

Beluga whale *Delphinapterus leucas* late summer habitat use and support for foraging areas in the Canadian Beaufort Sea

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ABSTRACT: The eastern Beaufort Sea beluga whale *Delphinapterus leucas* population aggregates in the Mackenzie Estuary every summer, and moves toward the continental shelf and offshore waters in the late summer. From 2007 to 2009, systematic aerial surveys recorded beluga whale locations beyond the estuary, over the Mackenzie Shelf and offshore waters, where distributions were observed to occur widely. It is thought that beluga use of the offshore is primarily driven by feeding opportunities, and historical abundance trends suggest that the offshore may have become more attractive to beluga in response to prey availability. To determine drivers of beluga late summer habitat use, a resource selection function (RSF) model was used to measure selection of 4 key environmental variables: (1) chlorophyll *a*, (2) sea surface temperature, (3) bathymetry and (4) distance from shore. Results revealed that all 4 variables contributed significantly to the individual 2007, 2008 and 2009 best-fit habitat models. Beluga preferred warmer sea surface temperatures (>2°C) and mid-to-high chlorophyll *a* concentrations (0.01–10 mg m⁻³), conditions that are indicative of enhanced local productivity and/or upwelling. Beluga distributions varied slightly between years, although high-use areas were identified in nearshore waters (0–50 m) offshore of the Tuktoyaktuk Peninsula, and along the continental shelf-slope (100–500 m), a region known to support a principal prey species, Arctic cod *Boreogadus saida*. This study improved knowledge of beluga habitat use in the offshore and revealed that selection of late summer oceanographic variables may provide support for foraging habitats, as these dynamic conditions are important to structuring forage fish ecosystems.

KEY WORDS: Beluga whale · Resource selection function · Aerial surveys · Beaufort Sea · Arctic cod · Climate change

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INTRODUCTION

Beluga whales *Delphinapterus leucas* are distributed in discrete populations around the circumpolar Arctic and occupy vast coastal and offshore habitats (Richard et al. 1998, Innes et al. 2002, COSEWIC 2004, Laidre et al. 2004). Although some beluga pop-

ulations remain in the same region year-round, many populations undertake large-scale annual migrations (Richard et al. 2001a, Hobbs et al. 2005, Hauser et al. 2014). In the western Canadian Arctic, the eastern Beaufort Sea population of beluga whales winter in the Bering Sea and migrate to summering areas in the Beaufort Sea and Amundsen Gulf (Allen &

Angliss 2013, Citta et al. 2016). Throughout the summer, beluga whales occupy the shallow waters of the Mackenzie Estuary (Fig. 1), forming one of the largest beluga summering aggregations in the world (Fraker & Fraker 1979, Norton & Harwood 1986). During late July and early August, beluga whales travel back and forth from the Mackenzie Estuary to deeper waters off the coast, moving along the continental shelf from Herschel Island to around Cape Bathurst (Fig. 1) (Harwood & Norton 1996, Richard et al. 2001a, Harwood & Kingsley 2013). During this time, their distribution becomes broad and is characterized by small groups dispersed across the shelf and offshore waters of the Beaufort Sea (Norton & Harwood 1986, Harwood & Kingsley 2013).

In the Mackenzie Estuary and southeast Beaufort Sea, beluga distribution and habitat use have been studied primarily using aerial surveys and satellite telemetry throughout the summer and fall (see Norton & Harwood 1986, Harwood et al. 1996, Barber et al. 2001, Richard et al. 2001b, Loseto et al. 2006). Systematic aerial surveys documented beluga in the offshore Beaufort Sea in August 1982–1985, with meth-

ods repeated in 2007–2009 (Harwood & Kingsley 2013). Findings from this work suggested that although beluga have become more common in the offshore Beaufort Sea since the 1980s, the reasons for this increase in abundance are not fully understood (Harwood & Kingsley 2013). As population growth alone cannot completely explain the increase in offshore whales (Harwood & Kingsley 2013), it is necessary to consider further information on habitat use, including oceanographic and biological drivers of movement and behaviour.

Foraging may be an important activity for beluga during late summer, contributing to distribution patterns and population changes in the region. Beluga often aggregate around points of land and exhibit ‘darting’ behaviour, which can be indicative of feeding (Norton & Harwood 1986). Thought to be opportunistic feeders, beluga whales forage on a spectrum of prey (Quakenbush et al. 2014). However, bio-tracers, such as fatty acids and stable isotopes, suggest that they largely feed on Arctic cod *Boreogadus saida* (Loseto et al. 2009). Unfortunately, specific species consumption and diet data are not readily available

