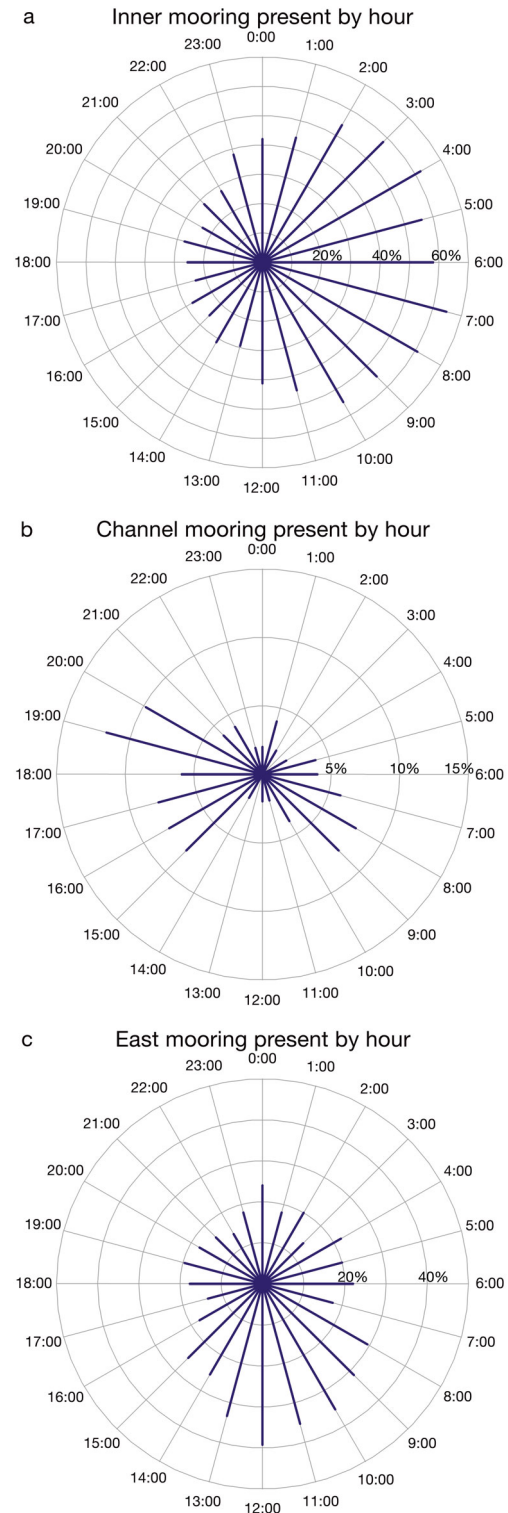


Fig. 5. Percentage of all sound recordings with beluga presence for each hour of the day at the (a) Inner, (b) Channel, and (c) East moorings (note the difference in scale). At the Inner mooring, presence was most common in the mornings, with beluga recorded at 07:00 h on 65% of days. At the Channel, detections were highest around 19:00 (13%) and 08:00 h (8%), and at the East mooring, detections were highest at 12:00 h (39%)

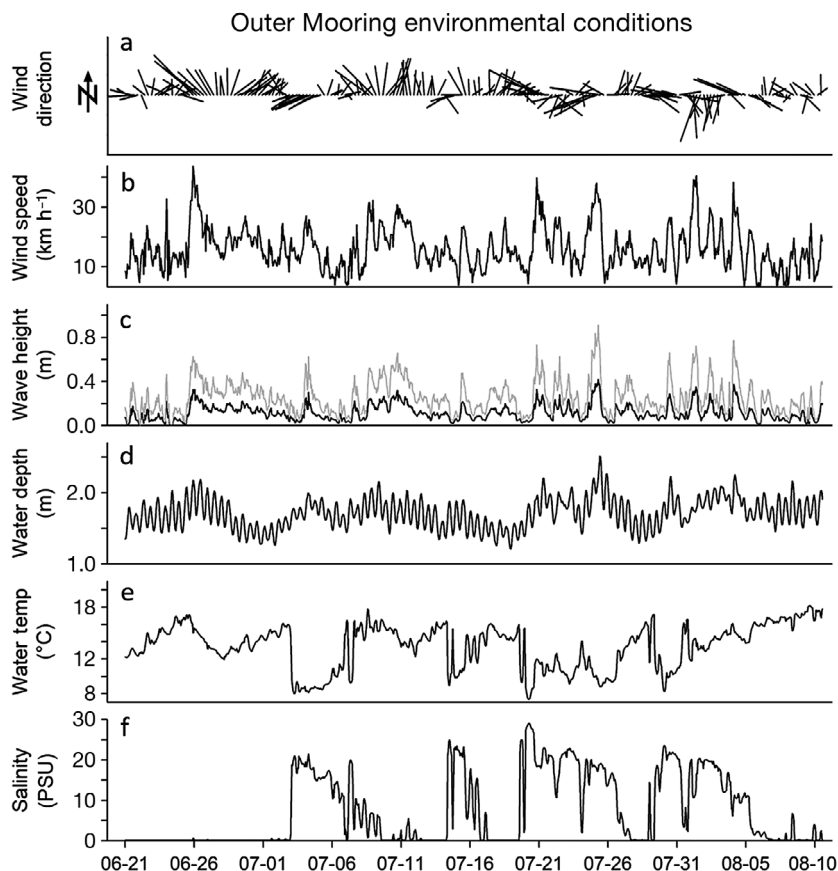


Fig. 6. Environmental conditions at the Outer mooring from 24 June to 10 August 2017. (a) Wind direction recorded at the East Whitefish weather station, presented as the direction from which the wind is blowing. The length of the stick is proportional to wind speed. For clarity, the 6 h centred average is shown. (b) Wind speed recorded at the East Whitefish weather station. (c) Average wave height (black) and maximum wave height (grey). (d) Water depth. (e) Water temperature. (f) Salinity. Environmental conditions at the other moorings are provided in Figs. S1–S3 in the Supplement

