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DISTRIBUTION AND ABUNDANCE OF THE EASTERN CANADA – WEST GREENLAND BOWHEAD WHALE POPULATION BASED ON THE 2013 HIGH ARCTIC CETACEAN SURVEY

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ABSTRACT

The hunting of bowhead whales (*Balaena mysticetus*) is an integral part of Inuit culture. An up-to-date abundance estimate of the entire Eastern Canada – West Greenland (EC-WG) bowhead population is necessary to support sustainable management of this harvest. The High Arctic Cetacean Survey (HACS) was conducted in August 2013, primarily to update abundance estimates for known stocks of Baffin Bay narwhal (*Monodon monoceros*). As the ranges of narwhal and bowhead largely overlap, the survey area was expanded to cover the summer range of bowhead whales. Bowhead whale abundance was estimated using 3 aircraft to cover the large survey area within a short time frame. Distance sampling methods were used to estimate detection probability away from the track line. Double platform with mark-recapture methods were used to correct for the proportion of whales missed by visual observers on the track line (perception bias). Abundance in Isabella Bay, an area known for high bowhead density, was estimated using density surface modelling to account for its complex shape and uneven coverage. Estimates were corrected for availability bias (whales that were not available for detection because they were submerged when the aircraft passed overhead) using a recent analysis of satellite-linked time depth recorders transmitting information on the diving behaviour of bowhead whales in the study area in August of the same survey year. The fully corrected abundance estimate for the EC-WG bowhead whale population was 6,446 (95% CI: 3,838–10,827). Possible sources of uncertainty include incomplete coverage and the diving behaviour of bowhead whales. These results confirm earlier indications that the EC-WG stock is continuing to recover from past overexploitation.

Keywords: bowhead whale, Baffin Bay, Eastern Canada - West Greenland, abundance, aerial survey, double-platform, distance sampling, density surface modelling, availability bias

INTRODUCTION

Bowhead whales (*Balaena mysticetus*) (Figure 1) are ice-associated baleen whales with a nearly circumpolar Arctic distribution. Subsistence hunts for bowhead whales are an important part of Inuit culture (Hay, Aglukark, Igutsaq, Ikkidluak, & Mike, 2000; Priest & Usher, 2004). Two populations were initially recognized in the Eastern Canadian Arctic: one in Hudson Bay-Foxe Basin and the other in Baffin Bay-Davis Strait. However, evidence from genetics and satellite telemetry studies (Dueck, Hiede-Jørgensen, Jensen, & Postma, 2006; Postma, Dueck, Heide-Jørgensen, & Cosens, 2006) indicate that bowhead whales from the Eastern Canadian Arctic are part of a single population that is shared with West Greenland.

This single Eastern Canada – West Greenland (EC-WG) population was historically overharvested by commercial whalers (Higdon, 2010) and the Committee on the Status of Endangered Wildlife in Canada recommended in 2009 that it be listed as a Species of Special Concern under the Species At Risk Act (COSEWIC, 2009). A limited subsistence hunt resumed in the Nunavut Settlement Area in 1996 and in the Nunavik Marine Region in 2008, with takes of 1 to 3 whales per year for both regions combined (DFO, 2015). These hunts are co-managed by the Nunavut Wildlife Management Board, the Nunavik Marine Region Wildlife Board, and Fisheries and Oceans Canada (DFO).

Figure 1. Bowhead whale, Cumberland Sound 2019. Photo credit: Ricky Kilabuk.

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Sustainable management of the population relies on up-to-date abundance estimates and the prediction of future trends under various harvest scenarios. In 1981, aerial surveys of the EC-WG winter range in Hudson Strait estimated population abundance at 1,349 (95% CI: 402–4,529; Koski, Heide-Jørgensen, & Laidre, 2006). Aerial surveys were also conducted in 2002, 2003, and 2004 in the summering areas in the Canadian Arctic, although these used a multi-year survey design because two separate populations of eastern Arctic bowhead whales were assumed at the time. Following the re-assessment as a single population, the 2002–2004 aerial surveys were reanalysed to yield a single population estimate of 6,344 (95% CI: 3,119–12,906; IWC, 2009). Although relatively imprecise, this estimate is consistent with Inuit Traditional Ecological Knowledge (TEK) and suggests the EC-WG population has increased substantially since commercial whaling stopped in the first half of the 20th century (Hay et al., 2000).

No aerial survey has covered the full extent of the bowhead whale summer distribution in the Eastern Canadian Arctic in a single year. While the primary target species of the High Arctic Cetacean Survey (HACS) conducted in August 2013 was the narwhal (*Monodon monoceros*; Doniol-Valcroze et al., 2020), the summer distribution range of narwhals overlaps to a considerable extent with that of EC-WG bowhead whales. Therefore, the HACS study area was expanded to achieve nearly complete coverage of the known summer range of EC-WG bowhead whales. Here we present the results of the 2013 aerial survey for bowhead whales, detailing new information on their distribution and abundance during the summer in the Canadian Arctic.

MATERIALS AND METHODS

The HACS was used to estimate both narwhal and bowhead abundance. Most of the data collection methods and analyses used to obtain an abundance estimate for bowhead whales are identical to those used for narwhals. Therefore, we provide only a brief description of the methodology here, with a focus on aspects that were specific to bowhead whales. Additional details on survey design, allocation of effort, data collection and management, and analytical approaches are available in Doniol-Valcroze et al. (2020).

Study area and survey timing

The objective of HACS was to sample the entire summering ranges of both the Canadian Baffin Bay narwhal stocks and EC-WG bowhead whales. The extent of the study area (Figure 2) was based on previous aerial surveys and telemetry tracking