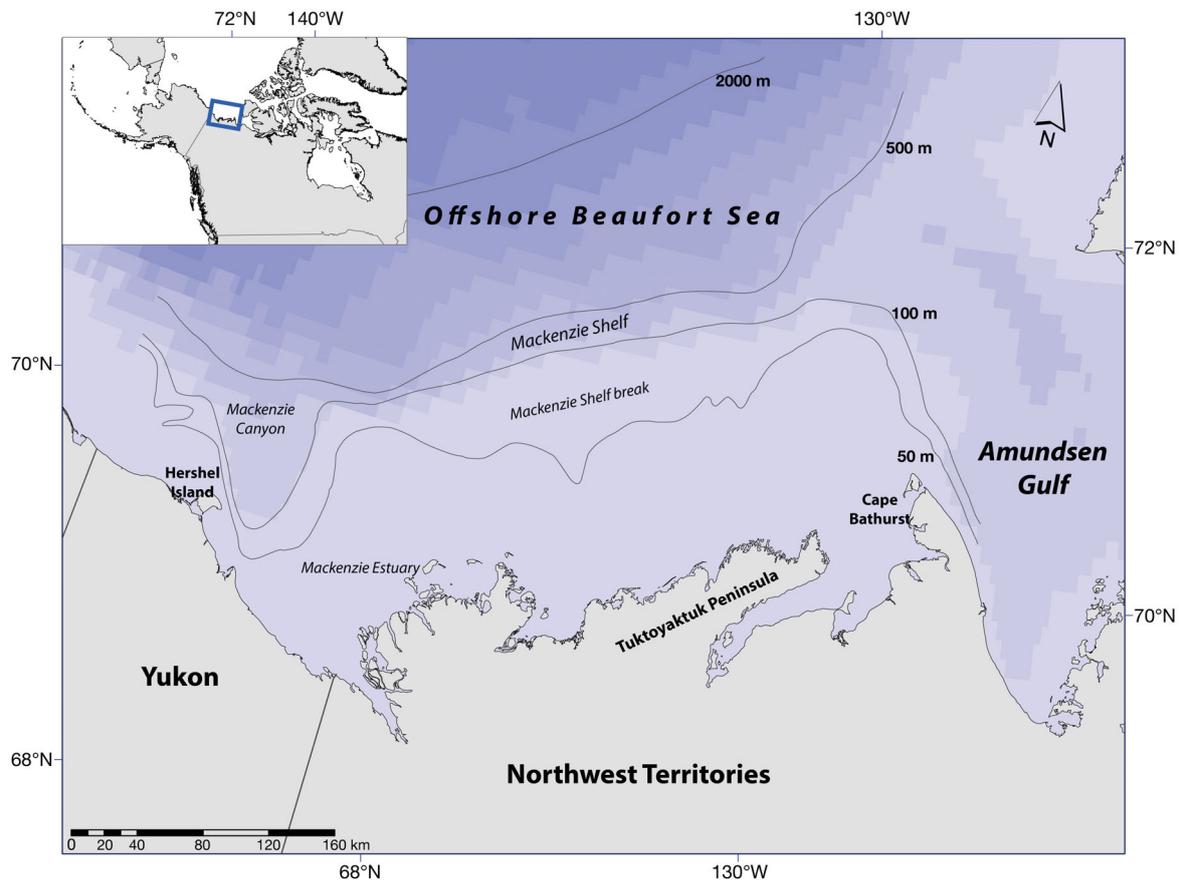


Fig. 1. Canadian southern Beaufort Sea and Mackenzie Shelf study area for 2007–2009 late summer aerial surveys of beluga whales *Delphinapterus leucas*

for beluga, as most whales harvested and sampled have empty stomachs, offering few insights into consumed prey. There have only been a few cases when beluga harvested in the late-season had full stomachs (Orr & Harwood 1998). Understanding beluga-habitat relationships (past and current) is underscored by the prediction that climate change will have a greater impact in polar regions, and on migratory species in the future (Laidre et al. 2008, Bailleul et al. 2012). Climate-induced prey shifts could potentially reduce the availability of key prey species (Gradinger & Bluhm 2004, Rose 2005, Wood et al. 2013), thus it is important to understand both the flexibility in beluga diet, feeding locations and drivers of beluga distribution, in order to predict how resilient these whales will be to changing prey resources.

The objective of this study was to contribute to the body of knowledge on Beaufort Sea beluga whale movement, distribution and habitat selection, by identifying environmental drivers contributing to late summer distribution patterns (2007–2009). To achieve this, a resource selection function (RSF) model was used to assess beluga habitat selection by measuring presence against available habitat. Dynamic oceanographic/biological features such as sea surface temperatures (SSTs), chlorophyll *a* (chl *a*) concentrations, eddies, gyres or currents influence densities of prey and are important in structuring Arctic habitats (Laidre et al. 2008). Since data on beluga prey and energetics are lacking, and distributions of prey are not well defined for this region, physical and oceanographic habitat features were linked to beluga whale observations. Four key summer environmental variables were investigated: (1) SST, (2) chl *a* concentration, (3) bathymetry (depth) and (4) distance to shore. These methods were also used to explore the hypothesis that in response to prey availability, caused by shifts in the ecosystem related to climate change, beluga have become more common in the offshore Beaufort Sea in recent years.

MATERIALS AND METHODS

Study area

The surveyed study area was the southern Beaufort Sea, including the Canadian Beaufort continental (Mackenzie) shelf (120 × 530 km) and slope region, which extends from the Alaska–Yukon border (141° W) eastward to Cape Bathurst (128° W), and from the 2 m isobaths seaward to the shelf break and beyond (Fig. 1). Harwood & Kingsley (2013) used the

term ‘offshore’ to represent the area surveyed beyond the inner Mackenzie Estuary. Similarly, for the purposes of this study, we define ‘offshore’ as the region beyond the estuary including the Mackenzie Shelf break, Mackenzie Shelf and slope area and area beyond the shelf.

Sizeable freshwater input from the Mackenzie River extends over the western part of the shelf, and is known as the Mackenzie River plume (Carmack & Macdonald 2002). The Mackenzie Shelf has been identified as an important region for birds, fish aggregations and marine mammal migration routes (Carmack et al. 2004). The upper portion of the water column (<220 m) in the southern Beaufort Sea is predominantly composed of relatively cold, fresh Pacific water entering through the Bering Strait, while water below is warmer (>0°C) and of Atlantic origin (Crawford et al. 2012). Strong winds promote upwelling that increase the production of ice algae and phytoplankton in the spring, and local circulation moves nutrient-rich water masses from greater depths on the shelf, spreading the river plume during the open-water season (Macdonald et al. 1987, Carmack et al. 2004, Tremblay et al. 2011). The nutrient-rich Pacific water upwelling near Cape Bathurst (Cape Bathurst polynya), Amundsen Gulf and the eastern part of the shelf increases productivity in this region, while zooplankton in the deeper offshore areas provides important food sources to higher trophic levels (Richardson et al. 1987, Stirling 1997, Walkusz et al. 2011). Upwelling events are generally weak in May and June, as sea ice clears away, and become more developed between July and September (Arrigo & van Dijken 2004, Tremblay et al. 2008, Citta et al. 2015).

Beluga sightings

Systematic aerial surveys were conducted in August of 2007–2009 to monitor the offshore distribution and relative abundance of beluga whales in the Beaufort Sea (Harwood & Kingsley 2013). A brief outline of survey design and raw beluga sightings (Fig. 2) is provided here; however, for a more detailed account of the survey methodology refer to Harwood & Kingsley (2013).

In each survey year, 24 systematic transects were flown, with a total survey area ranging from 4703 to 7959 km² (Table 1). All eastern, western and southern boundaries, as well as positions of north–south transects, were consistent and spaced systematically (about 20 km apart). A strip-transect method with a