with each other, we made correlation matrices for the Outer, Mid, Inner, and East moorings (Table 2). Wind speed was significantly positively correlated with water depth at all moorings (Table 2). Wave height, measured at the East and Outer moorings, was highest on the East side (Wilcoxon rank sum test:  $p < 0.0001$ ; Fig. 6c; also see Fig. S1). At both locations, wave height was significantly positively correlated with wind speed (East:  $r = 0.79$ ,  $p < 0.01$ ; Outer:  $r = 0.86$ ,  $p < 0.01$ ; Table 2). Wind direction was significantly correlated with all oceanographic variables at all moorings, except temperature at the East mooring (Table 2). Wind speeds from the north and west tended to be higher and brought colder water temperatures and increased salinity (Fig. 6b). Where observed, increases in salinity were aligned with cold oceanographic water surges (Fig. 6f, Table 2). Kruskal-Wallis tests revealed that temperature and salinity varied by

location (temperature:  $\chi^2 = 1556.7$ ,  $df = 3$ ,  $p < 0.0001$ ; salinity:  $\chi^2 = 1026$ ,  $df = 2$ ,  $p < 0.0001$ ), with post hoc analyses showing the coldest, saltiest conditions at the East mooring ( $p < 0.0001$  for both temperature and salinity), which was more saline than other sites for most of the summer (see Fig. S1). Oceanic influxes at the Outer mooring occurred on 4 occasions and followed salinity increases at the East mooring by about 2 d. Periods of intense NW winds caused these influxes to reach the Mid mooring on occasion, but these were smaller in magnitude and duration and followed those at the Outer mooring (see Fig. S2).

### 3.4. Detection of watercraft

Watercraft were detected as broadband signals lasting for several minutes but were almost never detectable for an entire 15 min sound file (see Fig. S4 for an example). These sounds are indicative of small, fast boats used by local hunters and travellers, rather than larger slow-moving vessels like ships, tug boats, and barges. Small-boat sounds were present in 64 files at the Inner mooring, 11 files at the Mid mooring, 4 files at the Channel, and 2 files at East mooring. No boats were detected at the Outer mooring. At the

Inner mooring, boat detections were most common in the afternoon (mean detection time: 15:52 h; circular variance: 0.76; Rayleigh test  $p = 0.02$ ) and when wind speed was low (Wilcoxon rank sum test:  $p < 0.0001$ ). Boat detections did not significantly differ with any other environmental predictors tested in the Inner mooring logistic regression model (Wilcoxon rank sum test: all  $p > 0.1$ ). At the Mid mooring, boat detections were more common when wind speed was low ( $p = 0.01$ ), with no significant mean detection time (Rayleigh test  $p = 0.36$ ).

### 3.5. Environmental drivers of habitat use

We performed multiple logistic regression models to determine if any of the environmental variables outlined above affected beluga presence/absence.

Table 2. Correlation matrices (Pearson  $r$ ) for environmental variables measured at the Outer, Inner, Mid, and East moorings (see Fig. 1 for site locations). Asterisks indicate significance: \* $p < 0.05$ , \*\* $p < 0.01$

Outer	Salinity	Temperature	Wind speed	Wave height	Water depth
Temperature	−0.79**				
Wind speed	0.075**	−0.026			
Wave height	0.028	−0.0035	0.86**		
Water depth	0.40**	−0.24**	0.30**	0.31**	
Wind direction	0.51**	0.33**	0.36**	0.32**	0.45**
East	Salinity	Temperature	Wind speed	Wave height	Water depth
Temperature	−0.85**				
Wind speed	−0.12**	0.11**			
Wave height	−0.21**	0.19**	0.79**		
Water depth	0.13**	0.027	0.21**	0.14**	
Wind direction	0.23**	0.028	0.36**	0.23**	0.47**
Mid	Salinity	Temperature	Wind speed	Water depth	
Temperature	−0.60**				
Wind speed	0.16**	−0.16**			
Water depth	0.36**	−0.13**	0.21**		
Wind direction	0.22**	0.30**	0.36**	0.44**	
Inner	Temperature	Wind speed	Water depth	Salinity at Outer	
Wind speed	−0.0025				
Water depth	0.10**	0.31**			
Salinity at Outer	0.078**	0.075**	0.37**		
Wind direction	0.31**	0.36**	0.38**	0.51**	

Other potential drivers, such as time of day, date, and the presence of boats, were also included in the models to determine their influence relative to environmental conditions. We did not complete a logistic regression model for the channel due to low detection rate; however, there appeared to be a tidal influence, with most detections made during high tide (mean detection time: 0.66 h after high tide; circular variance: 0.53; Rayleigh test:  $p < 0.001$ ; Fig. 7). Tide did not significantly influence beluga detections in any of the regression models at the other moorings.