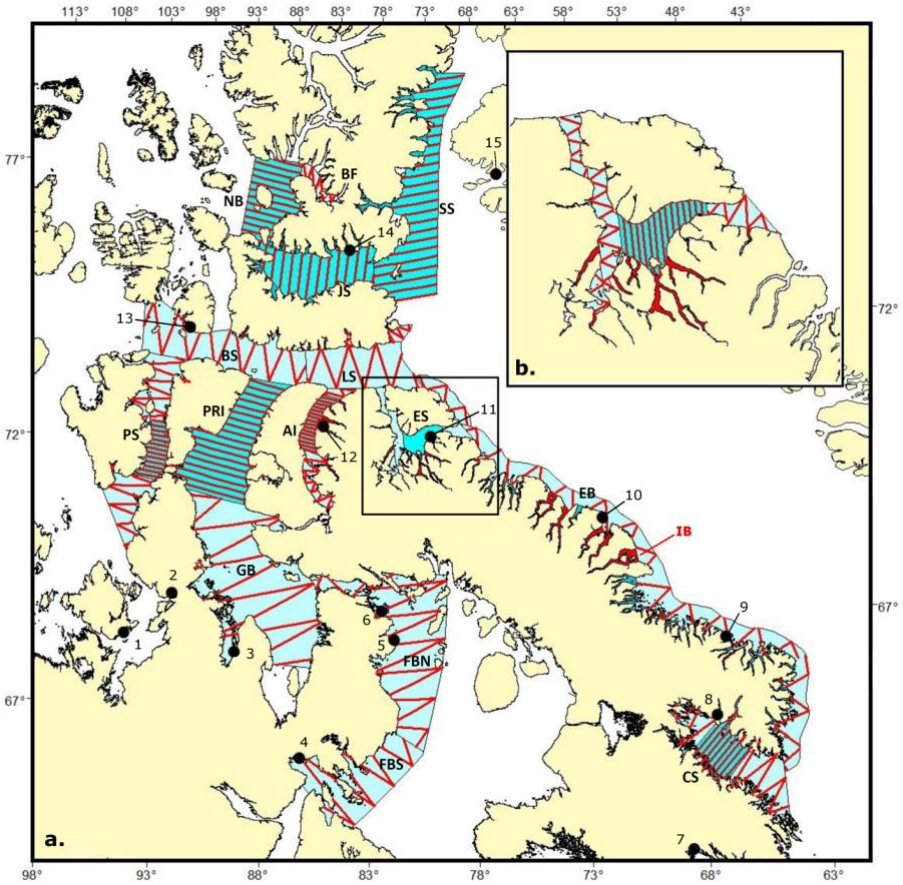

Figure 2. a. Map of planned survey strata (blue polygons), transect lines (red lines), and fjord strata (red areas). AI: Admiralty Inlet. BF: Baumann Fjord. BS: Barrow Strait. CS: Cumberland Sound. EB: East Baffin. ES: Eclipse Sound. FBN: Foxe Basin North. FBS: Foxe Basin South. GB: Gulf of Boothia. JS: Jones Sound. LS: Lancaster Sound. NB: Norwegian Bay. PRI: Prince Regent Inlet. PS: Peel Sound. SS: Smith Sound. Communities (black dots): 1. Gjoa Haven; 2.Taloyoak; 3. Kugaaruk; 4. Repulse Bay; 5. Sanirajak; 6. Igloolik; 7. Iqaluit; 8. Pangnirtung; 9. Qikiqtarjuaq; 10. Clyde River; 11. Pond Inlet; 12. Arctic Bay; 13. Resolute Bay; 14. Grise Fjord; 15. Qaanaaq (Greenland). Red line indicates position of Isabella Bay (IB, see also Figure 5 and Figure 10); b. inset: enlargement of the Eclipse Sound stratum (boxed area).

studies of both species, TEK, and recent observations by Inuit hunters (Hay et al., 2000). The priority areas for bowhead whales were identified as Prince Regent Inlet, Gulf of Boothia, Northern Foxe Basin, Admiralty Inlet, the eastern coast of Baffin Island (including fjords), and Cumberland Sound. Additional coverage was also desirable in Roes Welcome Sound, Barrow Strait, Lancaster Sound, and Eclipse Sound. Although, bowhead whales are also observed in Hudson Strait and Frobisher Bay in summer, we did not include these areas due to limitations on survey time and expectations of low whale density.

Dates for the survey were established based on the short window of relatively ice-free waters in the Arctic Archipelago and the timing of narwhals and bowhead whales aggregating on their summering grounds. The best time was determined to be August, when telemetry studies have shown that bowhead whales are relatively circumscribed within their summering range and the weather is also most favourable for flying. Using 3 aircraft allowed the entire survey area to be covered in a relatively short period of time (3 weeks of flying), which limited the risk of bias or double-counting due to potential movements of whales between survey areas.

Survey design

The survey was designed to cover the largest possible proportion of the population's summering range, while at the same time achieving greater precision than past surveys, which required coverage at a higher intensity. The resulting design reflects constraints imposed by the dual objectives of estimating narwhal and bowhead abundances. To minimize the sampling variance, we stratified the study area based on geographic boundaries as well as presumed densities of narwhals and bowhead whales (Figures 3, 4 and 5). For instance, a high-density area for bowhead whales was identified in the central portion of Cumberland Sound based on telemetry data and Inuit TEK (Figure 2).

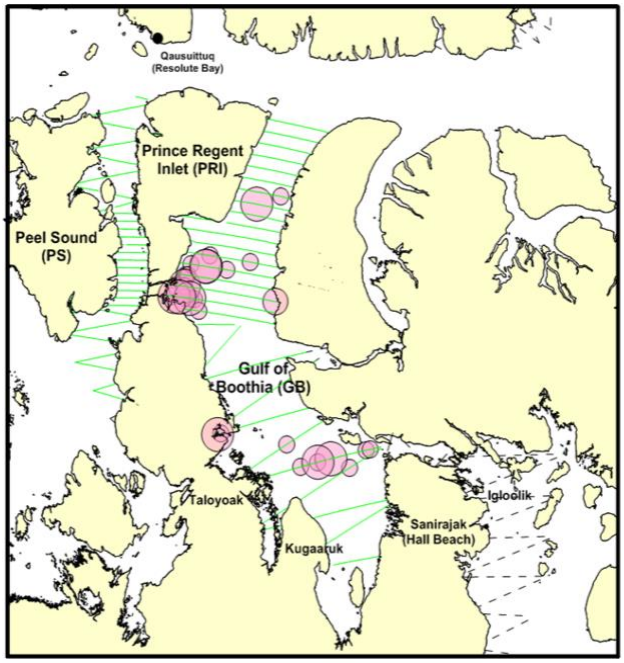

Figure 3. Somerset Island survey showing completed transects (green), un-completed planned transects (black dashed) and sightings of bowhead whales with symbol size proportional to group size (1–3).

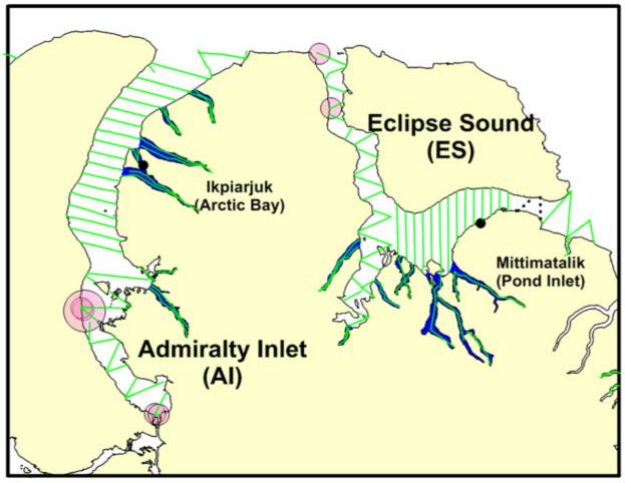

Figure 4. Admiralty Inlet and Eclipse Sound showing completed transects (green), un-completed planned transects (black dashed) and sightings of bowhead whales with symbol size proportional to group size (1–2). Surveyed fjord strata: blue.

Transect design was performed using Distance version 6.1 (Thomas et al., 2010). The design used was systematic, with a random start in each stratum. For presumed high density strata, we used systematic parallel transects, whereas areas where we expected lower densities were covered with equally spaced zigzag transects (Strindberg & Buckland, 2004). The sequence of stratum coverage was designed to survey areas in order of priority for narwhal stocks, which placed some bowhead strata among the first to be surveyed (e.g., Prince Regent Inlet, Gulf of Boothia), while other areas were planned for the end of the survey period (e.g., Cumberland Sound, Roes Welcome Sound). In an effort to avoid the effect of potential directed movements of whales within areas, attempts were made to survey each stratum within 1 or 2 days, and to survey neighbouring strata in quick succession.

