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# Behavioral responses affect distribution analyses of bowhead whales in the vicinity of seismic operations

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ABSTRACT: Aerial surveys are sometimes used to assess the densities of wide-ranging whales, as well as changes in their distributions in response to human activity. Such surveys also provide data used to estimate numbers of animals exposed to different received levels of seismic sound, as required by regulators. However, estimates of abundance are often biased because they fail to account for the effects of seismic operations on the surfacing and diving behavior of whales. Our objective was to determine the extent to which analyses of the distribution of bowhead whales *Balaena mysticetus* are affected by changes in visual 'availability' caused by seismic operations. We used aerial survey data collected during seismic operations in the Alaskan Beaufort Sea from late August to early October 2008 and fit spatial density surface models to bowhead sighting data to predict whale density in an ensonified area. We also incorporated availability correction factors to determine the sensitivity of density estimates to changes in surfacing and diving behavior caused by seismic operations. The influence of altered whale behavior was then evaluated by comparing a series of realistic simulated scenarios in which models incorporated undisturbed or seismic disturbance-related correction factors. Results suggest that the numbers of bowhead whales present in the vicinity of seismic operations during the bowhead autumn migration are underestimated if the behavioral effects of seismic operations on whales are ignored. Our study highlights the importance of accounting for changes in whale behavior that can affect sightability when estimating numbers and distribution of whales in the vicinity of industrial activity.

KEY WORDS: Bowhead whale · Seismic survey · Distance sampling · Beaufort Sea · Availability · *g*(0) · Alaska · Spatial models · Behavior · Generalized additive model



## INTRODUCTION

The overlap between human activities and some species of marine mammals in the Arctic is substantial (Moore et al. 2012, Reeves et al. 2014). As a result, Arctic marine environments are subject to increasing levels of anthropogenic sound (Moore et al. 2012, Reeves et al. 2012, 2014), including sounds related to seismic surveys. Seismic surveys are commonly used to map geological features of the seabed and are used extensively by the oil and gas industry to identify sources of oil and gas. Seismic operations typically employ an array of air guns that release high pressure bubbles of air at regular intervals, which travel through the water column to penetrate the seabed and substrate below (Caldwell & Dragoset 2000). Air guns produce intense sounds with nominal source levels ranging from ~222 to 264 dB re 1 µPa-$m_{p\text{-}p}$ (Richardson et al. 1995). Typical high-energy arrays emit most of their energy at low frequencies of <500 Hz (Potter et al. 2007), but higher frequencies also contribute to the emitted energy (Goold & Coates 2006). As a result, there is overlap with the calling and hearing frequencies of low-frequency specialists, such

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as the bowhead whale *Balaena mysticetus* (Clark & Johnson 1984, Würsig & Clark 1993).

The effects of seismic operations on bowhead whales have been studied in the US and Canadian Arctic since the early 1980s (e.g. Fraker et al. 1985, Richardson et al. 1985, 1986, 1987, Ljungblad et al. 1988, Greene et al. 1999, Blackwell et al. 2010, 2013, 2015). Bowhead whales have been observed in the presence of seismic operations in their summer feeding areas in the Canadian Beaufort Sea (Richardson et al. 1986, Miller et al. 2005, Harwood et al. 2008, 2010), as well as along parts of their westward autumn migration in the Alaskan Beaufort Sea (Davis 1987, Ljungblad et al. 1988, Blackwell et al. 2013, Quakenbush et al. 2013) and the Chukchi Sea (Moore & Clarke 1993, Quakenbush et al. 2010). Concerns surrounding the possible impacts of anthropogenic sound have resulted in regulations to limit the exposure of marine mammals to strong sounds associated with specific activities such as seismic operations (e.g. NMFS 2000, NOAA 2015).

Regulations for managing and protecting marine mammals have been implemented in the US under the Marine Mammal Protection Act (MMPA) and the Endangered Species Act (ESA). The MMPA requires that any activities that might harm or incidentally harass a marine mammal, or that would interrupt any Arctic aboriginal subsistence hunting activity in northern Alaska, be conducted in a way that minimizes potential impacts. Authorizations for such activities are issued with the understanding that, at most, only a small, predetermined number of animals will be subject to potential harassment, and that the activity will have negligible population-level impacts and can be mitigated to minimize any harm, harassment or availability of marine mammals to hunters (MMPA 1972, Moore et al. 2012). A key requirement involves the development of marine mammal monitoring and mitigation plans, where mitigation measures are intended to minimize harm to marine mammals, and monitoring is required to determine what effects there might be over an area larger than one in which mitigation can reasonably be implemented (Moore et al. 2012). Monitoring includes the collection of data to estimate how many animals might have been exposed to, or may have diverted from, the activity.

Seismic operations commonly employ marine mammal observers on ships for mitigation, and in the Arctic, aerial surveys have also been utilized for monitoring and mitigation purposes. Aerial surveys are an effective means of obtaining information about numbers and distributions of marine mammals over large areas in short periods of time. Aerial surveys are the only practical method to assess the presence and density of wide-ranging animals, such as the bowhead whale (Harwood et al. 2008, 2009, Funk et al. 2010, Bisson et al. 2013). They have been used in Canada to determine density and presence of feeding aggregations so that restrictions on the areas where industrial activities can be conducted may be implemented (Harwood et al. 2008, 2009). In the US, wide areas around seismic operations may be monitored using aerial surveys to assess distributions and to estimate numbers of whales present in areas with different estimated received sound levels. Documentation of marine mammal distributions around seismic operations is sometimes required by US regulators as a condition of permits to conduct activities (MMPA 1972, Moore et al. 2012). Such information on whale distribution relative to industrial activities is also useful to assess possible impacts of industrial activities on local Iñupiat whaling success.

Subtle behavioral reactions of whales to seismic operations could affect how visible whales are to observers. Not accounting and correcting for such behavioral variations could result in over- or underestimates of the number of animals that were present (Hain et al. 1999, Robertson et al. in press).

Bowhead whales have been found to vary their surfacing, respiration and dive behavior when in the vicinity of seismic operations at known ranges of up to 54–73 km, or where sounds related to seismic operations were <125 to ≥133 dB re 1 $\mu Pa_{rms}$ as determined from nearby sonobuoys (Richardson et al. 1995). The altered behavior included subtle changes in characteristics of their surfacing, respiration and dive behavior (Richardson et al. 1986, 1993, Ljungblad et al. 1988, Robertson et al. 2013). An analysis of these earlier bowhead behavior data supplemented with additional data collected up to 2000 determined that bowhead whales respire fewer times and have significantly shorter surfacing times when in the vicinity of seismic operations (Robertson et al. 2013). Variations in surface and dive behavior can, in turn, influence how visible a whale is to aerial observers because observers can only detect, and therefore count, whales that are at or near the surface of the water (Hain et al. 1999, Thomas et al. 2002, Robertson et al. in press). However, it is possible to account for whales that are submerged below the surface and not seen on surveys by calculating the probability that a whale will be at the surface and available for visual detection under different circumstances (Laake et al. 1997, Hain et al. 1999).

We used correction factors to account for the likelihood of whales being seen less frequently when in the vicinity of seismic operations and applied these correction factors to sighting data made available to us from an aerial survey program monitoring seismic operations in the southern Beaufort Sea in 2008. The objectives of our study were therefore to (1) predict corrected densities of bowhead whales in the southern Alaskan Beaufort Sea in areas ensonified to different sound level categories (≤120 to ≥140 dB re 1 $\mu Pa_{rms}$) by seismic operations, and (2) determine the extent to which predicted densities, and hence the predicted distribution, of bowhead whales change due to variations in availability associated with seismic operations. Distance sampling methods provided a means to succinctly address our objectives by allowing the sighting data and changes in behavior of whales while in the presence of varying levels of seismic sounds (categorized into broad bins of <120, 120–139 and ≥140 dB re 1 $\mu Pa_{rms}$ estimated received sound level) from seismic operations to be combined within the same modeling framework.

## MATERIALS AND METHODS

### Collection of effort and sighting data

Bowhead whale sighting data were collected during systematic line-transect aerial surveys in the southern Alaskan Beaufort Sea during the autumn of 2008. The surveys were designed to monitor the area in and near seismic operations conducted by Shell Offshore (Funk et al. 2010). Surveys consisted of randomly placed transect lines running perpendicular to the coast in a north–south direction. The length and density of the transects varied to reflect the monitoring requirements dictated by the different seismic operations being monitored in the area, but overall resulted in good coverage of the study area (Fig. 1) (Funk et al. 2010)

Surveys were conducted from a specially modified DHC-300 Twin Otter fixed-wing airplane. Modifications included a STOL (Short Take Off and Landing) kit to allow for slow survey speeds, bubble windows to enhance the viewing field available to observers, and an inverter that supplied 110 V AC power to run the survey equipment (Funk et al. 2010). The absence of a belly window can impact detection directly on the trackline; however, detectability on the trackline was assessed by plotting a lateral frequency distribution of all sightings during the analysis stage. All surveys were conducted at 305 m above sea level and at standard survey ground speeds of ~222 km $h^{-1}$. Flight durations were determined by fuel capacity, weather conditions and pilot daily flight hour limits.