The best model at the Outer mooring contained salinity, wind speed, date, and wind direction as predictors and had a reduction in deviance of 21.6%. Increased salinity negatively influenced beluga detections and contributed the greatest reduction in deviance of all predictors (without salinity:  $R = 10.4\%$ ; Table 3). At this mooring, all salinity influxes were paired with cold ocean surges (Fig. 6), so water temperature was not included in the model. Wind speed also had a negative influence on detection rate, and its inclusion in the model had the second greatest reduction in deviance (without wind speed  $R = 13.9\%$ ; Table 3). Date and wind direction were sig-

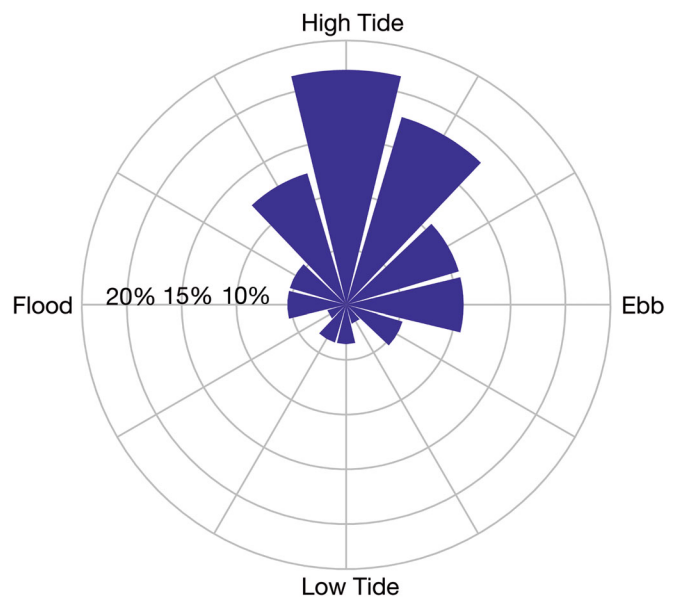


Fig. 7. Tidal effect on beluga presence at the Channel mooring from 24 June to 10 August 2017. The size of the triangle represents the percentage of all beluga detections at the Channel that were made at the indicated tidal level. This was the only location to show this relationship

Table 3. Logistic regression output for predicting beluga presence/absence at the Outer, Mid, Inner, and East moorings (see Fig. 1) from 24 June to 10 August 2017. The best logistic regression models (i.e. lowest Bayesian information criterion [BIC] score) for each location are given on the left including regression coefficients (\* $p < 0.01$ ) and standard error (SE). Model comparisons for each location are given on the right, with the reduction in deviance (R) and BIC of the best model (includes all predictors listed on the left), and the best model minus 1 of the predictors. Salinity at the Outer mooring ('Salinity at Outer') was used as a predictor for the Inner mooring model. Boat 6 h (Boat 10 h): detection of a boat on the hydrophone within the previous 6 (10) h

Logistic regression models			Model comparisons		
Predictor	Coefficient ( $\beta_i$ )	SE	Model	R (%)	BIC
<b>Outer</b>					
Intercept	0.799*	0.074	Full	21.6	1198.3
Wind direction (sin)	-0.417*	0.128	- Wind direction	20.9	1202.1
Date	-0.019*	0.006	- Date	20.8	1202.4
Wind speed	-0.117*	0.012	- Wind speed	13.9	1305.7
Salinity	-0.113*	0.009	- Salinity	10.4	1357.6
<b>Inner</b>					
Intercept	-0.026	0.080	Full	23.1	1259.8
Wind speed	-0.033*	0.010	- Wind speed	22.4	1263.6
Temperature	-0.288*	0.045	- Temperature	20.4	1294.4
Date	-0.040*	0.006	- Date	20.0	1301.0
Salinity at Outer	0.063*	0.009	- Salinity at Outer	19.5	1308.8
Time of day (sin)	0.823*	0.105	- Time of day	19.0	1317.6
Boat 6 h	-1.531*	0.184	- Boat 6 h	18.1	1331.6
<b>Mid</b>					
Intercept	0.873*	0.074	Full	13.4	1311.2
Salinity	-0.054*	0.017	- Salinity	12.7	1315.3
Boat 10 h	-1.224*	0.239	- Boat 10 h	11.7	1331.0
Wind speed	-0.074*	0.010	- Wind speed	9.6	1341.9
Date	-0.051*	0.005	- Date	6.9	1401.7
<b>East</b>					
Intercept	-1.307*	0.078	Full	8.1	1192.7
Depth	-1.540*	0.364	- Depth	6.7	1204
Time of day	-0.494*	0.103	- Time of day	6.3	1209.3
Wind speed	-0.059*	0.012	- Wind speed	5.9	1213.4
Salinity	-0.041*	0.007	- Salinity	5.7	1216

nificant but made minor contributions to the overall model (relative to salinity and wind speed).

Examination of the timing of oceanic influxes at the Outer mooring (Fig. 6) and the second peak in DHPD at the Inner mooring (Fig. 3) led us to hypothesize that belugas move further into the estuary during cold oceanic influxes. Therefore, we tested salinity at the Outer mooring as a predictor at the Inner mooring. The best model at the Inner mooring included the presence of a boat within the past 6 h, time of day, salinity at the Outer mooring, date, temperature, and wind speed as predictors ( $R = 23.1\%$ ). Increased salinity at the Outer mooring had a positive influence on beluga detections at the Inner mooring (without salinity,  $R = 19.5\%$ ; Table 3). Boats were commonly detected at this mooring, and presence of a boat within 6 h had the strongest negative influence on beluga detec-

tions and contributed the greatest reduction in deviance in the best model (without boat presence,  $R = 18.1\%$ ; Table 3). Date, temperature, and wind speed were all negatively associated with beluga detections at the Inner mooring (Table 3).

Logistic regression models at the Mid and East moorings had comparatively low reductions in deviance ( $R = 13.4$  and  $8.1\%$ , respectively). The best model at the Mid mooring included date, wind speed, boat presence (within the past 10 h), and salinity as predictors. Date was the best predictor of beluga detections at the Mid mooring, with fewer detections late in the season (Table 3). Increased wind speed, spikes in salinity, and the presence of a boat within the past 10 h were all negatively associated with beluga detections (Table 3). The best model at the East mooring included salinity, wind speed, time of day, and

water depth as predictors. Salinity, wind speed, and depth each had a negative association with beluga detections (Table 3).