Bowhead whales are often encountered in fjords during the summer. Since it was not logistically possible to survey every fjord in the study area, we used a subsampling approach. Following Thomas, Williams, and Sandilands (2007), we used a 2-stage sampling design. At stage 1, each fjord was considered a primary sampling unit (PSU) and a custom algorithm was used to select a subset of PSUs where each fjord had a probability of being selected proportional to its area in an attempt to maintain equal coverage probability within fjord strata. At stage 2, distance sampling was conducted within each selected PSU. In fjords, flights were planned as continuous tracks and adjusted on site by the navigator to follow the main axis of each fjord, while aiming to spread coverage uniformly according to distance from the shore when the fjords were wide enough, and to minimize duplicate coverage of any area. Data were collected using the same protocol as in non-fjord areas.

Survey methodology

The survey was flown at an altitude of 305 m and a target speed of 185 km/h using 3 de Havilland Twin Otter 300 aircraft, each equipped with 2 bubble windows on each side that allowed observers to view the track line directly below the aircraft. An observer was stationed at each of the bubble windows, with a 5th team member acting as a navigator and camera operator. The visual surveys were conducted as a double-platform experiment with independent observation platforms at the

front (primary) and rear (secondary) of the aircraft. The paired observers stationed on the same side of the aircraft were separated visually and acoustically to ensure independence of their detections. Observers recorded their observations vocally using hand-held recorders, including the time at which they sighted groups of whales ("spot time"), the time at which the animals passed abeam ("beam time"), the perpendicular declination angle of each sighting abeam, species, group size, and, when possible, direction of movement, presence of calves, and any other relevant observations. Primary observers recorded weather and observation conditions at the beginning and end of the transects or whenever changes in sighting conditions occurred. These included sea state (Beaufort scale), ice concentration (in tenths), cloud cover (%), fog (% cover and intensity), and angle of searching area affected by glare along with sun glare intensity.

In addition to visual observations, the 3 aircraft collected continuous photographic records below the aircraft using dual high-resolution digital SLR cameras (Nikon D-800, lens Zeiss Distagon-T 35 mm) mounted in a belly window, pointing downwards obliquely towards either side of the track line, at an angle of 27°. A 3 second interval between photographs produced a target overlap of 20% between successive photographs along the direction of aircraft travel at the survey altitude. At the target survey altitude, the swath width of the pictures taken was 420 m, with a total strip width of 840 m.

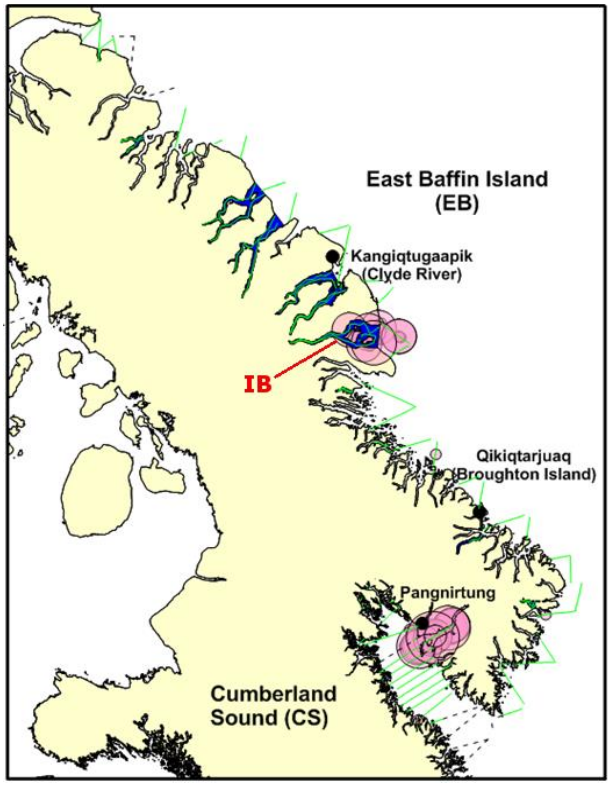

Figure 5. East Baffin and Cumberland Sound showing completed transects (green), un-completed planned transects (black dashed) and sightings of bowhead whales with symbol size proportional to group size (1–4). Surveyed fjord strata: blue; un-surveyed fjord strata: grey. IB: Isabella Bay (see Figure 10).

Data management and photo verification

Sightings where angles of declinations or group sizes had not been recorded or were coded as "uncertain" were compared to the photographic records. If a visual sighting could be identified without ambiguity on the corresponding photo, then the missing perpendicular distance was retrieved from the pixel position of the sighting on the photo, or the missing group size was estimated from the photo. If the sighting was not made within the swath width of the picture, could not be found, or could not be told apart from other sightings unambiguously, it was coded as missing distance (these sightings were not used in fitting the detection function but were added to the total count per transect to estimate encounter rates, as described below) or group size. Sightings with missing group size were given the mean group size in that stratum.

Data analysis

Duplicate identification

Due primarily to the extreme aggregation of cetacean sightings in some areas, we adapted and extended the methodology developed by Southwell, de la Mare, Underwood, Quartararo, and Cope (2002) to identify duplicates from the HACS visual survey data. For each sighting, the dataset was searched for all sightings made within the next 10 seconds by the other station on the same side (rear bubble for front sightings, front bubble for rear sightings). Any such sighting was then identified and paired with the initial sighting as a *potential duplicate*. The following covariates were considered as possibly useful in identifying duplicates: *T*: Difference in beam time in seconds; *D*: Difference in declination angle in degrees; *C*: Difference in group size; and *S*: Difference in species identity (see Table 2 in Doniol-Valcroze et al. (2020)). We followed Southwell et al. (2002) in estimating threshold covariate levels by examining graphs showing the number of potential duplicates as covariate levels changed. It was expected that such curves would show a sharp initial increase followed by a levelling-off, with the inflection being roughly equivalent to the covariate value below which most duplicates could be found.

In an effort to determine which covariates were most useful for identifying duplicates, we created a second dataset that contained sighting pairs between front and rear observers that occurred close together in time but, by definition, could not be duplicates. This was done in exactly the same way as the dataset described above, except that observer sightings were paired with stations on the opposite side of the aircraft. For example, a front right sighting would be paired with a back left sighting that occurred within the 10 second interval. Unlike the same-side dataset, this opposite-side dataset cannot possibly contain true duplicate sightings (Hamilton et al., 2018). Logistic regression was used to determine which covariates best discriminated among the 2 datasets, with the assumption that those same covariates were also useful to identify data that contained duplicate pairs. The response variable was same-side (1) vs. opposite-side (0). Candidate logistic regression models were fit using all combinations of individual covariates *T*, *D*, *C* (if *C*>30 it was considered missing), and *S*. For each case, the model with the highest Area Under Curve (AUC), representing the best reclassification performance, was chosen.