Surveys were conducted using standardized procedures. Survey teams consisted of 2 pilots and up to 5 trained observers. Two primary observers and up to 2 secondary observers sat at bubble windows on either side of the plane, continuously scanning the water for marine mammals within approximately 2 km of the transect line (Funk et al. 2010), while a data recorder entered sighting and effort-related data into a GPS-linked laptop computer. The observers rotated positions between primary, secondary and data recorder positions approximately every 2 to 3 transects in order to maintain alertness. Observers recorded environmental data (Beaufort wind force scale, ice cover percentage and type, amount of glare in the viewing area, and an overall measure of sightability) that could influence sightability at 2-min time intervals and at the end of each transect (Funk et al. 2010).

When a bowhead whale was sighted, observers recorded the time when the sighting was perpendi-

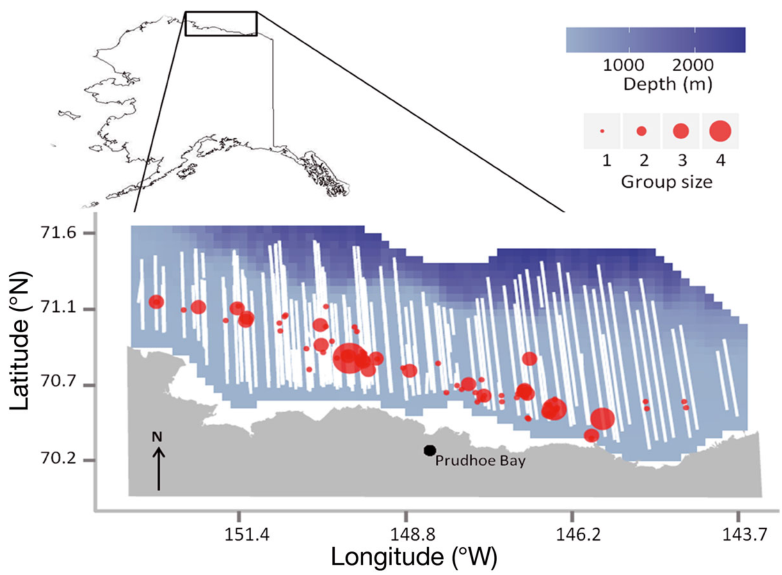


Fig. 1. Aerial surveys conducted over the southern Alaskan Beaufort Sea, 25 August to 10 October 2008. The usable transect lines are depicted by the white lines, while sightings of non-calf bowhead whales are shown by the red circles. The size of the circle corresponds with the recorded group sizes of 1 to 4 whales. Depth within the study area is also shown on a gradient scale (0–2500 m). The majority of the study area comprises the continental shelf, shown in light blue; the continental slope is shown in dark blue

cular to the aircraft heading, the group size, sighting cue, age class, activity, heading, swim speed and an inclinometer angle. The inclinometer angle and time were used to calculate the precise location of each sighting. The GPS position of the aircraft at the time of the sighting was obtained from the GPS log file and the angle reading allowed the perpendicular distance of the whale from the trackline to be calculated and the whale location to be determined (Funk et al. 2010). Primary and secondary observers were independent (i.e. secondary observers did not announce their sightings), and the sighting data of secondary observers were coded to reflect the observers' position. Observers recorded sighting and effort data onto digital recorders and transcribed data into an Excel spreadsheet after each survey. The spreadsheet was verified to ensure that all data were entered correctly.

Table 1. Sighting and environmental covariates considered for the detection function and density surface models fitted to the 2008 bowhead whale sighting data. Ice % was not included in either model because all sightings occurred in open water conditions with no ice present

| Model | Covariate | Scale |
|---|---|---|
| Detection function | Beaufort wind force | Beaufort scale 0–4 |
| | Sightability | Excellent – moderately impaired |
| | Half month | 25–31 Aug, 1–15 Sep, 16–30 Sep, 1–11 Oct |
| | Perpendicular distance | Meters |
| | Group size | |
| Density surface | Water depth | Meters, log transformed |
| | Distance from shore | Meters, square-root transformed |
| | Latitude | Meters – northing |
| | Longitude | Meters – easting |
| | Day of year | |
| | Distance to seismic survey | Kilometers, 10 levels (0–10, 11–20, 21–40, 41–60, 61–80, 81–100, 101–150, 151–200, 201–300, > 300) |
| | Estimated received level | <120 dB, 120–139 dB, ≥140 dB |

## Data analysis

Survey data collected from 25 August onward were selected for analysis because this is when the majority of the Bering-Chukchi-Beaufort population of bowhead whales migrates west through the southern Beaufort Sea (Richardson & Thomson 2002, Huntington & Quakenbush 2009, Citta et al. 2014). Only data considered as 'on transect' were selected. This included sighting and effort data collected while the aircraft was level and flying pre-determined north–south transect lines at the standard survey speed and altitude (Funk et al. 2010). To minimize the impact of poor sighting conditions (e.g. high sea states, glare, and low-lying cloud), the sighting and effort data were filtered so that only data that met the following criteria were retained for analysis. Useable sighting conditions included those where the Beaufort wind force was ≤4, glare covered ≤30% of the viewing area, and the overall sightability was subjectively described by observers as excellent to moderately impaired (Table 1) (Funk et al. 2010). Filtering the data to meet these strict criteria reduced the impact of poor sighting conditions on subsequent analyses of the data.

We used a 3-step process to predict bowhead whale density within the study area following a distance sampling methodology (Buckland et al. 2001, Thomas et al. 2010, Miller et al. 2013a). The first step involved fitting a detection function to the bowhead whale sighting data. The detection function model was then expanded into a spatial model that investigated the importance of a set of spatial and temporal covariates in relation to bowhead sightings. Finally, we used the results of the spatial model to predict a 2-D density surface for bowhead whales across the study area to assess the spatial extent of avoidance of the seismic operations by bowhead whales.

### Step 1: Detection function modeling

Distance sampling models were fitted to sighting data collected by both primary and secondary observers, to estimate the detection function $g(x)$ of bowhead whales detected at distance $x$ from the transect line. Standard distance sampling methods assume that all animals at the surface are observed on the transect center line. However, animals are harder to detect with increasing distance from that center line (Buckland et al. 2001, Thomas et al. 2010). A fitted detection function allows estimation of the proportion of animals missed during the survey as distance from the trackline increases.

We considered both conventional distance sampling (CDS) and multiple covariate distance sampling (MCDS) models for the detection function model. CDS models incorporate heterogeneity and are considered pooling-robust when many factors may affect detectability (Marques & Buckland 2004, Thomas et al. 2010), while MCDS models account for heterogeneity by allowing covariates to be included in the detection function model (Marques & Buckland 2004). Covariates considered likely to influence the detectability of bowhead whales included group size, Beaufort wind force and overall sightability. Ice percentage and glare are also assumed to influence detectability (Givens et al. 2010), but were not considered because all whale sightings in 2008 occurred in ice-free conditions and glare was considered in our evaluation of overall sightability. Prior to model fitting, we examined the covariate data using methods recommended by Zuur et al. (2010). We investigated outliers with Cleveland dotplots, and identified collinearity between covariates with Pearson's correlation coefficients and variance inflation factor (VIF) values (Zuur et al. 2010). We found that sightability and Beaufort wind force were collinear (Pearson's correlation coefficient = 0.7). We therefore retained Beaufort wind force and dropped sightability from further consideration to avoid issues with multicolliniarity and to minimize model performance issues (Zuur et al. 2010). Variables considered to affect detectability included Beaufort wind force, group size and half-month time period.

Detection function models were fitted to sighting data collected by primary and secondary observers that were coded as 'on-transect' using the R package 'Distance' v0.7.3 (Miller 2013, R Core Team 2013). A total of 91 sightings of 127 whales were available to fit the model. The use of primary and secondary observer sightings allowed us to maximize the sighting data available to us as >40 sightings are recommended for fitting a detection function in distance (Buckland et al. 2001). These sightings included both non-calf bowhead whales (classified as all subadult and adult whales without a dependent calf) and bowhead cows with a dependent calf. Two candidate detection function models were considered, the half-normal key function (Eq. 1) and the hazard rate key function (Eq. 2):

$$g(x) = \exp^{\left(-x^2/2\sigma^2\right)} \quad (1)$$

$$g(x) = 1 - \exp^{\left[\left(x/\sigma\right)^{-\beta}\right]} \quad (2)$$

where $x$ is the perpendicular distance from the transect line, σ is the scale parameter, and the hazard rate key function contains an additional parameter (β) that defines the shape of the detection function (Eq. 2) (Buckland et al. 2001).

Aerial survey sighting data often require some left truncation in the absence of a belly window (as was the case with these surveys) that allows the transect line to be observed directly. Investigation of several possible left truncation distances determined that the fitted detection function model for our sighting data remained robust with no left truncation. However, a right truncation (based on where the detection probability fell below 10%; Buckland et al. 2001) was required and resulted in exclusion of all sightings further than 2000 m from the transect center line. Akaike's information criterion (AIC) (Burnham & Anderson 2002) and visual inspection of the detection function histograms were used to assess model fit (Buckland et al. 2001, Thomas et al. 2010). AIC scores were computed over all candidate models, and the model with the smallest AIC score and realistic detection function was selected as the best model. This model was incorporated into the subsequent spatial model.