#### 4. DISCUSSION

We used acoustic data to estimate patterns of beluga whale habitat use over space and time. Our visual observations support acoustic results from our study as well as others in the area (i.e. Simard et al. 2014); this was in agreement with studies which noted that visual observations of belugas correspond with vocalizations in turbid water (Castellote et al. 2013). While larger groups of whales were more likely to be detected than small groups or lone animals (both aurally and visually), this should not affect our overall interpretation of habitat use patterns and environmental drivers, as large groups are more representative of the entire aggregation. We identified patterns that are consistent with previous studies (Harwood et al. 2014, Simard et al. 2014) but provide more spatial and temporal detail of beluga use of Kugmallit Bay. For instance, our results demonstrated the preference for hotspots identified by Harwood et al. (2014), to the west and south of Hendrickson Island, but also that belugas frequently used the area near the East Whitefish camp early in the season and in the mornings. We also identified short periods of habitat use at the Channel, consistent with findings by Simard et al. (2014), as well as similar duration bouts at the East mooring, which suggests that belugas primarily transited through these areas. However, the presence of high-frequency calls (which do not propagate far) in most sound files where belugas were detected, and the short duration of detectability of boat sounds when present, suggests that the maximum listening range for a PAM system in Kugmallit Bay is less than the 5–10 km estimated by Simard et al. (2014). Visual surveys did not provide enough evidence to make an updated estimate of detection range.

Pairing beluga detections with oceanographic variables allowed us to identify key environmental drivers, including salinity and wind speed. Strong winds were negatively associated with beluga detections at all moorings, while beluga presence near the East Whitefish camp late in the season appeared to be in response to oceanic influxes of cold/saline water pushing further into the bay. The movement of whales away from cold/saline influxes lends support to the hypotheses that estuar-

ine waters are attractive because they facilitate moulting, or provide a thermal advantage to young belugas (Sergeant 1973, Smith et al. 1992). The presence of small boats, particularly near the East Whitefish camp, also influenced patterns of habitat use throughout the season and was likely a key reason for the lower detection rate at the Inner mooring compared to the Outer and Mid moorings. These boats are often used to hunt belugas in Kugmallit Bay, so an avoidance of boats is unsurprising.

##### 4.1. Influences of habitat use

The negative association of beluga presence with high salinity in Kugmallit Bay suggests an attraction to warm, fresh waters. High salinity is also a likely explanation for the low presence on the east side of Hendrickson Island (East mooring), which was inundated with salt water for most of the season. Previous studies have shown that beluga presence in estuaries tends to be higher in locations with low salinity (Moore et al. 2000), but, to our knowledge, changes in beluga presence in association with changes in ocean chemistry at one location over time has not been reported. It has previously been suggested that water temperature is the main factor governing whale distributions in the Mackenzie Estuary and that salinity is less important (Fraker et al. 1979); however, we found it difficult to separate the 2 factors, given that the coldest water temperatures were almost always associated with increases in salinity. Decreases in water temperature that were not associated with increased salinity were less extreme and did not affect whale presence at the hotspot locations. Although salinity is the best proxy for oceanic influxes, we cannot rule out that belugas are responding to colder temperatures.

High wind speed was associated with increased wave height, and both were associated with fewer whale detections at all locations. While strong winds can mask beluga calls and reduce the detection range of the hydrophone, almost all files with beluga presence contained high-frequency calls, which were produced closer to the hydrophone than its maximum listening range. These types of calls were much less affected by masking because noise from wind is at a low frequency, and wave sounds were not continuous (see Fig. S4). During the windiest conditions, sound levels in the high frequency range were similar to those in quiet conditions most of the time, and the vocalizations identified during typical beluga presence would have been detectable during



manual analysis. Therefore, the lower detection rate likely indicates that belugas were absent during windy conditions.

Lower beluga presence during windy conditions could be due to difficulty travelling in such shallow water (~2 m) when the water is rough. During the windiest conditions, maximum wave height could exceed 1 m, which would be felt throughout the entire water column and thus would be energetically costly for belugas, especially young ones. Higher waves on the east side of Hendrickson, which is more exposed to the Beaufort Sea, could also explain the lack of whales at this location. In the Northern Bering Sea, it has been suggested that belugas react to high-speed winds by seeking calmer waters or shelter close to shore (Mymrin & Huntington 1999), and in the Nastapoka Estuary, belugas appear to favour the upper estuary during periods of high waves and strong winds (Caron & Smith 1990). In our study, wind speed was associated with a low detection rate at all locations; therefore, it could not be determined where belugas go during high-speed winds. Whales may have taken shelter closer to Richards Island, where they would have been outside the detection range of the hydrophones, or moved to deeper waters, where it is possible to dive below the surface roughness and avoid stranding, especially when resting, sleeping, or being inattentive for any reason.