Using the coefficients from the best model in each of these situations, regressions produced *p* values (coded here as *d*) corresponding to the probability that a particular sightings pair belonged to the same-side dataset, as opposed to the opposite-side dataset. Because the same-side dataset contained a mix of duplicate and non-duplicate pairs, these *d* values did not

correspond directly to the probability that a pair was truly a duplicate. However, since the main difference between these 2 datasets was the presence of duplicate pairs in the same-side dataset, these scores were interpreted as a relative index of the probability that a particular sightings pair was a duplicate.

For each of these models, we calculated $d(0)$ the value of d when all covariates were at 0 (i.e., the maximum value of d). To be able to pool scores from the 4 models, we scaled d values by dividing them by $d(0)$ and used $1-d$ to obtain a dissimilarity index ranging between 0 (most likely to be a duplicate) and 1. We then substituted the covariate thresholds obtained by graphical methods mentioned above into the regression equations to obtain a threshold value for d, identified as $d(T)$. This meant that a duplicate could exceed a threshold for a given covariate if the other covariate values were low, for example, a candidate pair with a declination difference of 12 degrees might have been considered a duplicate even if the threshold was 10 degrees, if its time, count and species differences were low enough to result in a score below $d(T)$. To avoid extremely unlikely values, however, we placed a limit of 20 degrees on D.

Duplicates were selected by ranking all potential duplicate pairs with a score below $d(T)$ by their d value from lowest to highest, then selecting those with the lowest scores while removing selected sightings from the list.

Abundance estimation

Design-based strata

Mark-recapture distance sampling (MRDS) was used to estimate bowhead abundance in the design-based strata. This approach involved fitting 2 models, each with potentially different covariates: a distance sampling model fitted to all unique sightings, and a mark-recapture model fitted to the double observer data.

First, we calculated estimates of the density $(\widehat{D})$ and abundance $(\widehat{N})$ of bowheads during a systematic survey of each design-based stratum, uncorrected for visible animals missed by observers on the line (perception bias) or animals that were submerged and not visible during the passage of the aircraft (availability bias), using conventional multi-covariate distance sampling (MCDS) techniques (Buckland et al., 2001). Analyses were carried out using the *mrds* package in R (Laake, Borchers, Thomas, Miller, & Bishop, 2019). The analyses were performed on the perpendicular distances of unique groups (i.e., duplicate sightings, plus sightings made only by observer 1 plus sightings made only by observer 2) of bowhead whales. For duplicate sightings, we used the distance recorded by observer 1 (the most experienced observer), unless it was missing and available from observer 2. A single, global detection curve was fitted to sightings from all strata, with the best model chosen by minimization of Akaike's Information Criterion (AIC; Buckland et al., 2001). Covariates considered for inclusion in the model were: ice cover, cloud cover, sea state, and glare. The expected group size in each stratum was estimated using the size bias regression method of the natural log of group size against the probability of detection. The regression was used if significant at $\alpha = 0.10$; otherwise the mean group size was used (Buckland et al., 2001).

Second, we used MRDS to estimate the proportion of available bowhead whales that were seen at distance 0, and thereby provide a correction for perception bias (Burt, Borchers, Jenkins, & Marques, 2014; Laake & Borchers, 2004). We used "point-independence" models, which relax the independence assumption such that independence is assumed only at distance 0 (Laake & Borchers, 2004), with an Independent Observer (IO) configuration, as our platforms were symmetrical and independent. MRDS models were built with different combinations of covariates and compared using AIC. By definition, all point-independent models included perpendicular distance as a covariate. Other covariates included the environmental variables described above, observer identity, and side of the aircraft.

Fjord Strata

To account for the complex shape and uneven coverage of fjords, we estimated bowhead abundance in these survey areas using a density surface model (DSM) of spatially-referenced count data, with the additional information provided by collecting distances to account for imperfect detection. Modelling proceeded in two steps: first, a detection function was fitted to the perpendicular distance data to obtain detection probabilities for groups of individuals. Counts were then summarised per segment (contiguous transect sections). A generalised additive model (GAM) (Wood, 2006) was then constructed with the per-segment counts as the response and segment areas corrected for detectability in the package *dsm* (Miller, Rexstad, Burt, Bravington, & Hedley, 2013).

Variance in spatial models of abundance was estimated using a Bayesian approach that simulates replicate parameter sets from the posterior distribution of the estimated parameters of the spatial model to obtain a measure of the variance in the spatial model (Wood, 2006). Spatial models also include variability that comes from estimating the parameters of the detection function because the effective area of each cell is based on the estimated strip half-width. Therefore, the total variance of abundance of each fjord (PSU) was estimated using the delta method to combine the variance of the effective area (detection model) with the variance from the spatial component (Hedley & Buckland, 2004).

As mentioned, within each fjord stratum, we used a 2-stage sampling design in which the first stage consisted of sampling with replacement among PSUs. Appropriate estimators for the density $\widehat{D}$ and total surface abundance $\hat{\tau}$ in a stratum were given by a ratio estimator (Cochran, 1977):

$$\widehat{D} = \frac{\sum_{i=1}^{n} \hat{y}_i}{\sum_{i=1}^{n} A_i}$$

$$\hat{\tau} = A_t \cdot \frac{\sum_{i=1}^{n} \hat{y}_i}{\sum_{i=1}^{n} A_i}$$

where A_i and $\hat{y}_i$ are respectively the area and the estimated abundance in each of the n surveyed fjords (PSU) in the stratum, and A_t is the total stratum area. Note that this is equivalent to averaging the estimated bowhead densities of all fjords, weighted by their respective areas. Note also that when all N possible fjords in a given stratum are surveyed (as in Admiralty Inlet and Eclipse Sound), $\sum_i^n A_i = \sum_i^N A_i = A_t$, and thus the equation simplifies to the sum of the abundance estimates, as per a standard stratified design (Buckland et al., 2001).

The sample variance of the estimated density among fjords, with fjords of unequal areas, was adapted from the formula proposed by Innes et al. (2002):

$$\widehat{Var}(\hat{D}) = s_a^2 = \frac{n}{A^2(n-1)} \cdot \frac{\sum_{i=1}^{n} A_i^2 \left(\frac{\hat{y}_i}{A_i} - \frac{\sum_{i=1}^{n} \hat{y}_i}{A}\right)^2}{n-1}$$

where $A = \sum_i^n A_i$ is the sum of the areas of the surveyed fjord.

Because we used a 2-stage sampling scheme, the variance of the total abundance has 2 components: among-fjord variance and within-fjord variance. The among-fjord variance is equal to $A_t^2 s_a^2$ with the addition of a finite population correction (1 - *f*) and the within-fjord component is the sum of the variances of each surveyed fjord, multiplied by the inverse of the sampling fraction. Thus, the estimator of the variance is:

$$\widehat{Var}(\hat{t}) = A_t^2(1-f) \cdot s_a^2 + \frac{1}{f} \cdot \sum_{i=1}^{n} s_i^2$$

where $f = \frac{n}{N}$ is the sampling fraction and s_i^2 is the variance of the *i*th fjord (obtained from the DSM) and s_a^2 is the among-fjord variance of the estimated density. Note that when all the fjords within a stratum are sampled (i.e., f = 1), the first term disappears and the multiplier of the second term becomes unity, i.e., the total variance is the sum of the within-fjord variances, as per a standard stratified design (Buckland et al., 2001).