### Step 2: Density surface modeling

The presence of potentially detectable air-gun activity in areas coinciding with regions where an aerial survey was flown on a given day was determined from 38 directional autonomous seafloor acoustic recorders (DASARs) distributed in 6 separate groups across the study area for the duration of the 2008 survey season (Blackwell et al. 2013). All but 2 surveys flown from 25 August to 11 October were conducted during periods when air-gun activity was detected by the DASARS and thus assumed to be audible to nearby bowhead whales. Recent analysis of bowhead whale calling behavior by Blackwell et al. (2015) indicates that whales alter their calling behavior when air-gun signals are audible. When low levels of seismic sounds are audible, bowheads increase their calling rate and appear to have continued to approach the seismic operations, but when whales approached distances at which received levels of the air-gun pulses were 160 dB re 1 μPa$_{rms}$, most whales stopped calling, supporting our use of 'audibility' as a possible threshold for changes in distribution and behavior. Therefore, only those surveys where air-gun activity was assumed to be detectable to whales were retained for analysis. However, some of the surveys included had relatively low levels of seismic sounds that originated from well outside of the study area (>200 km) or from arrays within the study area that were operating at reduced power. Transect lines were divided into segments of length $l_j$ based on combined

2-min time periods used by observers to record environmental effort data during each survey (Funk et al. 2010). This resulted in 729 segments with an average length of 14.26 km (range 7.03–21.64 km). Bowhead whales were detected in 44 (6.04%) segments, although neither abiotic nor biotic conditions varied appreciably within any given segment (Hedley & Buckland 2004, Miller et al. 2013a). Sightings recorded by a primary observer within 2000 m of the transect line when air-gun activity was presumably audible to the whales resulted in 65 sightings of 92 whales being available for spatial analysis. Of these sightings, only 6 were of mother–calf pairs. Given that the behavior of cows with dependent calves differs from that of other whales, we chose to avoid the potentially confounding issues related to influence of a dependent calf and only fit the models to the remaining 59 sightings of 80 non-calf whales.

Whale sighting data were also categorized by activity state. Whales were classified as feeding or traveling based on a combination of data recorded at the time of the sighting. These included behavior, orientation and swim speed. Whales recorded as swimming at medium to fast speed with a westerly orientation were classified as traveling, while whales observed with easterly orientations, moving slowly or not at all, with mouths open when they surfaced, or with mud streaming from their mouth or their body, were classified as feeding (Würsig et al. 1985, 1989, Koski et al. 2009).

Spatial and temporal covariate data assumed to influence the location of the whales in 2008 were summarized for each segment (Table 1). Covariate data associated with each segment included depth, distance to shore, day of year, distance-to-seismic operation (DS), estimated received sound level (ERL), latitude and longitude. The average water depth for each segment midpoint was calculated using bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO 2003), while distance to shore, latitude and longitude for each segment midpoint were determined using ArcMAP 9.3 (ESRI 2008). The seismic-related variables (DS and ERL) were included as a proxy for the possible sound levels that would have been audible to bowhead whales in 2008. DS was divided into 10 distance bins because the exact distance to some operations was unknown, and ERLs were divided into 3 bins: <120 dB, 120–139 dB and ≥140 dB re 1 $\mu Pa_{rms}$. Effort levels were too low to allow us to add further ERL categories where ERL was >150 dB re 1 $\mu Pa_{rms}$. Categorizing ERLs into bins allowed us to partly address issues related the underestimation of received sound levels that were known to occur in some circumstances, and also to integrate distant seismic operations whose air-gun signals were detected on the DASARs, and therefore would have also been audible to whales detected near the DASAR arrays.

Prior to model fitting, covariate data were subjected to the same exploratory analysis as detailed in the modeling of the detection function in Step 1. Water depth and distance from shore were collinear (Pearson's correlation coefficient = 0.9) and latitude also presented evidence of colliniarity with both distance from shore and depth. Therefore, both latitude and distance from shore were dropped from further consideration in the model to avoid multicolliniarity. Five final variables were considered for inclusion in the model: continuous variables included smoothed functions of water depth (log-transformed), longitude (standardized to easting, in meters) and day of year, while categorical variables included DS and ERL (Table 1).

We fit the spatial model using the 2-step count method proposed by Hedley & Buckland (2004) using the R package 'dsm' v2.0.1 (Miller et al. 2013b). This approach is also referred to as density surface modeling (Miller et al. 2013a). The number of whales per segment $n_j$ of contiguous transect was modeled within a generalized additive model framework as a function of spatial and temporal covariates, $z_{ik}$, where $z_{ik}$ is the value of the $k$th covariate in the $i$th segment (Hastie & Tibshirani 1990, Wood 2006, Givens 2009) with the structure:

$$E(n_i) = \hat{p}_i A_i \exp\left[\beta_0 + \sum_k f_k(z_{ik}) + z_{ik}\right] \quad (3)$$

where $f_k$ are smooth functions of the covariates and $\beta_0$ is the intercept term (Miller et al. 2013a). Segment area $A_i$ multiplied by the probability detection function, $\hat{p}_i$ modelled in Step 1, gives the effective area for segment $i$ (Thomas et al. 2010, Miller et al. 2013a), and is included in the model as an offset term.

A Tweedie distribution, in which variance is proportional to some power of the mean, was used to account for the zero-inflated count data (Jøergensen 1987, Shono 2008, Williams et al. 2011, Miller et al. 2013a). The Tweedie distribution is a flexible and straightforward method of modeling count data when there are a high proportion of zeros in the data (Miller et al. 2013a).

Smoothness selection was by restricted maximum likelihood (REML). The objective function optimized by REML has more pronounced optima than methods such as Generalized Cross Validation (GCV) or AIC, so models tend to be estimated more accurately (Wood 2006, 2011). We fit the model in a forward step-wise manner and the decision whether to retain a term or drop it from further consideration was based on examining the approximate p-values of each term, the AIC score (where possible) and the randomized quantile residual plots. AIC scores could only be compared when candidate models were fit with a combination of the same fixed effects. Once the smooth functions of the continuous covariates were selected, the value of the Tweedie parameter (θ) was assessed using quantile residual diagnostic plots generated from the qres function in the 'statmod' package in R (Dunn & Smyth 1996, Smyth et al. 2013). Visual inspection of residual plots for different values of θ is thought to be adequate as overall results are usually not very sensitive to θ (Williams et al. 2011). Finally, temporal and spatial residual autocorrelation were investigated using variograms and bubble plots.

### Step 3: Density prediction and variance estimation

Correction factors for availability (Marsh & Sinclair 1989, Laake & Borchers 2004) were incorporated into the selected density surface model by dividing the predicted density of each grid cell by the correction factor. The correction factor for availability [$a(x)$] of non-calf bowhead whales exposed to seismic operations in the autumn was selected because only surveys conducted during the autumn during which bowhead whales would have been exposed to airgun activity were considered in the density surface model. The correction factor values were calculated using surfacing and diving behavior of bowhead whales summarized in Robertson et al. (2013), following the method proposed by Laake et al. (1997):

$$a(x) = \frac{s}{s+d} + \frac{d\left[1-e^{\left\{-t(x)/d\right\}}\right]}{s+d} \quad (4)$$

where $s$ is the mean surface time and $d$ is the mean dive time of a bowhead whale, and $t(x)$ is the time that a patch of sea surface is in the view field of the observer (for the purposes of these data this was 21.6 s). A prediction grid divided into 5 km$^2$ grid cells was created in Quantum GIS 1.8.0 (QGIS 2004) to encompass the study area and values for each explanatory variable retained in the final model were generated for the midpoint of each grid cell. The availability-corrected model was used to predict the number of whales in each 5 km$^2$ grid cell of the study area, resulting in a 2-D density surface of whales. Variance estimation followed the variance propagation method detailed in Williams et al. (2011) and incorporated into the R-package 'dsm' (Miller et al. 2013a,b). This method incorporated the uncertainty in the estimation of the detection function into the variance of the spatial model (Williams et al. 2011, Miller et al. 2013a) and is considered computationally efficient and comparable to bootstrap equivalents (Miller et al. 2013a).

Following the same prediction procedures detailed in Step 3, the effects of variable availability related to the presence of seismic operations was assessed by comparing prediction grids generated from the use of availability correction factors based on the behavior of presumably undisturbed non-calf whales in the autumn with predictions corrected for the variable behavior of non-calf whales exposed to seismic operations in autumn (Table 2) (Robertson et al. 2013).

The density surface modeling and prediction steps were repeated for feeding non-calf whales and traveling non-calf whales, and predicted densities with their associated variances were estimated. The effects of variable availability related to presumed exposure of whales to seismic operations was assessed by again comparing the predicted densities corrected for variable behavior of presumably undisturbed non-calf whales with those predicted densities that were corrected for the variable behavior of whales in the presence of seismic operations.