Increased detection rates in the mornings at the Inner mooring were not matched by a corresponding change in detection rate at any other location, suggesting the diel pattern only occurs in the inner estuary. This diel pattern did not appear to be in response to any environmental variables and was likely in response to human activity. The presence of small boats negatively influenced beluga detections at the 2 locations where it was regularly identified (the Inner and Mid moorings), and boat noises were most common at the Inner mooring and most frequent in the early afternoon. This is unsurprising, as East Whitefish is a traditional hunting camp, and hunters are less active during the morning. Given the 25% duty cycle on the hydrophone and the short duration of detectability of boat sounds, it is likely that many boats went undetected and appeared in the model as the time of day variable. Hunting activity and ship traffic are known deterrents to beluga presence elsewhere in the Arctic and sub-Arctic (Caron & Smith 1990, Frost & Lowry 1990, Lesage et al. 2014). While diel patterns in vocalization activity have been observed in other studies (Castellote et al. 2013), visual observations in our study suggest that whales move in and out of the location rather than change

their vocalization patterns. This diel pattern in beluga presence was also noted in an aerial survey report, which stated that local observers frequently observed whales near the Whitefish Station (i.e. Inner mooring) in the mornings (Robertson & Millar 1984). Alternatively, it is possible whales are moving in to catch fish at the mouth of the river during the morning, although it seems unlikely that whales feed in this estuary (Harwood et al. 1996, Loseto et al. 2009).

Tidal cycle appeared to have a limited effect on beluga detections and only appeared to be important at the Channel mooring, where most detections occurred at high tide. This was also found in 2011 and 2012 by Simard et al. (2014). The low detection rate could be due to sound propagation properties at the mooring. This mooring was deployed in a narrow channel which may have caused an acoustic shadow, preventing sounds from reaching the hydrophone unless they were produced directly above or in the channel. Belugas may have avoided spending time directly above or in the channel, except when the inward flood of tide slowed the outward flow of the Mackenzie River. Experimental testing of detection range should be conducted at this location if moorings are to be deployed here in the future. Alternatively, the channel could merely be a transit location that is easier to move through at high tide. The peak detection time (07:00 h) at the Inner mooring often coincided with the first high tide of the day, but vocalization activity was lowest during the afternoon high tide. However, if human activity is preventing use of the area in the afternoon, these movements could still be related to tide. Many studies have examined tidal effects on belugas in coastal estuaries (Kleinenberg et al. 1964, Caron & Smith 1990, Ezer et al. 2008), but these were largely conducted in estuaries where water levels fluctuate greatly. For example, belugas in Cook Inlet use high tides that range from 8–10 m to access areas of the estuary unavailable at low tide, including mouths of streams and rivers used by anadromous fish species that are beluga prey (Ezer et al. 2008). In the Mackenzie Delta, tides rarely exceed 0.5 m; thus, tides likely have little influence on beluga movements.

#### 4.2. Explanations for estuarine use

The apparent movement of whales away from cold/saline influxes lends support to the hypotheses that estuarine waters are attractive because they facilitate moulting (Smith et al. 1992) or that the warm water provides a thermal advantage to whales,

especially calves (Sergeant 1973). Considering that whales of different age/size classes, sex, and reproductive status appear to have different habitat requirements within their summer range (Loseto et al. 2006), Beaufort Sea belugas may converge on the estuary at different times for different purposes. For instance, thermal advantage is a likely explanation given the number of calves in the estuary and explains why belugas remain in the estuary late into the season. However, it does not explain the early season detections at the Inner mooring that were not associated with oceanic influxes, nor why males frequent the delta. One hypothesis is that early in the season, when temperatures across the bay are low, moulting is more difficult (Watts et al. 1991), causing whales to seek out the more abrasive seabed material found at the Inner mooring (Loseto et al. 2015) to successfully moult. Indeed, water temperature was a determinant of whale presence at the Inner mooring, with increased detections associated with colder temperatures. Alternatively, whales may enter the estuary early in the season, eager to moult, and may seek out abrasive substrate once the warm, fresh water has had a chance to interact with their skin cells (Watts et al. 1991). The diurnal pattern in presence/absence may be explained by a trade-off between substrate use for moulting and avoidance of human interactions. Abrasive substrate at the Inner mooring may facilitate moulting (Smith et al. 1992), which may help to minimize the amount of human interaction in the estuary. This idea is further supported by studies that suggest a lack of feeding within the estuary (Harwood et al. 1996, Loseto et al. 2009) as well as a short residence time (Richard et al. 2001). Unfortunately, due to the high turbidity in Kugmallit Bay, testing this hypothesis would be difficult, although future tagging studies may provide insights into the behaviour of whales at different locations in the estuary.

## 5. CONCLUSION

While motives for beluga presence and movements in the estuary are still not fully understood, we provide evidence supporting both the moulting and thermal advantage hypotheses and suggest that the estuary may provide multiple benefits to belugas. Given the ongoing and impending changes to the Arctic ecosystem (Stroeve et al. 2012) and anticipated increases in human activity (Reeves et al. 2014), a clear understanding of drivers for beluga habitat use is necessary. Many of the uncertainties surrounding belugas and the effects of climate change stem from an unclear

understanding of drivers for habitat use and the relative importance of habitat features (Laidre et al. 2008). While estuaries only make up a portion of the belugas' annual migration, they are nonetheless of critical importance (Finley 1982). One of the immediate effects of climate change, namely the expected increase in storms (Vermaire et al. 2013), could impact beluga habitat use. Here we have shown that increased wind speed can disrupt habitat use at preferred locations within the estuary. Furthermore, more frequent wind events, especially from the north and northwest, could result in increased frequency and duration of ocean surges, bringing more oceanic water into the estuary, thus forcing belugas to change their habitat use patterns in the bay. These altered patterns of habitat use may put belugas in greater contact with humans. It is possible that ocean surges will be balanced by expected increases in precipitation in the Mackenzie Basin in the spring and summer (Yip et al. 2012) and associated increases in Mackenzie River discharge (Manabe et al. 2004); however, predicting how increased discharge and ocean surges will interact to affect the water chemistry at beluga hot spots is a difficult task. Some models suggest that despite overall increases in river discharge, discharge in the summer months will decrease (Nohara et al. 2006, Yip et al. 2012). Current research into the dynamics of the Mackenzie Estuary aims to better understand the system and will help in the prediction of climate change impacts on beluga whales in the Beaufort region (Loseto et al. 2018b). Even changes in the timing of estuary use could impact Northern community members and hunters who have relied on belugas in the estuary for centuries (Fraker et al. 1979).