Availability bias

To estimate abundance, visual and photographic aerial surveys of aquatic marine mammals should be corrected for availability bias (Marsh & Sinclair, 1989). For marine mammals this equates to animals that are not visible to observers because they are submerged. However, there is no experimental evidence to indicate how deep in the water column a bowhead whale can be detected from an aircraft. In previous studies, it has been assumed that bowhead whales can be detected to a depth of 2 m (Koski, Heide-Jørgensen, & Laidre, 2006; Rekdal et al., 2015) or 4 m (Dueck, Heide-Jørgensen, Jensen, & Postma, 2006; Dueck, Richard, & Cosens, 2007; IWC, 2009) below the sea surface when directly underneath the aircraft. To account for this uncertainty, Watt, Marcoux, Leblanc, and Ferguson (2015) calculated the time that tagged bowhead whales spent in a number of different depth bins so that corrections may be adjusted depending on environmental conditions and study objectives, and recommended using an estimate from combining multiple depth bins (0–2, 0–4, and 0–6 m bins) for the analysis of the 2013 survey results. To do this, we used a mixture distribution to combine the results for 3 different possibilities (i.e., that bowheads are visible from 0–2 m, or 0–4 m or 0–6 m), giving equal weight to each possibility.

The correction factor for availability bias when sightings are instantaneous is given by $C_I = 1/P_a$, where P_a is the proportion of time spent by whales in the combined 0–2, 0–4 and 0–6 m bins. Watt et al. (2105) analysed data from 22 bowhead whales fitted with satellite-linked time depth recorders near the communities of Igloolik and Pangnirtung (Figure 2) in 2012 and 2013. These instrumented whales were assumed representative of the population surveyed and of their behaviour during the survey period, therefore we used correction factors provided by Watt et al. (2015) that were specific to the geographic location of each stratum.

C_I is an appropriate correction factor when sightings are instantaneous (e.g., for photographic surveys). If sightings are not instantaneous, this correction factor positively biases the abundance estimate. McLaren (1961) developed a correction factor that incorporates the dive cycle of the animal and the search time of the observer. The model has 2 components: the probability that an animal is at the surface when entering the observer's view, expressed as $t_s/(t_s + t_d)$, with t_s being the time the animal can be seen at the surface and t_d the period when animals are submerged), and the probability that an animal is in a dive while entering the viewing area $t_d/(t_s + t_d)$ multiplied by the probability of surfacing within the viewing area, which Laake et al. (1997) proposed expressing as $\left(1 - e^{-\theta/t_d}\right)$, where θ is the time available for an observer to see a group (i.e., "time in view"). Therefore, for a given time-in-view θ, the correction factor for availability is given by:

$$C_M(\theta) = \frac{t_s}{t_s + t_d} + \frac{t_d \cdot \left[1 - e^{-\theta/t_d}\right]}{t_s + t_d}$$

However, the 22 satellite tags used for estimating P_a could not be used to estimate t_d and t_s. Instead, we used values from Wursig et al. (1984), which are based on summer observation of Bering-Chukchi-Beaufort bowhead whales in the Beaufort Sea in the years 1980–1982.

To estimate the empirical time in view of the HACS sightings, we examined the length of time from the initial recording of a detection (i.e., spot time) to the recording of the abeam declination angle measurement (i.e., beam time). Following the technique proposed by Richard et al. (2010) we used a weighted availability bias correction factor C_a:

$$C_a = C_I \cdot \frac{\sum_{i=1}^{n} f_i(1 - b_i)}{\sum_{i=1}^{n} f_i}$$

where n is the maximum time in view, f_i is the frequency of times in view of duration i seconds and b_i is the percent bias of an instantaneous correction C_I for i seconds:

$$b_i = \frac{C_M(0) - C_M(i)}{C_M(0)}$$

The surface abundance estimate (corrected for perception bias) of each stratum $\widehat{N}_s$ was then multiplied by the appropriate period-specific C_a to give a corrected abundance estimate $\widehat{N}_c$. The variance was calculated using the delta method (Buckland et al., 2001):

$$var(\widehat{N}_c) = \widehat{N}_c \cdot \left\{ \frac{var(\widehat{N}_s)}{\widehat{N}_s{}^2} + \frac{var(C_a)}{C_a{}^2} \right\}$$

RESULTS

Survey coverage and bowhead sightings

Realized survey coverage is shown in Table 1 and Figures 3, 4 and 5. Large areas were initially covered using 3 aircraft simultaneously. Prince Regent Inlet was surveyed in a single day (Figure 3). Individual aircraft were then dispatched to survey

independently. The first aircraft covered the Gulf of Boothia a week later over a 2-day period (Figure 4). Numerous bowhead sightings were made in these strata. However, Fury and Hecla Strait, Northern Foxe Basin, and Roes Welcome Sound, which have been important bowhead habitats in past surveys (Figure 2), could not be covered. The second aircraft surveyed Admiralty Inlet in 2 days, with a 4-day break in between due to bad weather (Figure 4), and bowhead whales were sighted in the southern part of the inlet. Eclipse Sound was covered immediately afterwards, in 2 successive days but few bowhead whales were sighted there. The third aircraft surveyed the eastern coast of Baffin Island and Cumberland Sound over a 2-week period (Figure 5).

The largest numbers of sightings were made in Cumberland Sound and Isabella Bay (the only PSU of the fjord strata in which bowhead whales were sighted), which together accounted for 67% of all sightings.

The majority of bowhead whale sightings (79%) were of single animals, with pairs comprising 19% and groups of 3 or more only 2% (Figure 6). Overall, there was no significant relationship between the probability of detection and the natural log of group size, and mean group size was used to produce abundance estimates (Table 1). The global average group size of sightings within truncation distances was 1.22 (CV=3.7%). Of the 225 sightings of bowhead whales, 75 were identified as duplicates, leaving 150 unique sightings.

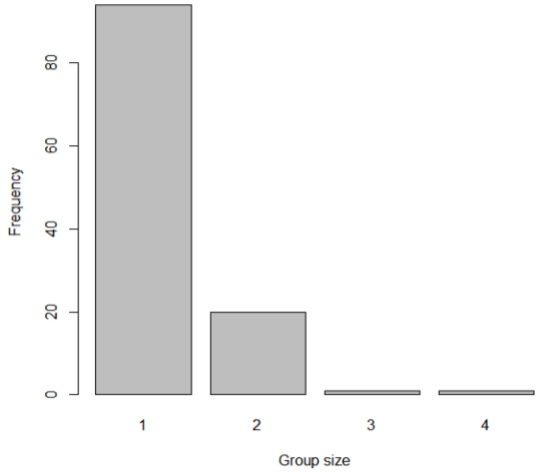

Figure 6. Group sizes of 117 unique sightings of bowhead whales in non-fjord strata.

Detection functions

Design-based strata

Examination of the histogram of the perpendicular distances of unique sightings indicated it was appropriate to right-truncate the data at 2,400 m, which left 117 observations. The shape of the histogram suggested that there was no need for left-truncation. Model selection was performed on the 3 key functions and all the combinations of environmental covariates. The model with the lowest AIC was that with a half-normal key function with no adjustment series and covariate "cloud cover" (Table 2, Figure 7). Selecting this model resulted in an average probability of detection of 0.52 and an effective strip half-width (ESHW) of 1,256 m (CV=7.8%).