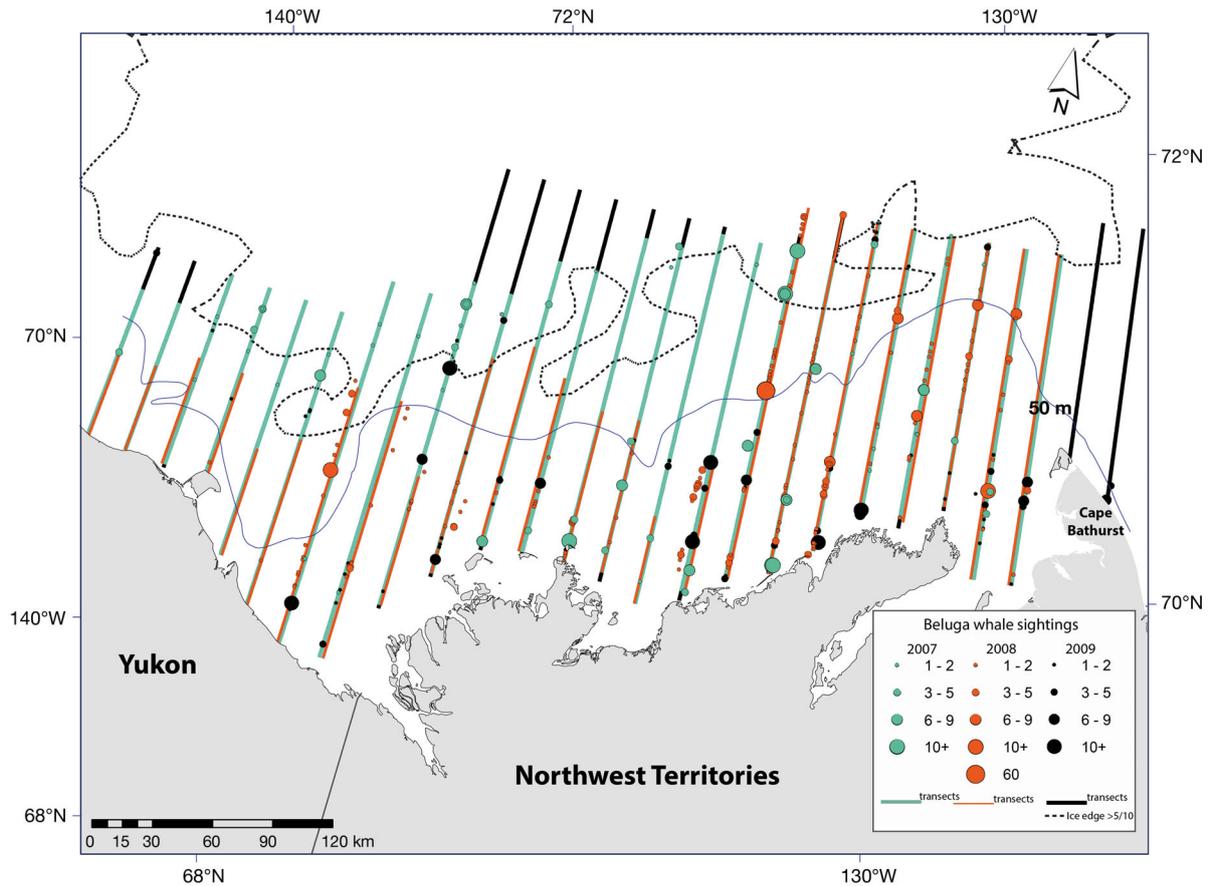


Fig. 2. Location of aerial survey transects and numbers of beluga whales *Delphinapterus leucas* sighted in the offshore Beaufort Sea during aerial surveys in August 2007 (green), 2008 (orange) and 2009 (black). The blue line denotes the 50 m isocline and the dashed line shows the approximate location of the 2009 ice edge at 5/10 or greater concentrations. The survey area was ice-free in 2007 and 2008

Table 1. Observed beluga whale *Delphinapterus leucas* sightings (on transect; used resource units, where a resource unit was defined as a $0.1 \times 0.1^\circ$ pixel in ArcGIS) and available resource units (unused pixels) for 2007, 2008 and 2009 resource selection function models. A total of 54 sightings that occurred within absent or patchy satellite data areas were removed from the analysis. Total resource units = Total used + Total available; NA: not applicable

Year	Used resource units (sightings)			Available resource units			Total resource units	Total surveyed area (km ²)
	Raw	Removed	Total	Raw	Removed	Total		
2007	337	NA	337	2236	93	2143	2480	7167
2008	401	15	386	684	54	630	1016	4703
2009	307	39	268	1520	224	1296	1564	7959
Total	1045	54	4347	4347	371	4967	4967	19829

de Havilland Twin Otter aircraft platform was used in all surveys, with a strip width of 2.0 km (1.0 km per side), delimited by marks or tape on bubble windows (Caughley 1977, Harwood & Kingsley 2013). The survey altitude was approximately 305 m, and target ground speed for all surveys was 200 km h^{-1} . Primary observers on the left and right side of the aircraft recorded marine mammals (on or off-strip), time and location of sighting, number in group, colour, appar-

ent swim direction and relative rate of movement. Observers used individual hand-held Garmin GPS Map 76 units to log the locations of sightings. The observers recorded sea state and ice concentration at the beginning and end of transects, and recorded conditions when they changed. Surveys were conducted in sea states of Beaufort 3 or less and were interrupted when sea state increased to Beaufort 4 (Harwood & Kingsley 2013). In all 3 years, left-side

data were collected by the same primary observer, partnered with other primary observers on the right. As noted by Harwood & Kingsley (2013), all observers had recent and extensive aerial survey experience.

The 2007 survey was completed the latest in the season (22 and 23 August) and in the shortest time, without any missed transects or portions of transects. A total of 337 beluga whales (Table 1) were observed on 92% of transects (Fig. 2). In 2008 (2, 4, 9 and 20 August), transects north of the Mackenzie Delta, western part of the study area, were shortened due to local fog and low cloud. Despite a decrease in surveyed area, 401 beluga whales (Table 1) were observed on 79% of transects (Fig. 2). In 2009 (15, 17, 18 and 20 August), several transects were truncated at the northeast end, owing to a more southerly ice edge (area defined as $\geq 50\%$ ice concentration); there was no ice present in 2007 and 2008 (Fig. 2). In 2009, Harwood & Kingsley (2013) recorded a total of 323 whales on 100% of transects. Only on-transect beluga observations were used for this study; thus during data processing, the number of beluga observations for 2009 was corrected to 307 (Table 1). All observations for 2007–2009, including systematic transect lines, were mapped using GIS software (ArcGIS 10.2).

Late summer habitat variables

SST and chl *a*

SSTs ($^{\circ}\text{C}$) and chl *a* concentrations (mg m^{-3}) for the Beaufort Sea and Mackenzie Shelf study area were obtained from satellite data acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS, <http://neo.sci.gsfc.nasa.gov/>). Surface SST and chl *a* products were available at daily and 8 d temporal periods, and with a spatial resolution of $0.1 \times 0.1^{\circ}$ (approximately 8 km pixel^{-1} ; Table 2). Satellite measurements of SST are reflective of the upper most ‘skin’ surface of the water and should not be interpreted as temperature at depth. Nevertheless, for our study these measurements were used as a proxy for surface temperature, as this is the best data set available for the region and time. Chl *a* concentrations were derived using satellite-based measurements of ocean colour and served as an index of ocean productivity (McClain 2009, Matishov et al. 2010). Measurements of algal pigment

chlorophyll (i.e. chl *a*) can be interpreted as the amount of algal biomass present in a system (Frey et al. 2015). As a result, regions with high phytoplankton productivity, and subsequent zooplankton abundances, will also have high concentrations of chlorophyll (Behrenfeld & Falkowski 1997, Pérez-Ruzafa et al. 2004, Matishov et al. 2010).

All satellite images (GeoTiff products) were imported into the GIS for each survey day and/or for 8 d composite for 2007, 2008 and 2009 (Table 2). If a map pixel in the exact survey day contained no data (i.e. the satellite data were poor or not available), then the 8 d composite value was used. In a few cases, neither the single day nor 8 d composite data were available; instead, a value for the pixel was calculated by interpolating from the nearest pixel on the transect line. This was only done for a maximum distance of 3 pixels. If larger sections of the study area were missing data (greater than 3 pixels along a transect), then these areas were removed from the analysis (Table 1). Due to extensive cloud cover in 2008 and 2009, resulting in poor satellite imagery and data coverage in sections of the study area, the 9 August survey day (15 total observations) was removed from the RSF analysis, along with 39 beluga observations in 2009 (Table 1).