This study only examined 1 year of data, and while patterns of habitat use are consistent with those found by Harwood et al. (2014) and Simard et al. (2014), year-to-year variation in wind, ice break-up, and river discharge likely play a role in patterns of habitat use. Future studies should investigate the variation in these patterns using multi-year mooring deployments, coupled with visual observations. Additional analyses should also explore other habitat features (e.g. seabed substrate, river outflow, and human settlements) similar to Goetz et al. (2012). Future studies should also quantify and categorize vocalization activity to explore patterns in vocalization in greater depth than presence/absence. These studies, together with satellite tagging of individual whales, may shed light on divergent habitat use of whales of different age, sex, and reproductive status throughout the estuary and help us better understand

inter-annual variations in movement pattern responses to environmental conditions. Finally, it should be noted that belugas are intelligent, gregarious animals (Frost & Lowry 1990), and other factors likely contribute to their distribution. For example, culture inheritance and natal philopatry have recently been shown to play a major role in determining the summer and wintering grounds and migration routes of belugas (O'Corry-Crowe et al. 2018). Whales may use the estuary for the benefits of warmth and freshness, but their spatial and temporal distribution within the estuary may be influenced by cultural inheritance.

**Acknowledgements.** Funding for this project was provided by Fisheries and Oceans Canada, Natural Resources Canada, the W. Garfield Weston Foundation, the Northern Scientific Training Program, and the Fisheries Joint Management Committee. In-kind field support was provided by the Polar Continental Shelf Program and the Aurora Research Institute. We acknowledge the wonderful partnerships with the Fisheries and Joint Management Committee, the Inuvialuit Game Council, and the Hunters and Trapper's Committees of the Inuvialuit Settlement Region who supported the collection of data. We also thank S. MacPhee, A. Gordon, and E. Way-Nee for field support; C. Day, R. Day, B. Joe, and F. Angasuk, our camp hosts; Y. Simard for the automated detector; and N. Kenkel for statistical advice.

#### LITERATURE CITED

- ✦ Au WWL, Carder DA, Penner RH, Scronce BL (1985) Demonstration of adaptation in beluga whale echolocation signals. *J Acoust Soc Am* 77:726–730
- ✦ Belikov RA, Bel'kovich VM (2006) High-pitched tonal signals of beluga whales (*Delphinapterus leucas*) in a summer assemblage off Solovetskii Island in the White Sea. *Acoust Phys* 52:125–131
- ✦ Belikov RA, Bel'kovich VM (2008) Communicative pulsed signals of beluga whales in the reproductive gathering off Solovetskii Island in the White Sea. *Acoust Phys* 54: 115–123
- Byers T, Roberts LW (1995) Harpoons and ulus: collective wisdom and traditions of Inuvialuit regarding the beluga ('qilalugaq') in the Mackenzie River estuary. Byers Environmental Studies, Winnipeg
- ✦ Carmack EC, Macdonald RW (2002) Oceanography of the Canadian Shelf of the Beaufort Sea: a setting for marine life. *Arctic* 55:29–45
- Caron LMJ, Smith TG (1990) Philopatry and site tenacity of belugas, *Delphinapterus leucas*, hunted by the Inuit at the Nastapoka Estuary, Eastern Hudson Bay. *Can Bull Fish Aquat Sci* 224:69–79
- Cassini MH (2013) Distribution ecology from individual habitat use to species biogeographic range. Springer, New York, NY
- ✦ Castellote M, Leeney RH, O'Corry-Crowe G, Lauhakangas R and others (2013) Monitoring white whales (*Delphinapterus leucas*) with echolocation loggers. *Polar Biol* 36: 493–509
- ✦ Castellote M, Stafford KM, Neff AD, Lucey W (2015) Acoustic monitoring and prey association for beluga whale, *Delphinapterus leucas*, and harbor porpoise, *Phocoena phocoena*, off two river mouths in Yakutat Bay, Alaska. *Mar Fish Rev* 77:1–10
- ✦ Castellote M, Small RJ, Lammers MO, Jenniges JJ, Mondragon J, Atkinson S (2016) Dual instrument passive acoustic monitoring of belugas in Cook Inlet, Alaska. *J Acoust Soc Am* 139:2697–2707
- Cobb D, Fast H, Papst MH, Rosenberg D, Rutherford R, Sareault JE (eds) (2008) Beaufort Sea Large Ocean Management Area: ecosystem overview and assessment report. *Can Tech Rep Fish Aquat Sci* 2780
- ✦ Dalal DK, Zickar MJ (2012) Some common myths about centering predictor variables in moderated multiple regression and polynomial regression. *Organ Res Methods* 15: 339–362
- ✦ Elwen SH, Best PB (2004) Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa. II. Within bay distribution. *Mar Mamm Sci* 20:583–601
- ✦ Ezer T, Hobbs R, Oey L (2008) On the movement of beluga whales in Cook Inlet Alaska: simulations of tidal and environmental impacts using a hydrodynamic inundation model. *Oceanography* 21:186–195
- Finley KJ (1982) The estuarine habit of the beluga or white whale, *Delphinapterus leucas*. *Cetus* 4:4–5
- Fisheries Joint Management Committee (FJMC) (2013) Beaufort Sea Beluga Management Plan, 4th amended printing. FJMC, Inuvik
- Ford JKB (1977) White whale: offshore exploration acoustic study. Prepared for Imperial Oil Limited, Calgary, Canada by F.F. Slaney & Company Limited, Vancouver
- Fraker MA, Gordon CD, McDonald JW, Ford JKB, Cambers G (1979) White whale (*Delphinapterus leucas*) distribution and abundance and the relationship to physical and chemical characteristics of the Mackenzie Estuary. *Fish Mar Serv Tech Rep* 863
- Frost KJ, Lowry LF (1990) Distribution, abundance, and movements of beluga whales, *Delphinapterus leucas*, in coastal waters of western Alaska. *Can Bull Fish Aquat Sci* 224:39–57
- ✦ Galley RJ, Key E, Barber DG, Hwang BJ, Ehn JK (2008) Spatial and temporal variability of sea ice in the southern Beaufort Sea and Amundsen Gulf: 1980–2004. *J Geophys Res* 113:1–18
- ✦ Goetz KT, Rugh DJ, Read AJ, Hobbs RC (2007) Habitat use in a marine ecosystem: beluga whales *Delphinapterus leucas* in Cook Inlet, Alaska. *Mar Ecol Prog Ser* 330:247–256
- ✦ Goetz KT, Montgomery RA, Ver Hoef JM, Hobbs RC, Johnson DS (2012) Identifying essential summer habitat of the endangered beluga whale *Delphinapterus leucas* in Cook Inlet, Alaska. *Endang Species Res* 16:135–147
- ✦ Harwood LA, Innes S, Norton P, Kingsley MCS (1996) Distribution and abundance of beluga whales in the Mackenzie estuary, southeast Beaufort Sea, and west Amundsen Gulf during late July 1992. *Can J Fish Aquat Sci* 53: 2262–2273
- ✦ Harwood LA, Iacozza J, Auld JC, Norton P, Loseto L (2014) Belugas in the Mackenzie River Estuary, NT, Canada: habitat use and hot spots in the Tatum Niryutait Marine Protected Area. *Ocean Coast Manag* 100:128–138
- Harwood LA, Kingsley MCS, Pokiak F (2015) Monitoring beluga harvests in the Mackenzie Delta and near Paulatuk, NT, Canada: harvest efficiency and trend, size