## RESULTS

### Detection function

A pooling-robust CDS model with a half-normal key function and no adjustment terms was selected as the best model through AIC and visual inspection

Table 2. Availability correction factors for foraging, traveling and non-calf bowhead whales in the autumn for both undisturbed whales and those exposed to seismic operations. Correction factors were calculated following the methods described in Robertson et al. (in press) using a field of view that assumed a 1.25 km swath of the water surface was in view from the plane on the transect line

| Category | Undisturbed $a(x)$ | Seismic $a(x)$ |
|---|---|---|
| Autumn | 0.161 | 0.096 |
| Traveling | 0.142 | 0.106 |
| Feeding | 0.182 | 0.137 |

of the detection curves (Table 3, Fig. 2). Beaufort wind force, group size or half-month in MCDS models did not improve the fit of the detection function (Table 3).

### Density surface model predictions of densities of non-calf bowhead whales

The best candidate model considered after forward stepwise selection was $N \sim s(\log(\text{depth}) + s(x) + s(\text{day of year}))$.

Smoothed functions of depth (log transformed), longitude (easting) and day of year were all important in explaining the numbers of bowhead whales in each segment; neither seismic-related variable (DS or ERL) significantly improved the model fit and so neither were considered further in the model (Table 4, Fig. 3). The model suggested that the whales had an apparent preference for shallower continental shelf waters instead of deeper slope waters. Higher numbers of non-calf whales were predicted earlier in the autumn (late August and early September), with numbers decreasing through the remainder of the season (late September and into October). Examination of model residuals revealed no serious issues with temporal or spatial correlation.

Table 3. Summary of detection function models fitted to the 2008 bowhead whale sighting data. The models are sorted from best to worst, as classified by Akaike's information criterion (AIC) and AIC differences ($\Delta_i$)

| Model | AIC | $\Delta_i$ |
|---|---|---|
| Half-normal | 1368.21 | 0 |
| Half-normal + Beaufort + ½ month | 1368.53 | 0.32 |
| Hazard rate + Beaufort | 1368.77 | 0.56 |
| Hazard rate | 1368.91 | 0.70 |
| Half-normal + Beaufort | 1369.36 | 1.15 |
| Half-normal + ½ month | 1369.79 | 1.58 |
| Hazard rate + group size + Beaufort | 1369.82 | 1.61 |
| Half-normal + group size | 1370.17 | 1.96 |
| Hazard rate + Beaufort + ½ month | 1370.37 | 2.16 |
| Half-normal + group size + ½ month + Beaufort | 1370.51 | 2.30 |
| Hazard rate + group size + ½ month + Beaufort | 1371.11 | 2.90 |
| Half-normal + group size + Beaufort | 1371.32 | 3.11 |
| Half-normal + group size + ½ month | 1371.69 | 3.48 |
| Hazard rate + ½ month | 1371.93 | 3.72 |
| Hazard rate + group size + ½ month | 1372.43 | 4.22 |

### Predicted densities for non-calf bowhead whales

The predicted densities indicated that non-calf whales were concentrated in the central southeast portion of the study area west of Camden Bay, but were present in much lower densities in the southwest region of the study area (from Prudhoe Bay into Harrison Bay), with the exception of a small area of higher densities on the extreme western edge of the study area (Fig. 4B). The estimates of relative abundance, their associated variances, and the mean and maximum whale density per 5 km$^2$ grid cell are summarized over 5 selected dates

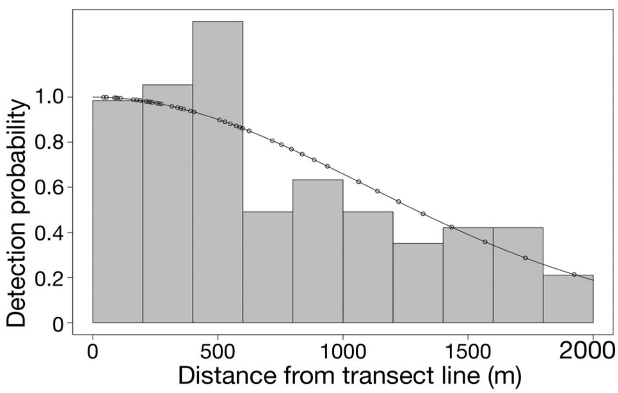


Fig. 2. The fitted detection function for the selected distance sampling model for sightings of bowhead whales collected during aerial surveys in the southern Alaskan Beaufort Sea in 2008. The best model was a pooling-robust conventional distance sampling (CDS) model with a half-normal key function and no adjustment terms. Where the line is the fitted detection function, the data points are the sightings and the grey bars the scaled histogram of observed distances of sightings from the transect line

Table 4. Density surface model results for the general density of non-calf bowhead whales in the southern Alaskan Beaufort Sea, late August to early October 2008. Significant relationships are in **bold**. A total of 729 segments of useable effort and 59 sightings of 80 bowhead whales were available for the model

| Parametric coefficient | Estimate | SE | p |
|---|---|---|---|
| **Intercept** | **−21.813** | **3.322** | **< 0.0001** |
| Approx. significance of smooth terms | edf | Ref. df | p |
| **s(day of year)** | **1.696** | **2.130** | **< 0.0102** |
| **s(*x*)** | **3.917** | **4.962** | **< 0.0006** |
| **s(log(depth))** | **2.012** | **2.181** | **0.0323** |
| $R^2$ (adjusted) | 0.06 | | |
| REML score | 264.53 | | |
| Deviance explained | 25.90 % | | |

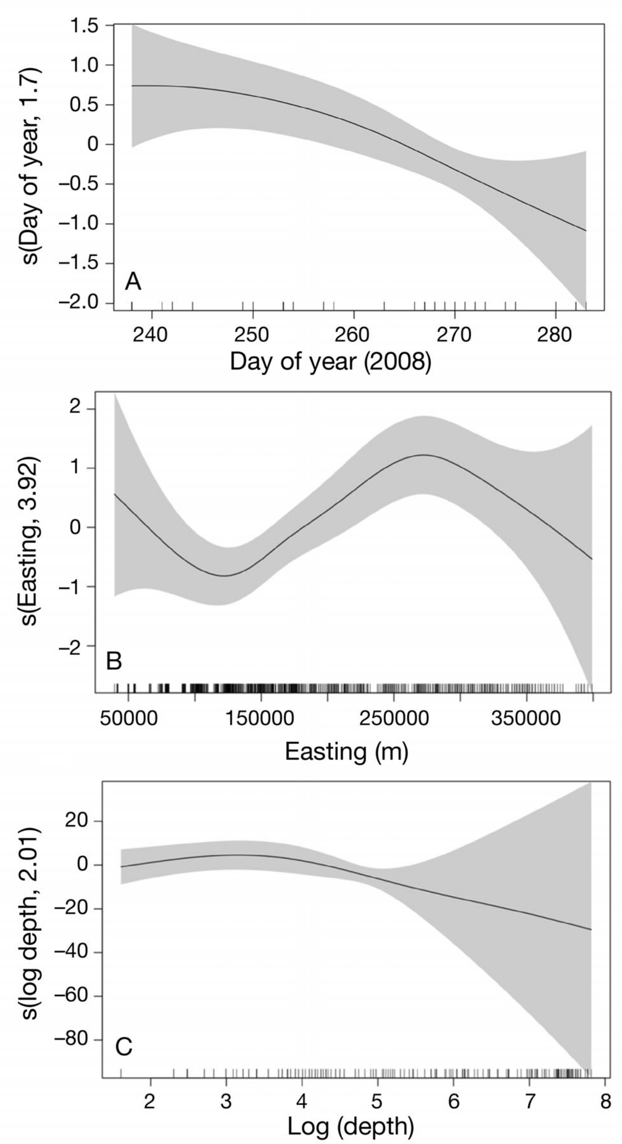


Fig. 3. Significant smoothed functions for the variables (A) 'day of year', with 1.7 degrees of freedom, (B) longitude, on a standardized easting scale with 3.92 degrees of freedom, and (C) depth, on a log-transformed scale with 2.01 degrees of freedom. These plots indicate that the highest numbers of whales occurred in depths of around 25–55 m, that whales were concentrated in the eastern-central and far western parts of the study area, and that numbers of whales in the study area decreased as the season progressed from late August into early October in 2008. The distributions of data points for each covariate are displayed along the *x*-axis by the rug plot and the shaded area illustrates the variance at 2 × SE bands around the fitted smooth functions

through late August to early October in Table 5. The highest densities of whales were predicted for late August with densities decreasing through September and into October, when the lowest densities of whales were predicted (Fig. 4B). Whales appeared to be concentrated in the nearshore waters, with little or zero densities predicted in the deeper slope waters (Fig. 4B).