Table 2. Late summer environmental covariates associated with offshore beluga whale *Delphinapterus leucas* locations in 2007–2009, along with units, bin categories and scales (spatial and temporal) used in the resource selection function model; NA: not applicable

Covariate	Unit	Bin categories	Spatial scale	Temporal scale
Sea surface temperature	$^{\circ}\text{C}$	–2–2	$0.1 \times 0.1^{\circ}$	2007: daily
		2–6		2008: daily + 8 d
		6–10		2009: daily + 8 d
		10–14		
Chlorophyll <i>a</i>	mg m^{-3}	0.01–0.3	$0.1 \times 0.1^{\circ}$	2007: daily
		0.3–1.0		2008: daily + 8 d
		1.0–3.0		2009: 8 d
		3.0–10		
		10+		
Bathymetry (depth)	m	0–50	NA	NA
		50–100		
		100–500		
		500–2000		
Distance to shore	km	0–40	NA	NA
		40–80		
		80–120		
		120–160		
		160–200 ^a		

^aThis transect distance was only achieved in 2007

Beluga observations (by day/year) were joined spatially with SST and chl *a* satellite data (by survey day/week), and locations were given a numeric value. Numerical values for SST and chl *a* were then binned into discrete biologically relevant categories before running the RSF models (Table 2). This step is necessary as it isolates the environmental variables into habitat categories (i.e. low to high chlorophyll concentrations). Due to limited environmental data, and in some cases the inability to ground truth these data, it remains difficult to directly link remotely sensed SST and chl *a* data with beluga foraging. However, for the purpose of this study, we separated these bins based on previously established literature on regional productivity (Niemi et al. 2015) and temperature ranges associated with a key prey species, Arctic cod (Crawford et al. 2012, Majewski et al. 2016).

Bathymetry

The late summer surveys were flown over deeper waters of the offshore Beaufort Sea but also captured nearshore shallow areas (0–50 m) and the shelf-slope region. The Mackenzie Shelf break occurs between the 80 and 120 m isobaths, with the shelf and slope area contained in the 200 to 500 m isobath region (Carmack et al. 1989). Bathymetry data for the Beaufort Sea were supplied by the International Bathymetric Chart of the Arctic Ocean version 3.0 (available at www.ngdc.noaa.gov/mgg/bathymetry/arctic/downloads.html; Jakobsson et al. 2012). The data were given in 50, 100, 500 and 2000 m contours, thus this variable was binned into 4 key depth areas: (1) nearshore-shelf 0–50 m (area between the shore and Mackenzie Shelf break (including the shallow Mackenzie Estuary), (2) offshore-shelf 50–100 m (Mackenzie Shelf break), (3) upper-slope 100–500 m (Mackenzie Shelf and slope area leading to the offshore) and (4) lower-slope 500–2000 m (offshore area beyond shelf). These regions and depths also align with marine fish groupings in the Beaufort Sea (Majewski et al. 2017). Since the survey area did not extend beyond Cape Bathurst, and within our study area the 500 m and 200 m isobaths are adjacent to the shelf edge, the 500 m line was treated as the continental shelf edge.

Distance to shore

Due to the wide spatial coverage of the surveyed area and varied distribution of belugas between

years, it was also important to assess if distance to shore was a variable influencing habitat selection. In 2007, full transects were completed with the maximum surveyed distance approximately 190 km from shore. In 2008 and 2009, the amount of offshore area covered by the survey was limited due to cloud cover and presence of an ice edge. Distance to shore was calculated for each observed beluga location using the Nearest Feature tool in ArcGIS. Distance to shore was not binned and was left as a numeric value (i.e. continuous variable).

RSF

We employed an RSF model to assess the significance of each environmental variable to beluga habitat selection in the offshore. RSF is increasingly used in ecological studies to identify critical resources for marine mammal populations and to predict species occurrence (Gillies et al. 2006). Logistic regression yields the probability of use of a 'resource unit' in the form (Manly 2002):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 \dots + \beta_p x_p) \quad (1)$$

where $\beta_1 \dots \beta_p$ are the regression coefficients, $x_1 \dots x_p$ are the independent variables, and w is the estimated probability of a beluga sighting. A 'resource unit' is a discrete unit, which is either observed to be selected or available (Boyce 2006). For this study, a resource unit was defined as a $0.1 \times 0.1^\circ$ pixel in ArcGIS. For line transect data, observers are less likely to detect whales farther from the aircraft, thus the probability of detecting an individual and coding a resource unit area as used depends on how far the whale is from the transect line (Manly 2002). In our study, all transect surveys covered a 2.0 km strip. To account for the maximum viewing distance by the observers (approximately 1.0 km per side), each track line was buffered by a total of 2.0 km, and only pixels within the buffered range were used as available resource units (note: truncated transects in 2008 and 2009 reduced the number of available resource units, see Table 1). Each pixel within the buffered lines was then classified as either selected (= 1) or available (= 0) habitat and assigned a numeric value of SST, chl *a* and a range of bathymetry (depths). Distance to shore was calculated for each pixel from the centre point using the Nearest Feature tool in ArcGIS.

A correlation analysis (Pearson's product-moment correlation) was first completed to examine the correlation between all 4 environmental variables (Table 3). Although a simple correlation involving 2

Table 3. Pearson correlation matrix for 2007–2009 beluga whale *Delphinapterus leucas* resource selection function variables (covariates): sea surface temperature (SST), chlorophyll *a* (chl *a*), bathymetry (depth) and distance to shore (distance)

	SST	Chl <i>a</i>	Depth
Chl <i>a</i>	0.251		
Depth	-0.199	-0.142	
Distance	-0.200	-0.419	0.456

variables at a time does not provide a complete description of the relationships between all 4 variables, the strength of each pair of variables is revealed. The RSF model was carried out on each year separately and for all 3 years (2007–2009) combined (Table 4). This assessment is important, as habitat selection can change between years, due to fluctuating resources, shifts in climate, and/or from changes in local distributions that result in changes in abundance (Boyce et al. 2002). All RSF model combinations were analysed in R statistical software, version 0.98 (R Development Core Team 2005), using the ‘Resource Selection’ package (see Lele & Keim 2006, Lele 2009). Model fit, i.e. whether the model deviated from the random null models, was assessed using a Hosmer and Lemeshow goodness of fit test, and each model combination was ranked using Akaike’s information criterion (AIC), which is a powerful approach for model selection from a set of plausible alternatives (Burnham & Anderson 1998).