- and sex of landed whales, and reproduction, 1970–2009. Can Manuscr Rep Fish Aquat Sci 3059
- ✦ Hauser DDW, Laidre KL, Suydam RS, Richard PR (2014) Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). Polar Biol 37:1171–1183
- ✦ Heithaus MR, Delius BK, Wirsing AJ, Dunphy-Daly MM (2009) Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. Limnol Oceanogr 54:472–482
- Hill P, Demaster DP (1999) Alaska marine mammal stock assessments, 1999. NOAA Tech Memo NMFS-AFSC-110.
- Hoover C, Ostertag S, Hornby C, Parker C, Hansen-Craik K, Loseto L, Pearce T (2016) The continued importance of hunting for future Inuit food security. Solutions 7: 40–51
- Hosmer DW, Lemeshow S, Sturdivant RX (2013) Applied logistic regression, 3<sup>rd</sup> edn. John Wiley & Sons Incorporated, Hoboken, NJ
- Huntington HP (1999) Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the Eastern Chukchi and Northern Bering Seas, Alaska. Arctic 52: 49–61
- Kleinenberg SE, Yablokov AV, Bel'kovich VM, Tarasevich MN (1964) Beluga (*Delphinapterus leucas*): investigation of the species. Nauk SSSR, Moscow
- ✦ Laidre KL, Stirling I, Lowry LF, Wiig Ø, Heide-Jørgensen MP, Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecol Appl 18(Suppl):S97–S125
- Lesage V, McQuinn IH, Carrier D, Gosselin J, Mosnier A (2014) Exposure of the beluga (*Delphinapterus leucas*) to marine traffic under various scenarios of transit route diversion in the St. Lawrence Estuary. DFO Can Sci Advis Sec Res Doc 2013/125
- ✦ Loseto LL, Richard P, Stern G, Orr J, Ferguson SH (2006) Segregation of Beaufort Sea beluga whales during the open-water season. Can J Zool 84:1743–1751
- ✦ Loseto LL, Stern GA, Connelly TL, Deibel D and others (2009) Summer diet of beluga whales inferred by fatty acid analysis of the eastern Beaufort Sea food web. J Exp Mar Biol Ecol 374:12–18
- Loseto LL, Whalen D, Hansen-Craik K, Swainson D (2015) What the belugas already know. Habitat mapping in the Kugmallit Bay Area. Proc ArcticNet Annual Science Meeting 7–11 Dec 2015, Vancouver, BC, Université Laval, Quebec City
- Loseto LL, Brewster JD, Ostertag SK, Snow K and others (2018a) Diet and feeding observations from an unusual beluga harvest in 2014 in Ulukhaktok, Northwest Territories, Canada. Arct Sci 4:421–431
- ✦ Loseto LL, Hoover C, Ostertag S, Whalen D and others (2018b) Beluga whales (*Delphinapterus leucas*), environmental change and marine protected areas in the Western Canadian Arctic. Estuar Coast Shelf Sci 212: 128–137
- ✦ Manabe S, Milly PCD, Wetherald R (2004) Simulated long-term changes in river discharge and soil moisture due to global warming. Hydrol Sci J 49:625–642
- ✦ Marcoux M, Ferguson S, Roy N, Bedard J, Simard Y (2017) Seasonal marine mammal occurrence detected from passive acoustic monitoring in Scott Inlet, Nunavut, Canada. Polar Biol 40:1127–1138
- Moore SE, Shelden KEW, Litzky LK, Mahoney BA, Rugh DJ (2000) Beluga, *Delphinapterus leucas*, habitat associations in Cook Inlet Alaska. Mar Fish Rev 62:61–80
- ✦ Morisaka T, Yoshida Y, Akune Y, Mishima H, Nishimoto S (2013) Exchange of 'signature' calls in captive belugas (*Delphinapterus leucas*). J Ethol 31:141–149
- Muto MM, Helker VT, Angliss RP, Allen BA and others (2016) Alaska marine mammal stock assessments, 2015. NOAA Tech Memo NMFS-AFSC-323.
- ✦ Mymrin NI, Huntington HP (1999) Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the Northern Bering Sea, Chukotka, Russia. Arctic 52: 62–70
- ✦ Nohara D, Kitoh A, Hosaka M, Oki T (2006) Impact of climate change on river discharge projected by multimodel ensemble. J Hydrometeorol 7:1076–1089
- O'Corry-Crowe G, Suydam R, Quakenbush L, Potgieter B and others (2018) Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). PLOS ONE 13:1–32
- Panova EM, Belikov RA, Agafonov AV, Bel'kovich VM (2012) The relationship between the behavioral activity and the underwater vocalization of the beluga whale (*Delphinapterus leucas*). Mar Biol 52:79–87
- ✦ Quakenbush LT, Suydam RS, Bryan AL, Lowry LF, Frost KJ, Mahoney BA (2015) Diet of beluga whales, *Delphinapterus leucas*, in Alaska from stomach contents, March–November. Mar Fish Rev 77:70–84
- ✦ Reeves RR, Ewins PJ, Agbayani S, Heide-Jørgensen MP and others (2014) Distribution of endemic cetaceans in relation to hydrocarbon development and commercial shipping in a warming Arctic. Mar Policy 44:375–389
- Rice DW (1998) Marine mammals of the world. Society for Marine Mammalogy, Lawrence, KS
- Richard PR, Martin AR, Orr JR (2001) Summer and autumn movements of belugas of the eastern Beaufort Sea stock. Arctic 54:223–236
- Robertson I, Millar JD (1984) White whale monitoring in the Mackenzie Estuary, 1983. Ian Robertson Consulting, Surrey, BC
- ✦ Roy N, Simard Y, Gervaise C (2010) 3D tracking of foraging belugas from their clicks: experiment from a coastal hydrophone array. Appl Acoust 71:1050–1056
- ✦ Schwarz G (1978) Estimating the dimension of a model. Ann Stat 6:461–464
- ✦ Sergeant DE (1973) Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. J Fish Res Board Can 30:1065–1090
- ✦ Simard Y, Roy N, Giard S, Gervaise C, Conversano M, Ménard N (2010) Estimating whale density from their whistling activity: example with St Lawrence beluga. Appl Acoust 71:1081–1086
- Simard Y, Loseto L, Gautier S, Roy N (2014) Monitoring beluga habitat use and underwater noise levels in the Mackenzie Estuary: application of passive acoustics in summers 2011 and 2012. Can Tech Rep Fish Aquat Sci 3068
- ✦ Sjare BL, Smith TG (1986) The vocal repertoire of white whales, *Delphinapterus leucas*, summering in Cunningham Inlet, Northwest Territories. Can J Zool 64:407–415
- ✦ Smith TG, St. Aubin DJ, Hammill M (1992) Rubbing behaviour of belugas, *Delphinapterus leucas*, in a high Arctic estuary. Can J Zool 70:2405–2409
- ✦ St. Aubin DJ, Smith TG, Geraci JR (1990) Seasonal epidermal moult in beluga whales, *Delphinapterus leucas*. Can J Zool 68:359–364
- ✦ Staniland IJ, Reid K, Boyd IL (2004) Comparing individual and spatial influences on foraging behaviour in Antarctic