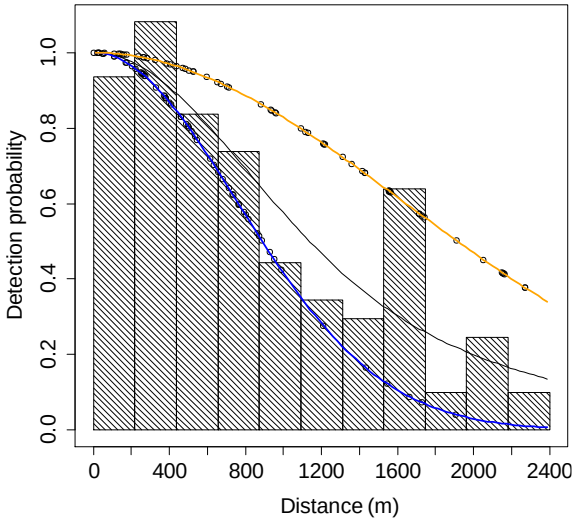

Figure 7. Bowhead whale detection function for non-fjord strata. Circles are the probability of detection for each sighting given its perpendicular distance and covariate value "cloud cover". Lines are the fitted model for the average (black), low level of the covariate (blue) and high level of the covariate (orange, cloud cover > 50%).

Selection among Mark Recapture (MR) models was performed on all the combinations of environmental covariates as well as covariates "observer" and "side of plane". The null MR model had the lowest AIC and none of the covariates improved the fit (none of the covariate models were within a ΔAIC of 2 from the best model, and thus we do not discuss them further). Therefore, the overall combination with lowest AIC was the

Table 1. Survey coverage, sightings, and abundance estimates of bowhead whales by stratum. L – transect length; n/L – encounter rate; E(s) – expected group size; N_s – surface abundance, corrected for perception bias but not for availability. Only strata with bowhead sightings are shown. AI: Admiralty Inlet. CS: Cumberland Sound. EB: East Baffin. ES: Eclipse Sound. GB: Gulf of Boothia. PRI: Prince Regent Island. Low/high refer to sub-strata of low or high density coverage.

Stratum	Area (km²)	Transects /PSU's	L (km)	n	n/L (km⁻¹)	CV	E(s)	CV	Prob. detection	CV	N_s	CV
AI (low)	4,526	18	387	5	0.0129	0.86	1.20	0.17	0.51	0.08	21	0.94
CS (high)	9,100	8	640	70	0.1093	0.46	1.20	0.05	0.51	0.08	439	0.48
CS (low)	15,029	6	231	1	0.0043	0.52	1.00	0.00	0.51	0.08	35	0.53
EB	43,419	28	1,140	11	0.0096	0.65	1.18	0.10	0.51	0.08	231	0.68
ES (low)	4,334	29	335	2	0.006	0.70	1.00	0.00	0.51	0.08	8	0.71
GB	63,178	11	1,627	8	0.0049	0.40	1.25	0.13	0.51	0.08	192	0.51
PRI	29,178	18	1,888	20	0.0106	0.21	1.30	0.08	0.51	0.08	219	0.29
EB Fjords	10,091	9		24							284	0.69
Total	178,855			141							1,429	

MCDS model described above and an MR model including no covariates other than perpendicular distance (Figure 8). This resulted in an estimated detection probability on the trackline $p(0)$ of 0.97 (CV=1.6%) for the combined platforms.

Table 2. Detection function models for MCDS in design-based strata, ranked by Δ-AIC. ESHW: effective strip half-width. "Null" is a model without covariates (i.e., with only perpendicular distance).

Key	Covariate	ESHW (m)	AIC	Δ-AIC
Half-normal	Cloud	1256	2019.05	0
Half-normal	Cloud+Glare	1255	2020.45	1.4
Hazard-rate	Beaufort+Cloud	1129	2020.61	1.56
Half-normal	Beaufort+Cloud	1254	2020.84	1.79
Hazard-rate	Cloud	1425	2020.85	1.8
Half-normal	Beaufort+Cloud +Glare	1250	2021.81	2.76
Hazard-rate	Beaufort+Cloud +Glare	1129	2022.6	3.55
Hazard-rate	Cloud+Glare	1417	2022.72	3.67
Hazard-rate	Beaufort	1010	2029.18	10.13
Hazard-rate	Beaufort+Glare	1007	2031.15	12.1
Hazard-rate	Null	1233	2036.65	17.6
Half-normal	Beaufort	1352	2037.66	18.61
Hazard-rate	Glare	1245	2038.24	19.19
Half-normal	Null	1371	2038.32	19.27
Half-normal	Glare	1361	2038.5	19.45
Half-normal	Beaufort+Glare	1349	2038.99	19.94

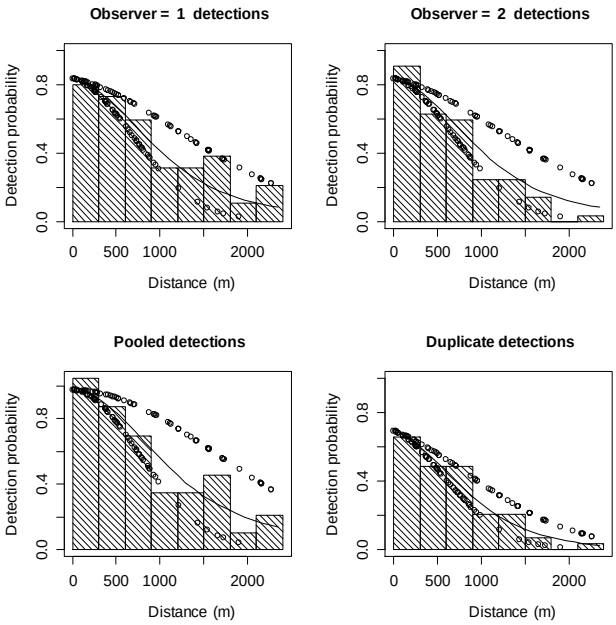

Figure 8. Mark-Recapture detection function plots assuming point independence between observers. Circles are the probability of detection for each sighting given its perpendicular distance and covariate value "cloud cover". Lines are the fitted models.

Fjord strata

All fjords in Admiralty Inlet and Eclipse Sound were surveyed. In the East Baffin Island fjord stratum, we selected 10 fjords out of 54, and were able to survey 9 of these. In Isabella Bay (i.e., East Baffin PSU 14), 39 bowhead sightings were recorded by primary and secondary observers, of which 15 were duplicates, which resulted in 24 unique sightings for a total of 38 individuals. No sightings were made in any of the other PSUs.