RSF models can have limitations in sampling areas where habitat changes temporally (e.g. seasonal sea ice) or in situations where species migrate, which can result in habitat usage changing both spatially and temporally (Loseto et al. 2006). As such, it is important to note that our final best-fit models represent ‘localized’ models of habitat use in the offshore Beaufort Sea; when applied to other areas or seasons, they may not remain robust. The habitat variables used

Table 4. Beluga whale *Delphinapterus leucas* resource selection function models for 2007, 2008, 2009 and 2007–2009, supported by Akaike’s information criterion (AIC) with *k* parameters and model significance (*p*); *n*: total number of resource units (used and available; see Table 1)

Year	df	<i>n</i>	<i>k</i>	AIC	<i>p</i>
2007	8	2480	4	4836	<0.01
2008	8	1016	4	4035	<0.01
2009	8	1564	4	3540	<0.01
2007–2009	8	5060	4	16082	<0.01

were all chosen based on availability of environmental and biological information in the area during the surveyed days, thus applying this model to a new area or different time period could result in changes in the environmental conditions and subsequent selection (Boyce et al. 2002). In regards to survey methodology, the percent of available habitat can depend on sampling intensity, for example, a more extensive search might result in previously recorded unused sites being reclassified as used sites (Boyce et al. 2002). We assumed temporal autocorrelation between days to be negligible, since belugas are able to move and change location sufficiently to consider the daily survey locations independent. Each transect was surveyed in 3 consecutive years, but was only surveyed once per year; thus to achieve less uncertainty in each model, a large representative sample of used versus available units must be used in order to minimize errors associated with sampling intensity.

RESULTS

The Pearson correlation analysis showed no significant correlation between the environmental variables ($p < 0.05$) (Table 3); hence, all 4 variables (SST, chl *a*, depth and distance to shore) were considered independent in the RSF models. An RSF model was run for each year individually, as well as for a pooled 3 yr data set (Table 4). Final models were selected according to the AIC criteria, and the model with the lowest AIC value was taken to be the best approximating model (Burnham & Anderson 1998). The 3 yr pooled model had the highest AIC value (16082), and model fit improved when examining each year separately (AIC < 4836, Table 4). For 2007, 2008 and 2009, all possible model combinations using 4 and 3 variables were examined and ranked again by AIC (Table 5). All 4 variables contributed significantly to each fitted model (Table 5) and according to the AIC criteria, there were no competing models to the selected model (i.e. AIC values for alternative models were >5 units higher than the selected model; Burnham & Anderson 1998).

In 2007, beluga whales selected all 3 available categories of SST; however, the highest proportion of whales were found in 2–6°C ($p < 0.001$) and 6–10°C water ($p < 0.001$), with 89% of the units selected out of the 95% available in the 2 combined temperature ranges (Fig. 3). The remaining whales were found in temperatures of –2 to 2°C ($p < 0.001$), in which only 5% was available and 11% was used (Figs. 3 & 4).

Table 5. Beluga whale *Delphinapterus leucas* resource selection function (RSF) models for 2007, 2008 and 2009 supported by Akaike's information criterion (AIC) with k parameters. RSF variables (covariates) were sea surface temperature (SST), chlorophyll a (chl a), bathymetry (depth) and distance to shore (distance); $\Delta_i = \text{AIC}_i - \text{min AIC}$ for each i

Model	k	AIC	ΔAIC
2007			
SST+ chl a + depth + distance	4	4836	0.0
chl a + depth + distance	3	4955	112.1
SST + depth + distance	3	4993	119.7
SST+ chl a + distance	3	4948	157.0
2008			
SST+ chl a + depth + distance	4	4035	0.0
SST+ chl a + distance	3	4159	124.1
chl a + depth + distance	3	4187	152.1
SST + depth + distance	3	4703	668.0
2009			
SST+ chl a + depth + distance	4	3540	0.0
chl a + depth + distance	3	3569	29.1
SST+ chl a + distance	3	3576	36.3
SST + depth + distance	3	3593	52.7

Beluga selection of chl a was significant in the concentrations of 3.0–10 mg m⁻³ ($p < 0.001$) followed by 0.01–3.0 mg m⁻³ ($p = 0.001$); both chl a categories were used (64%) by belugas more than what was available (41%) in 2007. The proportion of belugas sighted in areas with chl a concentrations of 1.0–3.0 mg m⁻³ ($p = 0.164$) was significantly less, with only 9% of these habitats used vs. 24% available (Fig. 3). The proportion of belugas found in each bathymetry bin was relative to what was available throughout the study area, with 95% of all depths available, and selected, being <500 m (Fig. 3). Belugas were primarily observed 0 to 120 km ($p < 0.001$) from land (Fig. 2).

In 2008, whales were again most often detected in areas with warmer SST, and used (88%) the 2 temperature ranges 2–6°C ($p < 0.001$) and 6–10°C ($p < 0.001$) more than what was available (69%; Figs. 3 & 4). A higher temperature range of 10–14°C was available in 2008, but only 2% was selected (Fig. 3). For chl a , the 2 lowest concentrations of 0.01–0.30 mg m⁻³ ($p < 0.001$) and 0.30–1.0 mg m⁻³ ($p < 0.001$) had the highest selection probability (55% used vs. 38% available, Fig. 3). The higher chl a range of 3.0–10 mg m⁻³ was selected 34%, yet an almost equal 38% was available (Fig. 3). Beluga selected the 0–50 m bin ($p < 0.001$) over any other depth range (87% used vs. 69% available); habitat selection was not significant in bathymetry ranges of 100–500 m ($p =$

0.404) and 500–2000 m ($p = 0.741$; Fig. 3). Individuals were distributed at all distances uniformly across the study area, and results of the variable 'distance to shore' alone were not significant ($p = 0.239$) in the 2008 model.

Temperatures across the study area were colder in 2009, with 93% of the available habitat ranging from –2 to 2°C and 2–6°C. Within these 2 temperature ranges, 68% of the habitat was selected by belugas (Fig. 3). Of the remaining 7% of available habitat, ranging from 6–10°C, 33% was used ($p < 0.001$; Figs. 3 & 4). Belugas preferentially selected chl a concentrations of 3.0–10 mg m⁻³ ($p = 0.005$) over 0.3–1.0 mg m⁻³ ($p = 0.018$; Fig. 3), with both bins used 64% vs. the 28% available. All bathymetry ranges were selected, with the highest proportion of whales selecting the 0–50 m depth range in 2009 (88% used sites vs. 52% available, Fig. 3). Distance to shore was selected uniformly across the study area and was not a significant ($p = 0.255$) variable in 2009.

DISCUSSION

To better understand the factors influencing offshore distribution, our study augmented aerial survey data (2007–2009) of beluga whales in the Beaufort Sea (Harwood & Kingsley 2013) by quantifying habitat selection of key late summer environmental conditions. Further, to examine if the offshore habitat has become more attractive to beluga in response to prey availability (Harwood & Kingsley 2013), we modelled 2 dynamic environmental conditions, viz. chl a and SST, and 2 static conditions, viz. bathymetry (depth) and distance to shore. Dynamic environmental conditions are known to influence movement and habitat use of migratory marine mammals over a range of spatial and temporal scales (Goetz et al. 2007, Hauser et al. 2017). Here we provide support for beluga foraging areas in the offshore Beaufort Sea by associating primary prey, Arctic cod, with late summer conditions of chl a , SST and depth, which were all strong predictors of beluga habitat selection in 3 individual best-fit RSF models for 2007, 2008 and 2009.