- fur seals *Arctocephalus gazella*. Mar Ecol Prog Ser 275: 263–274
- ✦ Stroeve JC, Serreze MC, Holland MM, Kay JE, Malanik J, Barrett AP (2012) The Arctic's rapidly shrinking sea ice cover: a research synthesis. Clim Change 110:1005–1027
- ✦ Usher PJ (2002) Inuvialuit use of the Beaufort Sea and its resources, 1960–2000. Arctic 55:18–28
- Vergara V, Michaud R, Barrett-Lennard LG (2010) What can captive whales tell us about their wild counterparts? Identification, usage, and ontogeny of contact calls in belugas (*Delphinapterus leucas*). Int J Comp Psychol 23:278–309
- ✦ Vermaire JC, Pisaric MFJ, Thienpont JR, Courtney Mustaphi CJ, Kokelj SV, Smol JP (2013) Arctic climate warming and sea ice declines lead to increased storm surge activity. Geophys Res Lett 40:1386–1390
- ✦ Watts PD, Draper BA, Henrico J (1991) Preferential use of warm water habitat by adult beluga whales. J Therm Biol 16:57–60
- ✦ Yang D, Shi X, Marsh P (2015) Variability and extreme of Mackenzie River daily discharge during 1973–2011. Quat Int 380–381:159–168
- ✦ Yip QKY, Burn DHH, Seglenieks F, Pietroniro A, Soulis EDD (2012) Climate impacts on hydrological variables in the Mackenzie River basin. Can Water Resour J 37:209–230

Editorial responsibility: Peter Corkeron, Woods Hole, Massachusetts, USA

Submitted: September 20, 2018; Accepted: May 27, 2019  
Proofs received from author(s): September 5, 2019