Right-truncation at 1,400 m removed 1 distant sighting and left 23 unique sightings: 22 were seen by the primary observers, 16 by the secondary observers, and 15 were seen by both (i.e., duplicates). Left truncation was not used. We fitted MRDS models to the data with different key functions, with and without covariates. None of the models with covariates had significant support (which might be because sightings in fjords were made in relatively homogeneous conditions, giving the model little information on the effect of covariates). The model that best fit the data was a hazard-rate key function with no covariates in either the MCDS or the MR models (Figure 9a), which estimated ESHW as 864 m (CV=18.5%) and an estimated $p(0)$ of 0.98 (CV=3.2%) for the combined platforms. Mean group size in Isabella Bay was 1.61 (CV=22%), with a larger proportion of pairs and trios than in non-fjord strata (Figure 9b), and a gathering of 9 whales that were recorded as a single group.

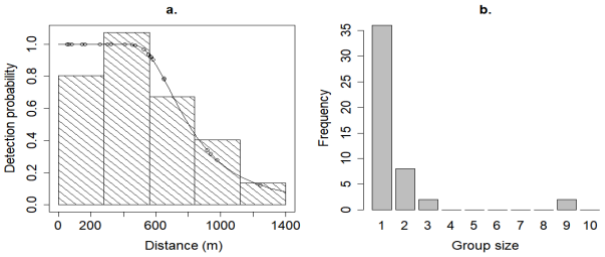

Figure 9. a. Detection function for bowhead whales in Isabella Bay (line is the fitted model). b. Group sizes within truncation distance in Isabella Bay.

Density surface model

Spatial model selection for Isabella Bay sightings showed that a soap filter without covariates and a negative binomial distribution provided the best fit to the counts-per-segment. The resulting density surface (Figure 10) shows how the soap filter prevented density gradients from being smoothed over islands and land boundaries, thus handling well the complex shape of this fjord.

The surface density was integrated to yield an abundance estimate (uncorrected) of 128 bowhead whales within Isabella Bay (CV=57.7%, of which 10% originates from the variance in the detection function and 90% is due to the variance in the GAM). Once corrected for perception bias with the fjord-specific $p(0)$ of 0.98, and when extrapolated to un-surveyed fjords along East Baffin Island, the surface abundance estimate for the entire stratum was 284 (CV=69.4%).

Figure 10. Spatial density surfaces of bowhead abundance in Isabella Bay (PSU14 in the East Baffin Island fjord stratum). Red line: track of aircraft. Red circles: sightings. Darker shading indicates higher predicted density. Estimated surface abundance (uncorrected) was 128 (CV=58%).

Availability correction and time-in-view data

Based on the results of Watt et al. (2015) and on the timing of bowhead sightings in each stratum, we used instantaneous, site-specific correction factors of 4.05 (± 0.838) in Prince Regent Inlet, 3.44 (± 0.838) in the Gulf of Boothia, 4.12 (± 0.766) in East Baffin Island fjords, 3.98 (± 0.840) in Admiralty Inlet, Eclipse Sound and the offshore area of East Baffin Island, and 5.68 (± 0.533) in Cumberland Sound.

There were 116 unique bowhead sightings within truncation distances for which both a spot time and a beam time were available. Time in view ranged from 0 to 40 seconds (and 1 outlier at 80 seconds), with an average time of 10.36 seconds (Figure 11).

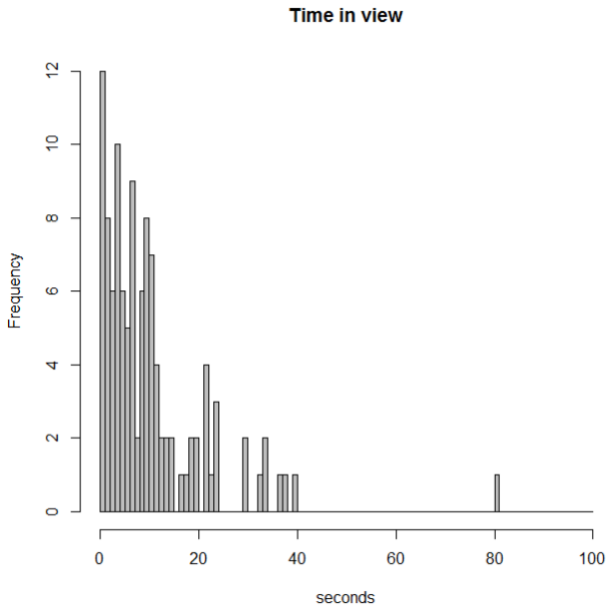

Figure 11. Time in view of 116 unique bowhead sightings with perpendicular distances within 2400 m.

Abundance estimates

Estimates of abundance for each stratum are given in Table 3. Density and abundance were highest in the Cumberland Sound High Intensity and East Baffin Fjord strata, which together comprised 57% of the total corrected abundance for the EC-WG population of 6,446 bowhead whales (CV=26.4%).

DISCUSSION AND CONCLUSIONS

Potential biases

Coverage and timing

Accurate abundance estimates require that all individuals from the population of interest have the possibility, i.e. a non-null probability, of being sampled (Buckland et al., 2001), which implies that their entire distribution range be surveyed. Based on TEK and telemetry studies available at the time of the survey, we attempted to sample the entire area known to be used by EC-WG bowhead whales in summer.

Due to unfavourable weather conditions, it was not possible to survey all of the planned areas. In particular, the Foxe Basin and north-western Hudson Bay regions were not surveyed. Although they can be important spring and summer habitats, these areas are not considered important aggregation areas for bowheads at the time of our survey in August (Cosens and Innes, 2000; Chambault et al., 2018). The Repulse Bay area had an estimate of approximately 75 whales in 1995 (uncorrected for either perception or availability biases). Whales have been observed in Frobisher Bay and Hudson Strait in summer where communities have harvested them recently; however we expected low densities and did not include these areas in our survey design. The Lancaster Sound area was thought to have bowhead whales in summer; however, telemetry studies have indicated large numbers of whales transit the area during spring and fall migration but tend not to remain long (Fortune, 2020; Chambault et al., 2018). Bowhead whale abundance estimates have sometimes exhibited high variability (e.g., Vacquié-Garcia et al., 2017), which has been attributed in part to patchy, variable distribution within a stock's range. However, movements of bowhead whales in the EC-WG have been well documented in recent years (e.g., Dueck et al., 2006; Chambault et al., 2018). Therefore, we consider it unlikely that the 3 regions we intended to survey, but were unable to, would represent a source of significant negative bias in our final estimate.

In addition, Nielsen, Laidre, Larsen, & Heide-Jørgensen (2015) used the diving patterns of satellite-tagged bowhead whales to identify important areas of summer feeding habitat in the Canadian Arctic. While most of these feeding habitats were covered in our survey, Frobisher Bay, Hudson Strait, and southern Foxe Basin were not. This could result in some additional negative bias to our estimate, but based on telemetry

Table 3. Abundance estimates by stratum. 'Surface abundance': corrected only for perception bias. 'Abundance (corrected)' includes a correction factor C_a for availability bias (from Watts et al., 2015). The 95% CI assume a log-normal distribution. For strata names, see Figure 2 and Table 1.