### Predicted densities for feeding bowhead whales

For feeding whales, the best model included the smooth functions of depth (log transformed), longitude (easting) and day of year (Table 6, Fig. 5). Densities of feeding non-calf whales were predicted to occur in the study area after correcting for variable availability of feeding non-calf whales in the presence of seismic operations [$a(x)$ = 0.14]. Whales engaged in feeding activities were observed during the first half of September, and the 2-D density surfaces indicated that the whales were predominantly feeding in the southeastern part of the study area, with the exception of a small region at the far western edge of the study area (Fig. 6B, see Fig. S1B in the Supplement at www-int-res.com/articles/suppl/m549p243_supp.pdf). There were few, if any, feeding whales in the central and southwestern portions of the study area (Fig. 6B, see Fig. S1B in the Supplement). The maximum predicted density within the survey area was 19.04 whales 5 km$^{-2}$ and occurred on the 6 September, while the mean density predicted across the study area ranged from 0.84 to 0.67 whales 5 km$^{-2}$ (Table 7, see Fig. S1B in the Supplement). Abundance estimates for the number of whales engaged in feeding within the study area on a given day ranged from 1341 whales on 6 September to 1063 whales on 19 September (Table 7).

### Predicted densities for traveling bowhead whales

For traveling non-calf whales, the best model again included the smooth functions depth (log transformed), longitude (easting) and day of year (Table 8, Fig. 7). Traveling whales were observed throughout the study period, and numbers fluctuated with peaks predicted for late August and during the latter half of September and early October (Table 7). Densities of traveling non-calf whales were predicted in the study area for 29 August, and 19 and 29 September after correcting for variable availability of traveling non-calf whales in the presence of seismic operations [$a(x)$ = 0.11] (see Fig. S2B in the Supplement). Estimates of relative abundance, their associated variances, and the mean and maximum whale density per 5 km$^2$ grid cell by date (Table 7) were very different from those for feeding non-calf whales. Traveling whales were predicted to have occurred rather uni-

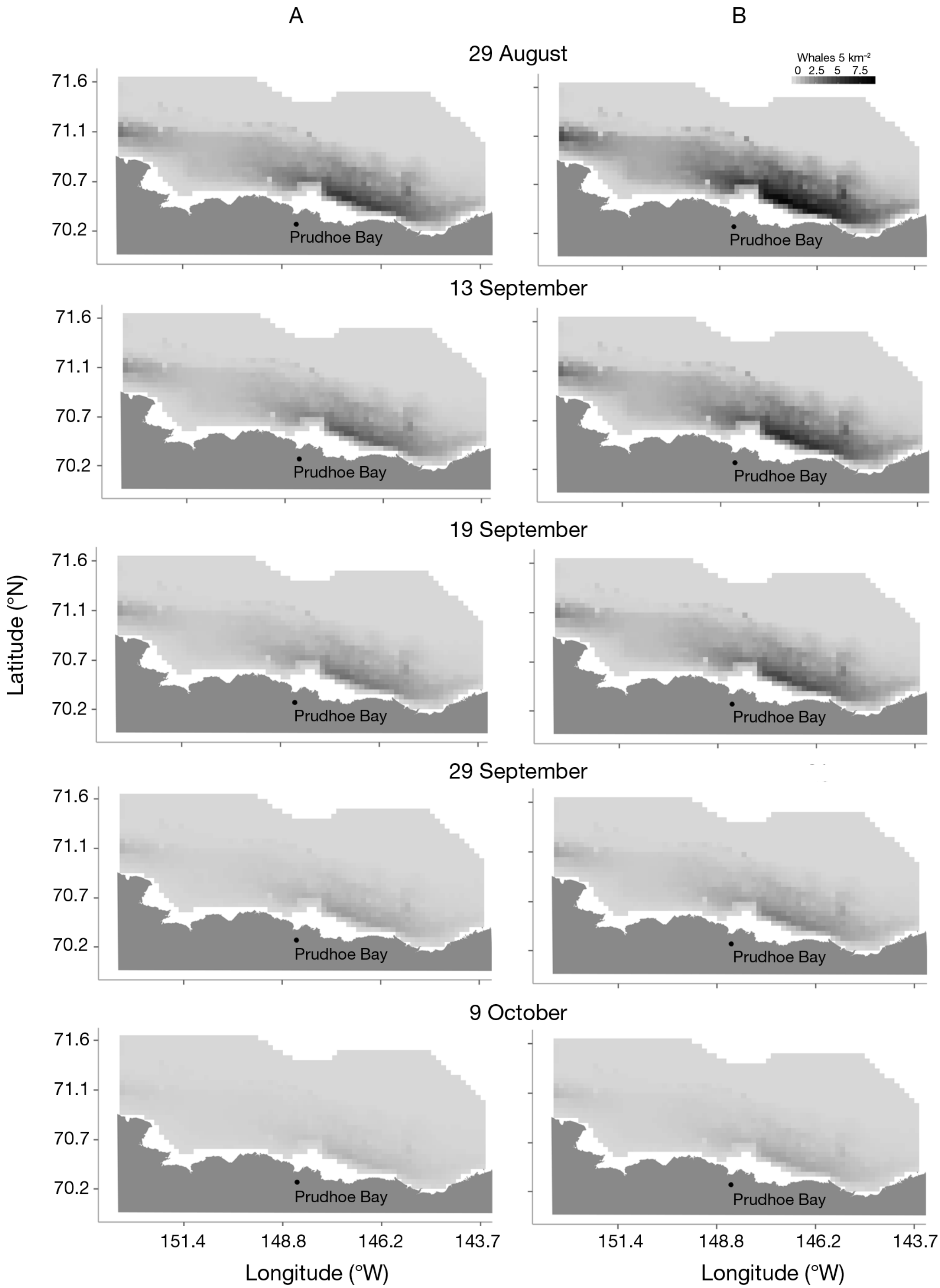


Fig. 4. Predicted densities (number of whales per 5 $km^2$ grid cell) for non-calf bowhead whales in the southern Alaskan Beaufort Sea, late August to early October 2008. Plots in (A) have been corrected for availability bias for undisturbed bowhead whales, while plots in (B) have been corrected for the availability bias of non-calf whales exposed to seismic survey operations

Table 5. Relative abundance estimates, associated variances, and mean and maximum densities of non-calf bowhead whales exposed to air-gun pulses within the survey area for selected dates from late August to early October 2008

| Date | Estimate | SE | CV | 95%CI | Mean density 5 km$^{-2}$ | Max. density 5 km$^{-2}$ |
|---|---|---|---|---|---|---|
| 29 Aug | 1718 | 683.79 | 0.40 | 810–3643 | 1.06 | 9.06 |
| 13 Sep | 1219 | 351.51 | 0.29 | 7010–2121 | 0.75 | 6.43 |
| 19 Sep | 9198 | 250.43 | 0.27 | 5443–15532 | 0.57 | 4.84 |
| 29 Sep | 499 | 160.52 | 0.32 | 270–923 | 0.31 | 2.63 |
| 09 Oct | 2787 | 168.84 | 0.61 | 93–834 | 0.17 | 1.46 |

formly throughout the study area in low densities, while feeding whales were predicted to have occurred predominantly in nearshore waters east of Prudhoe Bay and west of Harrison Bay, as illustrated for 19 September in Fig. 6. The predicted mean densities of traveling whales fluctuated over the season and were also much lower than those for feeding whales — as much as 33.5 times lower. The maximum density predicted for traveling non-calf whales was 2.51 whales 5 km$^{-2}$ on 29 August, while the mean density across the study area ranged from 0.42 traveling whales 5 km$^{-2}$ in late August to 0.02 whales 5 km$^{-2}$ in mid-September and 0.22 whales 5 km$^{-2}$ in late September (Table 7, see Fig. S2B in the Supplement). These results, combined with those for feeding whales, suggest that non-calf whales did not feed in the central southwest region of the study area in 2008, but rather traveled through the area. This is also supported by the lower predicted densities.

Table 6. Density surface model results for feeding non-calf bowhead whales in the southern Alaskan Beaufort Sea, late August to early October 2008. Significant relationships are in **bold**. A total of 729 segments of useable effort and 30 sightings of 41 non-calf whales were available for the model

| Parametric coefficient | Estimate | SE | p |
|---|---|---|---|
| **Intercept** | **–40.415** | **5.789** | **<0.0001** |
| Approx. significance of smooth terms | edf | Ref. df | p |
| **s(day of year)** | **4.453** | **5.073** | **0.011** |
| **s(*x*)** | **3.999** | **4.934** | **<0.0001** |
| **s(log(depth))** | **1.986** | **2.135** | **0.0004** |
| $R^2$ (adjusted) | 0.25 | | |
| REML score | 113.86 | | |
| Deviance explained | 74% | | |