Beluga habitat selection: an assessment of prey associations

Beluga whales are known to exploit upwelling zones, shelf breaks and ice edges, where food may be readily available (see Richard et al. 2001b, Harwood

& Smith 2002, Asselin et al. 2012, Hornby et al. 2016). Arctic cod is an important lipid-rich prey for many species (Welch et al. 1993) and has been identified as a major summer food source for belugas in the Beaufort Sea (Loseto et al. 2009, Quakenbush et al. 2014). Significant consumers of zooplankton (Walkusz et al. 2011), Arctic cod distributions can be influenced both by temperature (Crawford et al. 2012, Majewski et al. 2016) and local productivity (Logerwell et al. 2011). In the Canadian Beaufort Sea, the largest aggregations of Arctic cod have been found along the upper continental slope (250–350 m) at depths which coincide with hydrographic fronts (Majewski et al. 2017). It is hypothesized that either density differences between the Pacific and Atlantic water masses entrain planktonic organisms along the upper slope, or physiological responses to the transition between negative and positive water temperature concentrate zooplankton at the Pacific–Atlantic water mass boundary (Majewski et al. 2016).

In the late summers of 2007–2009, beluga frequently occurred along the upper Beaufort Sea continental slope and in nearshore regions (offshore of the Mackenzie Estuary and Tuktoyaktuk Peninsula), where mixing and nutrient input from land can increase primary productivity and temperature (Stewart & Barber 2010). Selection of chl *a* concentrations were not consistent across years, although higher chl *a* levels (3.0–10 mg m⁻³) were preferentially selected by beluga whales in 2007 and 2009. Due to limited *in situ* data, we are unable to specifically link surface chl *a* concentrations selected by belugas with key prey aggregations. Alternatively, the amount of chl *a* present in a region can be correlated with different magnitudes of primary production, or the rate at which energy is converted to organic substances (Frey et al. 2015). As such, we suspect that habitats used by belugas with higher concentrations of chl *a* are indicative of regions with enhanced local productivity and/or upwelling. High

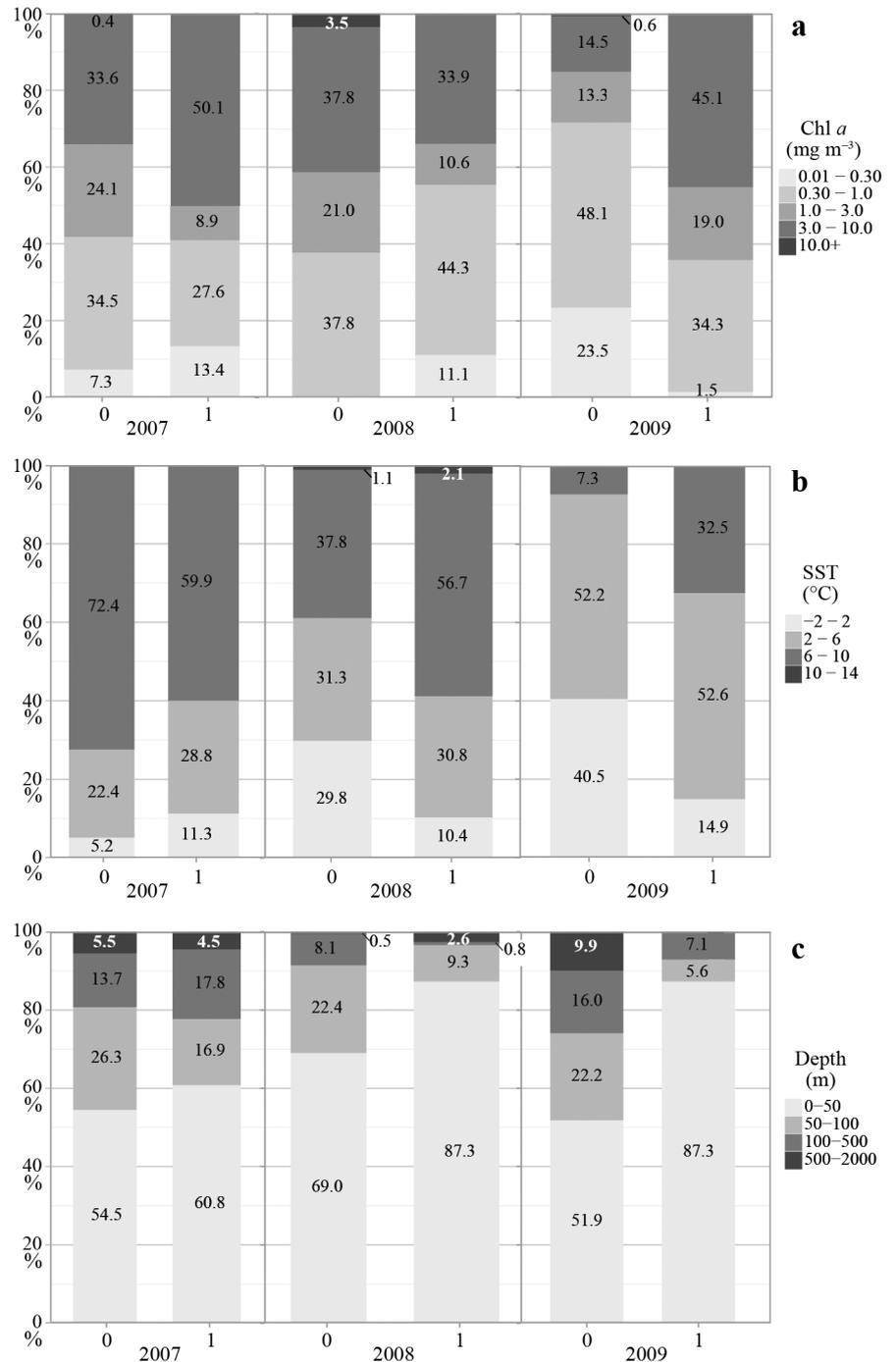
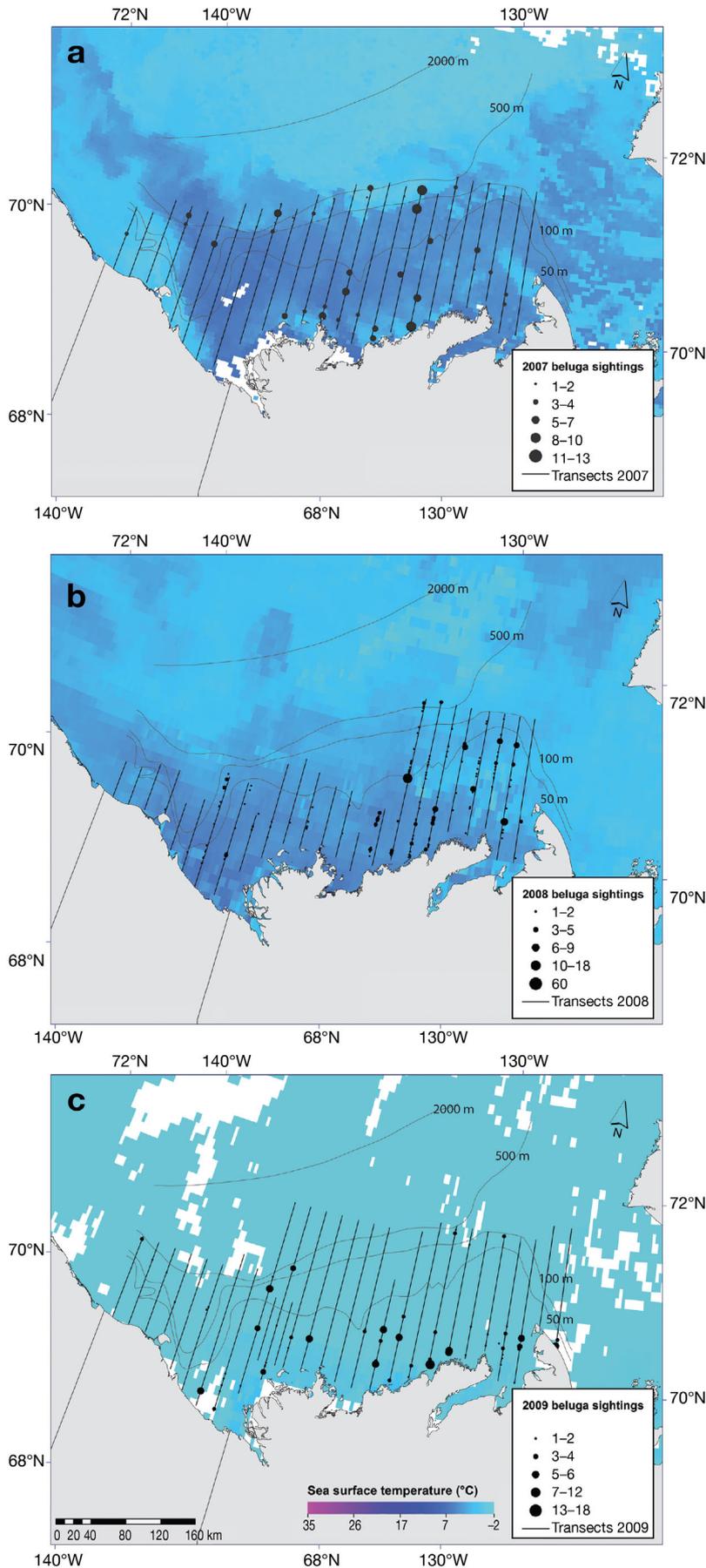