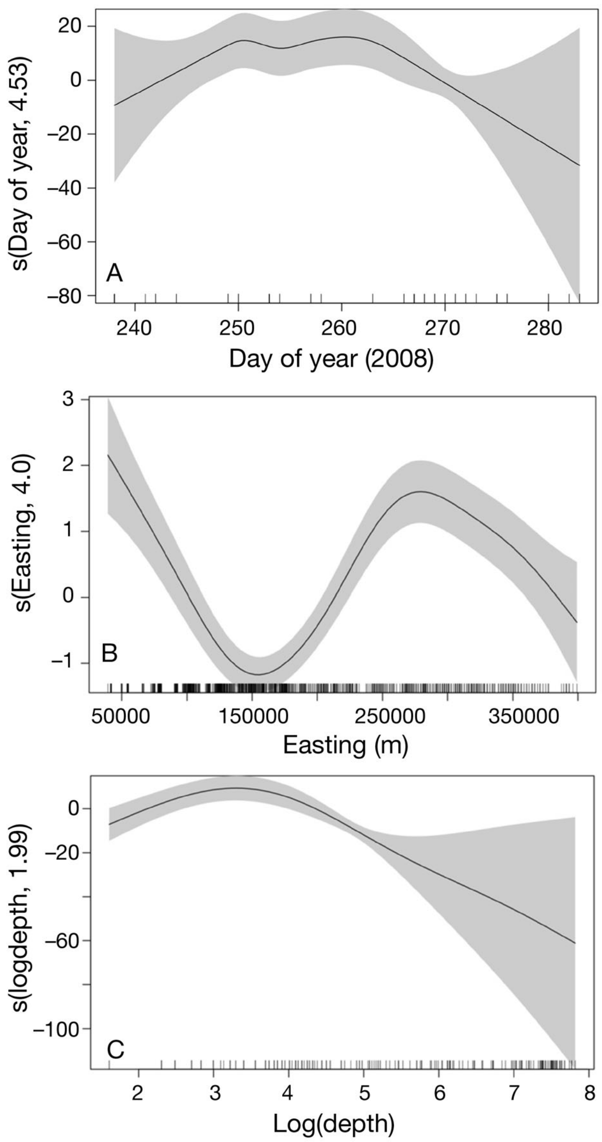


Fig. 5. Significant smoothed functions for (A) day of year, with 4.53 degrees of freedom, (B) longitude, on a standardized easting scale with 4.0 degrees of freedom, and (C) depth, on a log-transformed scale with 1.99 degrees of freedom for foraging non-calf bowhead whales in the southern Alaskan Beaufort Sea, 25 August–10 October 2008. The plots predict that numbers of feeding whales are highest at depths of 25–55 m, and that whales were concentrated in the central-eastern and far western parts of the study area during early September. The distributions of data points for each covariate are displayed along the *x*-axis by the rug plot and the shaded area illustrates the variance at 2 × SE bands around the fitted smooth functions

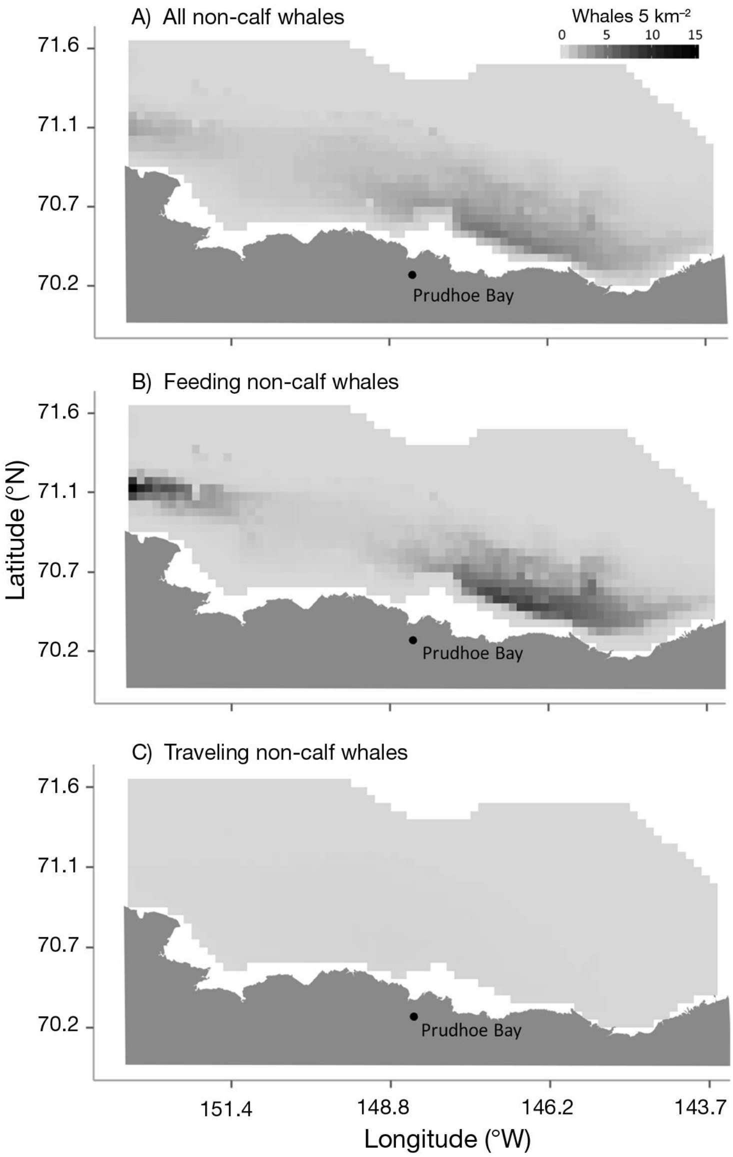


Fig. 6. Predicted densities (number of whales per 5 km$^2$ grid cell) of (A) all, (B) feeding and (C) traveling non-calf bowhead whales across the study area on 19 September 2008. All predicted densities exhibited in these maps were corrected for the variable availability of whales exposed to seismic survey operations

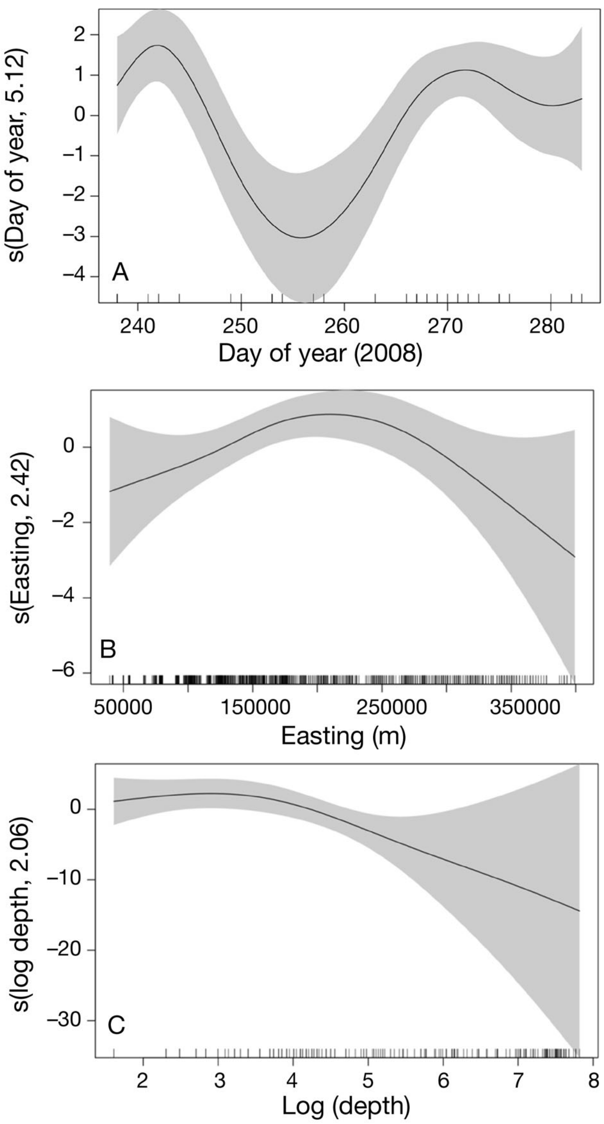


Fig. 7. Significant smoothed functions for the variables (A) day of year, with 5.12 degrees of freedom, (B) longitude, on a standardized easting scale with 2.42 degrees of freedom, and (C) depth, on a log-transformed scale with 2.06 degrees of freedom for traveling whales. These plots indicate that higher numbers of whales occurred in waters 30–50 m deep and in the central part of the study area more than to the east and west. There was a clear dip in numbers of traveling whales in the middle of the season that corresponded with the peak in feeding activity. The distributions of data points for each covariate are displayed along the *x*-axis by the rug plot and the shaded area illustrates the variance at 2 × SE bands around the fitted smooth functions

## Comparisons of densities with corrections for disturbed and non-disturbed whales

Not accounting for changes in surface and dive behaviors that occur in the vicinity of seismic survey operations results in lower density and abundance estimates of whales in the study area and the general distribution of whales being more restricted to inshore waters in 2008 (Table 9, Fig. 4). The predicted densities that account for changes in behavior due to exposure to sounds related to seismic operations indicate that non-calf whales were widely distributed across the southern region of the study area, with

Table 7. Relative abundance estimates and associated variances of feeding and traveling non-calf bowhead whales exposed to air-gun pulses within the survey area. Predictions for the density and abundance of feeding whales were calculated for 3 equally spaced days during the first half of September, when bowhead whales were observed feeding within the study area in 2008. Predictions for traveling whales were made for late August and the second half of September; traveling whales were observed predominantly during the latter half of the survey season in 2008

| | Estimate | SE | CV | 95% CI | Mean density 5 km$^{-2}$ | Max. density 5 km$^{-2}$ |
|---|---|---|---|---|---|---|
| Feeding whales | | | | | | |
| 06 Sep | 1370 | 430.81 | 0.31 | 751–2501 | 0.84 | 19.04 |
| 13 Sep | 1086 | 208.23 | 0.19 | 749–1576 | 0.67 | 15.10 |
| 19 Sep | 1095 | 179.03 | 0.16 | 797–1506 | 0.67 | 15.22 |
| Traveling whales | | | | | | |
| 29 Aug | 684 | 349.52 | 0.51 | 26–1758 | 0.42 | 2.51 |
| 19 Sep | 35 | 25.64 | 0.73 | 10–127 | 0.02 | 0.13 |
| 29 Sep | 35 | 156.84 | 0.45 | 152–810 | 0.22 | 1.29 |

Table 8. Density surface model results for traveling non-calf bowhead whales in the southern Alaskan Beaufort Sea, late August to early October 2008. Significant relationships are in **bold**. A total of 729 segments of useable effort and 29 sightings of 39 non-calf whales were available for the model

| Parametric coefficient | Estimate | SE | p |
|---|---|---|---|
| **Intercept** | **–21.28** | **1.035** | **<0.0001** |
| Approx. significance of smooth terms | edf | Ref. df | p |
| **s(day of year)** | **5.123** | **6.300** | **0.0002** |
| **s(*x*)** | **2.415** | **3.065** | **0.024** |
| **s(log(depth))** | **2.061** | **2.471** | **0.022** |
| $R^2$ (adjusted) | 0.03 | | |
| REML score | 157 | | |
| Deviance explained | 36.80% | | |

higher densities occurring to the southeast, towards Camden Bay, resulting in 68% more whales estimated to be present within the study area when taking account of changes in behavior due to the presence of the seismic operations. Similar results were seen for feeding whales (Table 10, see Fig. S1A,B in the Supplement) and for traveling whales (Table 10, see Figs. S1B, S2A in the Supplement).

In summary, our models predicted a primarily nearshore distribution of bowhead whales in the southern Alaskan Beaufort Sea in autumn 2008, regardless of ongoing seismic survey activities. Bowhead whales occurred in higher densities in the region just to the west of Camden Bay, which was close to the main seismic survey (within 10–40 km), during September and early October, and at lower densities from Prudhoe Bay into Harrison Bay a region where primarily traveling whales were found. Density predictions were found to be influenced by variations in whale behavior associated with the presence of seismic operations. Correcting for variable detectability related to the presence of seismic operations resulted in density predictions ranging from 33 to 68% higher than predictions that only corrected for the variable detectability of whales that were not exposed to sounds from any type of industrial activity.

## DISCUSSION

Our study highlights the influence of whale behavior on density and distribution analyses of bowhead whales in the vicinity of seismic operations where received sound levels may reach up to 150 dB re 1 $\mu Pa_{rms}$, and suggests that whales were not avoiding areas with seismic operations to the extents previously thought. Rather, numbers of whales in the vicinity of, and thus potentially exposed to different levels of, seismic sound may be higher than previously thought.

### Predicted distribution and density of bowhead whales in the vicinity of seismic operations

In accounting for the behavioral responses of whales to seismic operations, we found that bowhead whales presumably within audible range of seismic operations during autumn 2008 were widely distributed in the nearshore southern Alaskan Beaufort Sea. Bowhead whales have shown a preference for nearshore shallow-water habitat during low-ice years (Moore et al. 2000, Moore & Laidre 2006, Treacy et al. 2006) and our results supported this finding by highlighting similar spatial patterns during 2008, a year in which the fourth lowest sea-ice extent occurred since records began in 1979 (Fetterer et al. 2002). Whales appeared to prefer the shallow nearshore continental shelf waters of the southern Alaskan Beaufort Sea despite the ongoing seismic operations, suggesting that there was no major offshore shift in the whales' migration corridor in response to the seismic survey activity. Whales did not appear to have been displaced more than a few 10s of km within the area where air-gun sounds would have been audible to whales in 2008.

Temporal patterns were also evident, with higher densities of whales predicted during the earlier part of the study season, but declining as the season progressed. Acoustic studies of bowhead migration have revealed pulsed patterns in calling rates, with clustering in space and time during the westward migration (e.g. Blackwell et al. 2007), that are also consistent with patterns of whale occurrence described by local whalers (Koski et al. 2005). We did not detect the pulsed nature of the migration in 2008, despite modeling our sighting data on a daily temporal scale. Whether we missed detecting these calls because the surveys were not conducted each day is unknown, but this is the most likely explanation.

Our models predicted higher than expected densities and relatively large numbers of feeding whales in the study area during early-to-mid September, particularly in the Camden Bay area despite proximity to the main seismic survey. The high predicted densities suggest that, at least on some days during the autumn migration period, whales were congregating to take advantage of apparently dense zooplankton concentrations. Prey aggregations must have been sufficiently dense to result in predicted densities that at times exceeded 10 whales 5 $km^{-2}$ (Walkusz et al. 2012). It is likely that the ocean conditions that cause zooplankton to concentrate in nearshore waters off the Yukon coast and extend west into Alaska (Thomson et al. 1986, Moore et al. 2000, Richardson & Thomson 2002) were prevalent in 2008 as there were numerous observations of feeding whales from both the aerial surveys and vessels associated with a seismic survey operating in the area in 2008 (Koski et al. 2009). Similarly, feeding whales were observed in the same region during 2007, also during seismic operations (Koski et al. 2009).

The high densities associated with feeding whales in 2008 would have obscured any temporal and seasonal movement patterns. Just as the timing of the migration varies from year to year (Moore and Reeves 1993, Quakenbush et al. 2013), so does the importance of the western Camden Bay area for feeding whales. Recent tagging studies of mostly sub-adult whales, which are the most likely segment of the population to use nearshore habitats (Koski & Miller 2009), suggest that they were not spending significant time in the Camden Bay area during the autumn. Rather, they appeared to be simply traveling through Camden Bay (Quakenbush et al. 2013) (although 2 of 13 tagged whales were within the study area for 5 and 6 d). The overall low use of Camden Bay has also been confirmed by recent analysis of movement patterns and core range use of 54 whales tagged from 2006 to 2012 (Citta et al. 2014). However, it is apparent from both the observations of feeding whales and the results of our models that the Camden Bay area did provide at least some opportunistic feeding opportunities that were exploited by some migrating whales in 2008 despite the presence of seismic operations.

There is increasing evidence to suggest that foraging whales will tolerate seismic operations and other human activities (Richardson et al. 1986, Koski et al. 2009, Robertson et al. 2013). In 2008, some feeding whales observed within our study area appeared to tolerate received levels of seismic sounds up to ~180 dB re 1 $\mu Pa_{rms}$ (Koski et al. 2009) and showed no evidence of avoidance in areas where seismic sounds were <150 dB re 1 $\mu Pa_{rms}$. Other species of foraging whales have also been observed in the vicinity of seismic operations, from within 20 km to over 140 km (similar distances to which bowhead whales in this study were detected in relation to the seismic surveys taking place in the Beaufort Sea in 2008), including gray whales (seismic exposure levels ≤163 dB re 1 $\mu Pa_{rms}$; Gailey et al. 2007, Johnson et al. 2007, Yazvenko et al. 2007) and sperm whales (135 to < 160 dB re 1 $\mu Pa_{p\text{-}p}$; Madsen et al. 2002, Miller et al. 2009). Neither of the seismic-related variables considered in our models significantly contributed to explaining the numbers of whales encountered during the 2008 surveys, providing further evidence of the apparent tolerance of feeding bowhead whales to sound levels up to ~150 dB re 1 µPa in the vicinity of seismic operations, and suggesting that other factors were likely more important in determining the presence of bowhead whales in our study.

In other parts of our study area we predicted much lower densities of whales, particularly in the southwest (from Prudhoe Bay toward Harrison Bay), an area that has previously been noted for its low density (Givens 2009). The area of low density predicted by our overall model corresponded with where traveling whales were predicted to have occurred in 2008. From 2006 to 2012, 83.3% of tagged whales spent an average of 2 d in the Prudhoe Bay area. Because it would take whales approximately 2 d to travel through that area if they did not stop to feed, Quakenbush et al. (2013) suggested that whales were primarily migrating through this area rather than feeding there.