Fig. 3. Percentage of available (0) versus selected (1) habitat for (a) chlorophyll *a* (chl *a*) concentration, (b) sea surface temperature (SST) and (c) bathymetry (depth) in 2007 ($n = 2480$), 2008 ($n = 1016$) and 2009 ($n = 1564$)

primary production of phytoplankton is essential for supporting large benthic biomass and providing food for organisms at higher trophic levels (Munger et al. 2009). Smith et al. (1986) hypothesized that the distribution and abundance of some cetaceans can be defined by the coastal surface-water mass, which is



rich in chlorophyll. Similarly, Hauser et al. (2017) predicted that beluga whale habitat selection in the Beaufort Sea was most influenced by features such as depth, slope and proximity to bathymetric features, which together promote and guide regional productivity and foraging opportunities.

The waters in and around Cape Bathurst are highly productive and maintained by upwelling and easterly winds during the open-water season (Stirling 1997, Walkusz et al. 2012). Although the Tuktoyaktuk Peninsula is not specifically identified as a region of upwelling, it does receive downstream inputs from Cape Bathurst, and is likely a niche for certain prey on an episodic basis (Williams & Carmack 2008, Walkusz et al. 2012). This region has also been identified as a summer biological ‘hotspot’, known to promote the concentration of calanoid copepods and to attract other large predators such as seals and bowhead whales *Balaena mysticetus* (Walkusz et al. 2012, Citta et al. 2015). Further, beluga whales landed offshore of the Tuktoyaktuk Peninsula in the fall had stomach contents containing Arctic cod, sand lance *Ammodytes* spp. and Arctic cisco *Coregonus autumnalis* (Orr & Harwood 1998).

Similar to chl *a*, beluga selection of a specific SST range was not consistent across years; however, belugas did prefer regions with warmer temperatures (>2°C) in all years. In 2007, due to elevated temperatures in the Beaufort Sea, 72% of the available habitat was >6°C, and belugas selected temperatures equal to what was available. In subsequent years, temperatures were less uniform and belugas preferentially selected regions >6°C. We suspect that beluga

Fig. 4. Sea surface temperatures (source: MODIS) for (a) 22 August 2007, (b) 20–27 August 2008 and (c) 13–20 August 2009, along with beluga whale *Delphinapterus leucas* sightings and aerial survey transects flown each year. White patches represent areas with no available data due to cloud cover and/or the presence of ice

habitat use of warmer waters, often found within the Mackenzie River Plume, was associated with increased local productivity and prey availability in the late summers of 2007–2009. Forage fish aggregations are primarily driven by temperatures below the surface layer and features such as the thermocline or halocline (Crawford & Jorgenson 1996, Ferguson et al. 2006). Recent sampling along the Beaufort continental shelf and slope revealed that Arctic cod prefer temperatures $>0^{\circ}\text{C}$, specifically in the upper portion (250–350 m) of the Atlantic water mass (Crawford et al. 2012, Eert et al. 2015, Majewski et al. 2017). Satellite-tagged beluga whales in the region have also been observed diving to depths where hydrographic conditions are known to concentrate Arctic cod (Richard et al. 2001b, Hauser et al. 2015). The upper-Atlantic water mass and associated upper-slope habitat also supports other potentially important bottom-dwelling prey sources, such as Greenland halibut *Reinhardtius hippoglossoides* (Dehn et al. 2006, Majewski et al. 2017), emphasizing the need for enhanced data on beluga dive behaviour and seasonal prey preferences. We recognize that remotely sensed SST data are limited to the surface, therefore further investigation into how surface temperatures and productivity relate to prey abundance below the surface is needed. In addition, other variables not tested here, such as freshwater flow (Hornby et al. 2016), currents/eddies (Llinás et al. 2009) and/or ice edges (Hauser et al. 2017), could play a role in prey availability and beluga distributions.