Table 9. Relative abundance estimates of non-calf bowhead whales for each half-month period in an area of the southern Alaskan Beaufort Sea ensonified by seismic operations in 2008. Predictions on the left (undisturbed whales) have not been corrected for variable behavior due to the presence of seismic operations, while predictions on the right (potentially disturbed) have been corrected for the variable behavior of whales exposed to seismic operations

| Non-calves | $a(x)$ = undisturbed whales | | | | $a(x)$ = potentially disturbed | | | | % |
|---|---|---|---|---|---|---|---|---|---|
| | Estimate | SE | CV | 95% CI | Estimate | SE | CV | 95% CI | Change |
| 29 Aug | 1024 | 404.00 | 0.39 | 486–2158 | 1718 | 683.79 | 0.40 | 810–3643 | |
| 13 Sep | 727 | 205.94 | 0.28 | 422–1253 | 1219 | 351.51 | 0.29 | 701–2121 | |
| 19 Sep | 548 | 146.40 | 0.28 | 328–917 | 919 | 250.43 | 0.27 | 544–1553 | 68 |
| 29 Sep | 298 | 94.37 | 0.32 | 162–546 | 499 | 160.52 | 0.32 | 270–923 | |
| 09 Oct | 166 | 100.28 | 0.61 | 55–495 | 278 | 168.84 | 0.61 | 93–834 | |

Table 10. Predicted point estimates of feeding and traveling non-calf whales in an area of the southern Alaskan Beaufort Sea ensonified by seismic operations in 2008. Predictions on the left (undisturbed whales) have not been corrected for variable behavior due to the presence of seismic operations, while predictions on the right (potentially disturbed) have been corrected for the variable behavior of whales exposed to seismic operations

| Non-calves | $a(x)$ = undisturbed whales | | | | $a(x)$ = potentially disturbed | | | | % |
|---|---|---|---|---|---|---|---|---|---|
| | Estimate | SE | CV | 95% CI | Estimate | SE | CV | 95% CI | Change |
| Feeding whales | | | | | | | | | |
| 06 Sep | 1031 | 323.49 | 0.31 | 566–1880 | 1370 | 430.81 | 0.31 | 751–2501 | |
| 13 Sep | 818 | 155.70 | 0.19 | 565–1184 | 1086 | 208.23 | 0.19 | 749–1576 | 34 |
| 19 Sep | 824 | 133.53 | 0.16 | 61–1130 | 1095 | 179.03 | 0.16 | 797–1506 | |
| Traveling whales | | | | | | | | | |
| 29 Aug | 511 | 258.53 | 0.51 | 200–1302 | 684 | 349.52 | 0.51 | 266–1758 | |
| 19 Sep | 26 | 19.06 | 0.73 | 7–94 | 35 | 25.64 | 0.73 | 10–127 | 33 |
| 29 Sep | 262 | 115.68 | 0.44 | 114–599 | 35 | 156.84 | 0.45 | 152–810 | |

**Effects of variable availability on bowhead whale density estimates**

Variations in bowhead surface and dive behaviors resulted in underestimates of densities of whales in areas presumably ensonified by seismic survey operations if the appropriate availability correction factors were not used. Our study is the first to incorporate behavioral responses of bowhead whales to the presence of human activities in the Alaskan Beaufort Sea into analyses of density and distribution. We found no evidence of changes in distribution of whales exposed to sound levels up to ~150 dB re 1 μPa$_{rms}$, whereas Richardson et al. (1999) found avoidance. This suggests that earlier analyses of displacement by bowhead whales of seismic operations are likely to have overestimated displacement because the numbers of whales in areas ensonified by seismic operations may have been as much as 33–68% higher than were previously estimated. This implies that at least some whales are not avoiding these areas on the large scales suggested in earlier studies by Richardson et al. (1999) and Davis (1987). Our results suggest that the data from these earlier surveys could be re-examined in light of the changes in behavior that likely occurred between experimental and control periods to determine whether the displacement by traveling whales is as great as has been suggested in the past. Our findings suggest that feeding whales were widely distributed in the southern region of our study area, with higher densities of whales occurring toward the southeast region despite the presence of air-gun activity within 10–40 km. Thus, avoidance on the previously reported large scales for traveling whales did not occur for feeding whales in 2008. Importantly, our results also suggest that there was no obvious offshore displacement of whales away from the coast in 2008, something that has been a primary concern to the local hunters.

The lack of wide-scale avoidance or offshore displacement suggested by our results supports recent acoustic evidence that whales continued to use areas of the Alaskan Beaufort Sea ensonified by seismic operations (Blackwell et al. 2013, 2015). In 2008, bowhead whale calls were recorded on acoustic receivers throughout the study area (Funk et al. 2010). Blackwell et al. (2013) investigated bowhead calling behavior in the same region in 2007 and found a statistically significant drop in the detected number of bowhead calls at the onset of seismic air-gun activity in areas where received levels were 116–129 dB re 1 $\mu Pa_{rms}$, but no change or a slight increase in calling rates when received levels near the whales were >108 dB re 1 μPa (Blackwell et al. 2013). Deflection was thought to be an unlikely explanation for the variation in calling rates, partly because the whales would not have been able to move out of the area fast enough to account for the changes in calling rates when air-gun activity was shut down due to the slow swim speeds of bowheads (Blackwell et al. 2013). While whales initially increase their calling rates as soon as air-gun sounds became audible, they reduce their calling rate as the cumulative sound exposure level exceeds ~127 dB re 1 $\mu Pa^2$-s (equivalent to ~112 dB re 1 $\mu Pa_{rms}$) and cease to call altogether or divert away from the sources as the cumulative sound exposure level rises above ~160 dB re 1 $\mu Pa^2$-s (~153 dB re 1 $\mu Pa_{rms}$; Blackwell et al. 2015).

## Study caveats and considerations for future research

Aerial surveys were flown to monitor and help mitigate exposure of bowhead whales to sound levels >180 dB re 1 $\mu Pa_{rms}$ from seismic survey operations in the southern Alaskan Beaufort Sea in 2006–2008 and in 2010. We restricted our analyses to data collected in 2008 because that survey season provided the greatest coverage of the study area as well as the greatest number of sightings. This reduced the sample size of sightings that we used, particularly for the models that assessed feeding and traveling whales separately. However, fewer sightings and more variable effort in the other years did not allow us to incorporate yearly variation into our models. Had there been better coverage in other years, these data would have greatly strengthened our models and allowed us to incorporate yearly variation. The timing of the autumn migration, and the distribution of whales while migrating through the southern Alaskan Beaufort Sea, is subject to natural year-to-year variation in relation to variables such as ice conditions, and prey distribution and availability (Moore & Reeves 1993, Quakenbush et al. 2013). The inclusion of zooplankton data in our models, had it been available, might have helped to further explain why some parts of the study area were apparently more important to feeding whales than others. However, the presence or absence of feeding by bowheads was presumably related to the presence of prey, so our inclusion of feeding activity can be considered a surrogate for prey.

While the presence of prey appears to have been the main factor influencing whale distribution within the study area in 2008, a significant limitation of our study was the lack of precise sound levels near the whale sightings, and so we were forced to coarsely bin both seismic variables. Neither seismic variable improved the model fit, which meant that neither variable was selected for the final model. With finer detail on sounds from seismic operations, we might have been able to detect the distance or sound levels at which avoidance begins to occur. The lack of survey effort in areas where whales could have been exposed to sound levels >150 dB also reduced our ability to document those distances or sound levels. Two operational strategies implemented to minimize the impact of the seismic operations on the whales contributed to the low effort near whales. First, air guns were shut down whenever bowheads were detected approaching the seismic operations before they would be exposed to levels that could harm them, and second, when feeding bowheads were found near the operation in 2008, the seismic operation was moved farther north to an area where few whales had been seen.

Future analyses of aerial survey data would benefit by including additional variables related to prey presence, other industry activities, measured sound levels near whales, and subsistence hunting activities. Adding these covariates may strengthen the predictions provided by the models. By incorporating year-to-year variation and a parameter for geographic area, we might be able to explain why whales occurred at higher densities in the southeast of our study area but at much lower densities in the central-southwest.

Additionally, future research investigating the impacts of seismic survey operations on bowhead distribution would benefit from incorporating specific behavioral response studies. The availability correction factors incorporated into our analyses had their own limitations. The availability correction factors were calculated using fine-scale behavior data comprising surfacing and diving behavior (Robertson et al. 2013). These behavioral data were mostly collected opportunistically, particularly behavioral observations of whales exposed to seismic sounds, resulting in only approximate information on the highly variable seismic sound levels to which the whales were likely exposed (Robertson et al. 2013). The correction factors therefore only account for how whale behavior varies when seismic operations are presumably nearby compared with when they are absent, without taking account of the varying sound levels at the whales' locations. As highlighted by Blackwell et al. (2015), it is likely that the level of response exhibited by whales to seismic sounds is related to both received sound level as well distance to the sound source. By understanding how whales vary their behavior under different circumstances we can better quantify the distribution and density of whales in areas ensonified by seismic operations and thus better assess the extent of avoidance of those activities.

Finally, our analyses did not address the fine-scale deflections related to seismic survey operations, which can only be addressed with greater effort conducted close to the operations (which is currently unavailable). The mitigation measures implemented (i.e. shut downs and relocation of the survey) for the seismic surveys in 2008 prevented us from assessing whether whales would have approached close enough that they might have suffered temporary or permanent hearing damage; however, we were able to show that there was no large-scale offshore deflection of non-calf bowhead whales during active seismic operations in 2008. In addition, our analyses provide further support for the hypothesis that feeding whales are more tolerant of seismic operations than whales engaged in other activities such as traveling. Future research on this issue should be conducted on a finer spatial scale to determine the sound levels at which whales will display immediate avoidance behavior of active air guns and whether their tolerance while feeding could put them at risk for temporary or permanent hearing damage.

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