Both increases in open water extent and duration of the open water season have contributed to an overall increase (ca. 30% from 1998 to 2012) in primary production in the Arctic Ocean (Barber et al. 2008, Arrigo & van Dijken 2015). Specifically, years with earlier break-up and warmer SST are known to have higher chl *a* concentrations and overall production (Orlova et al. 2005, Frey et al. 2015). In 2007 and 2008, early melting of sea ice and contributions of large amounts of fresh water in the surface layer resulted in increased SSTs in the Beaufort Sea (Proshutinsky et al. 2009). It is possible that these warmer summers may have influenced the magnitude and persistence of chl *a*, enhancing the offshore environment and maintaining productive foraging habitats for belugas. Further, whales seemed to be more widely distributed in 2007 and 2008, suggesting that when productive areas are extensively available, belugas may exhibit broader habitat use. Conversely, temperatures in the offshore were colder in 2009, and the proportion of used versus available habitat was 4 times higher for the warmer SST bin ($6\text{--}10^{\circ}\text{C}$) and

3 times higher for the intermediate to high chl *a* concentration bin ($3.0\text{--}10\text{ mg m}^{-3}$). In this case, belugas seemed to be clumped closer to the shore in limited areas of warmer water, where production was likely contained.

Beluga distributions and model interpretation

As described above, late summer beluga distributions observed in this study were wide and varied among surveyed years. This broad distribution may also be a function of sexual segregation, where beluga whales of different ages and sexes may use different habitats and feeding strategies in inshore and offshore areas (Loseto et al. 2006, Hauser et al. 2017). Geographic segregation can also be driven by avoidance of predators (i.e. killer whales *Orcinus orca*) specifically by reproductive females (Main et al. 1996). Between years, habitat selection can appear different when the relative abundance of belugas is higher, resulting in individuals occupying a more diverse range of habitat types than in years when abundance is lower (Boyce et al. 2002, Harwood & Kingsley 2013). Harwood & Kingsley (2013) concluded that the number of surfaced belugas used in our study was similar in all of the 2007–2009 surveys, with no apparent trend toward increasing or decreasing relative abundance. Additionally, the RSF model accounted for the varied availability of habitat feature measurements throughout the study area, and we estimate that the minor alterations to survey effort across years did not greatly impact our results.

In 2007, whales proportionally selected distance to shore and depth similar to what was available, with the majority of whales sighted within 120 km of the mainland. Belugas preferentially selected the 0–50 m depth range in 2008 and 2009. A greater number of whales distributed within the nearshore-shelf could be an artefact of changes in migration timing out of the Mackenzie Estuary towards the offshore and/or timing of the surveys (2008 and 2009 surveys occurred earlier in August than in 2007). Including distance to shore in the 2008 and 2009 RSF model improved the overall model fit, but alone it was not significant. This may be an artefact of statistical limitations, such as positive spatial autocorrelation (i.e. observations measured at nearby locations are more similar than randomly associated pairs of observations) (Redfern et al. 2006). As such, modelling beluga observations at an individual level can present some limitations. For example, 60 individuals were

detected at the 50 m isobath in 2008. This large aggregation (associated with the same habitat type) could have potentially skewed the results of the RSF model and the significance of each habitat category. Examining the size and composition of the beluga groups may have more accurately described the relationship between distribution, habitat use and the associated activity in that habitat (Bailleul et al. 2013).

Harwood & Kingsley (2013) identified that belugas were noticeably absent in waters offshore of the Yukon coast, shallower than 50 m, with none observed in a 50–200 m deep region in the middle of the study area about 120–160 km offshore. Truncated transects in 2008 could have resulted in limited sightings in the deeper offshore habitats, and the presence of an ice edge in 2009 may have physically limited belugas, driving them towards the shore and shallow areas. These factors could have contributed to an observed absence in certain offshore areas, yet interestingly, this region also overlaps with the Beaufort Sea petroleum leasing sites, as well as hydrocarbon vents and pingo-like features identified within the same region of the continental shelf (Paull et al. 2007, Saint-Ange et al. 2014). The effect of these unique submarine features on local productivity and water chemistry is not known. Research to understand the biological significance of these features for beluga whales would benefit from better interpretation of beluga presence and absence in this area.

Climate change and future considerations

Arctic summer sea ice extent reached a record minimum in 2007, with a dramatic reduction in area of coverage, relative to the previous record in 2005 (Richter-Menge et al. 2007). Since 2007, a series of warm summers in the Beaufort Sea, with concomitant largely ice-free conditions, have the potential to cause long-term shifts in the regional climate (Wood et al. 2013). Inter-annual variability can also lead to broad changes (either spatially or temporally) in local habitat features (Galley et al. 2008, Wood et al. 2013) and influence migration and habitat use by beluga whales. For example, a change in oceanographic conditions or physical processes could result in a movement of resources and decreased prey availability for belugas (Carmack & Macdonald 2002), potentially resulting in changes in beluga distributions in the Beaufort Sea. In combination, the extreme sea-ice retreat may favour advection of invasive prey species onto the Beaufort Sea shelf,

allowing belugas to concentrate their foraging effort in areas with more dependable or augmented concentrations of prey (Rose 2005, Moore & Laidre 2006, Falardeau et al. 2014).

Harwood & Kingsley (2013) hypothesized that a reason the offshore habitat may have become more attractive to beluga whales in recent years is due to shifts in the ecosystem related to climate change. Enhanced upwelling of nutrients along the Beaufort slope, followed by increased pelagic marine productivity, could have resulted in belugas accessing resources in the offshore Beaufort Sea to a greater extent or for longer periods of time, when compared to previous 1980s survey data (Harwood & Kingsley 2013). We acknowledge that this 3 yr study presents limitations in our ability to interpret patterns and/or changes in habitat use over time. However, our results suggest that beluga habitat selection can vary in geographic location from year to year and that dynamic variations in selection may be linked to, or predicted by, certain conditions of SST, chl *a* and depth. To strengthen this regional assessment, we recommend a historical analysis of offshore beluga-habitat relationships comparing the results of this study (2000s) to the complementary survey data collected in the 1980s (Harwood & Kingsley 2013). This would also provide an improved baseline with which to assess how belugas may benefit or suffer from climate-induced environmental changes.

In the late summer, belugas frequently used habitats along the Mackenzie Shelf and shelf-slope break, and nearshore waters offshore of the Tuktoyaktuk Peninsula, lending further evidence of the overlap between the habitat of Arctic cod and offshore beluga whales (Orr & Harwood 1998, Richard et al. 2001b, Harwood & Kingsley 2013, Hauser et al. 2017, Majewski et al. 2017). By examining seasonally appropriate environmental variables and the strength of associations with beluga prey, we improved our knowledge of beluga habitat use in the late summer. Nonetheless, we recognize that the ecological significance of each modelled variable and the direct link between belugas, prey densities and productivity remains imperfect. In order to better understand foraging within areas of beluga whale occurrence, future work requires more precise information on the environmental conditions selected by Arctic cod and other potential prey. The findings from this study are important, as dynamic habitat variables play a key role in structuring forage fish ecosystems and will likely be affected by future climate change locally and across the circum-polar Arctic.

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