Stratum	Surface abundance	CV	C_a	CV_{ca}	Abundance (corrected)	CV	95% CI
AI (low)	21	0.94	3.98	0.21	82	0.97	13–510
CS (high)	439	0.48	5.68	0.09	2,495	0.49	709–8,781
CS (low)	35	0.53	5.68	0.09	201	0.54	43–941
EB	231	0.68	3.98	0.21	920	0.72	232–3,645
ES (low)	8	0.71	3.98	0.21	32	0.74	7–123
GB	192	0.51	3.44	0.24	660	0.56	187–2,334
PRI	219	0.29	4.05	0.21	886	0.36	415–1,893
EB Fjords	284	0.69	4.12	0.19	1,170	0.72	264–5,193
Total	**1,429**				**6,446**	**0.26**	**3,838–10,827**

studies (e.g., Chambault et al., 2018), we believe these biases would likely be of small magnitude.

A total of 24 bowhead sightings (38 individuals) were recorded in Isabella Bay, an area known for its large concentration of bowhead whales during the summer (Finley, 1990; Hay et al., 2000). The resulting (uncorrected) surface estimate was 128 (CV=58%). An earlier survey of Isabella Bay conducted later in the season (September 2009) resulted in a higher surface estimate of 221 (CV=34%, Hansen, Heide-Jørgensen, & Laidre, 2012) but the confidence intervals of these estimates overlap. Moreover, the 2009 survey included larger parts of the waters immediately outside the bay (where bowhead whales were observed during HACS, but this area was part of our design-based stratum rather than the fjord stratum). The possible sensitivity of our results to the limits of the fjord stratum are also hinted by the density gradients (Figure 10), which suggested density was higher towards the mouth of the bay. Together, these results have showed the continued importance of Isabella Bay for bowhead whales in recent years, which has also been shown by the long residency patterns of tagged individuals in this area (Chambault et al., 2018).

Isabella Bay was the only fjord along the eastern coast of Baffin Island where bowhead whales were observed. Because this survey aimed primarily at estimating narwhal abundance, this fjord was treated as a primary sampling unit (PSU) like any other fjord within the design of the survey. However, it could be argued that for the specific purpose of estimating bowhead abundance, this area should have been a separate stratum, since few bowhead whales were expected in other East Baffin fjords. Such a stratification scheme would have resulted in 128 bowhead whales in Isabella Bay and 0 in the rest of the fjords (instead of the 284 estimated for the entire fjord stratum), thus reducing our total abundance estimate by 11%. This stratification scheme would also have resulted in a lower CV (because it would have reduced variation within strata and increased variation among strata). However, Nielsen et al. (2015) identified other areas along the East Baffin coast (including Clyde Inlet and Broughton Island) as bowhead summer feeding habitat, and telemetry studies confirm their presence and long residency patterns along the East Baffin coast (Chambault et al., 2018), which we feel justifies our use of the extrapolated estimate.

Overall, our survey achieved the most complete and intense coverage ever in a single season, and covered most important areas of bowhead habitat, making our fully corrected estimate of 6,446 (95% CI: 3,838–10,827) the most complete survey estimate for the stock. A genetic mark-recapture study covering a 5-year time frame up to 2013 estimated a similar abundance for the EC-WG population (7,660; 95% High Density Interval 4,500–11,100; Frasier et al., 2015).

Perception bias

We estimated the proportion of visible bowhead whale sightings that were missed by observers using MRDS methods, which required the identification of between-platform duplicate sightings. This was much more straightforward for bowhead whales than for narwhals, which often occurred in large aggregations (due to their higher densities and grouping behaviour), resulting in many sightings over a short period of time (Doniol-Valcroze et al., 2020). In contrast bowhead sightings tended to be more isolated in time, making the identification of duplicates unequivocal in most cases.

Our estimates of perception bias for the combined platforms were 0.97 for the design-based strata and 0.98 for the fjord strata (i.e., Isabella Bay), which is significantly higher than the estimate of 0.34 (CV=28%) from the previous survey series carried out from 2002–2004 (Dueck et al., 2007). However, the earlier surveys used aircraft with flat rather than bubble windows, which limited visibility close to the track line, and the MR analysis was based on 34 sightings, including only 5 duplicate sightings. Our higher estimate of sighting probability for bowhead whales is based on a much larger sample size and is similar to that from aerial surveys using similar methods for whales of similar size and colour, such as humpback whales (*Megaptera novaeangliae*) (Hansen et al., 2019; Pike, Gunnlaugsson, Sigurjónsson, & Víkingsson, 2020).

Availability

Our correction for bowhead whales that were not seen because they were submerged during the passage of the aircraft (availability bias) is based on the diving behaviour during daylight hours of 22 bowhead whales tagged with satellite-linked time/depth recorders between 2012 and 2013 in Cumberland Sound and Northern Foxe Basin (Watt et al., 2015). These whales were tracked in Prince Regent Inlet and the Gulf of Boothia as well as Foxe Basin (PRI/GoB/FB). The data were restricted to the month of August and to daylight hours to conform with the period of the survey. As we lack comparable data for other strata, we applied the average correction value for Cumberland Sound and PRI/GoB/FB to other areas. However, bowhead whale diving behaviour can vary substantially between areas. For example, in mid-August, bowhead whales spent 17.6 ± 1.65% of their time in the 0–2, 0–4, and 0–6 m combined depth bins in Cumberland Sound and 29.1 ± 7.09% in PRI/GoB/FB. Most sightings outside of these areas were made in East Baffin and particularly Isabella Bay, making the correction for this area uncertain.

Unlike the case for narwhal (Doniol-Valcroze et al., 2020), there is no experimental evidence to suggest how deep in the water column a bowhead whale can be detected from an aircraft, making it difficult to determine which depth bins to use to calculate an instantaneous availability bias correction factor. To account for this uncertainty, we have combined multiple depth bins (0–2, 0–4 and 0–6 m bins), giving equal weight to each bin. Previous estimates of Eastern Arctic bowhead whales have used depth intervals of 0–2 m (Koski, Heide-Jørgensen, & Laidre, 2006; Rekdal et al., 2015) or 0–4 m (Dueck et al., 2007). Bowhead whales are largely of dark colouration dorsally with white patterns along the mouth and tail stock for older individuals (Figure 1), resulting in variable distinctive markings that may or may not be seen reliably from an aircraft to a depth of 4 or 6 m. Some of our sightings were made in fjord areas with turbid water, which reduces sub-surface visibility, and we did not make adjustments for turbidity in fjords as has been done for narwhal (Watt et al., 2015). For these reasons we consider our estimate of instantaneous availability, P_i, to be conservative in that it is likely to be positively biased and the availability correction factor, C_a, negatively biased. While comparable estimates are not available for Eastern Arctic bowhead whales, Krutzikowsky and Mate (2000) combined several studies of Western Arctic bowhead whales based on visual observations

to derive an average instantaneous availability from an aircraft of 16.2%, which also suggests that our estimate is conservative.

Our availability correction would be appropriate if sightings were instantaneous (e.g., for photographic surveys). During HACS, visual sightings were not instantaneous and thus the correction factor does not account for the search time available for observers to detect animals. Use of an instantaneous estimate of availability with a non-instantaneous detection process can positively bias the corrected estimate of abundance (McLaren, 1961). Ideally, data on the dive cycle of bowhead whales in August in the study area, combined with estimates of the average time in view for bowhead whales from the survey, would be used to adjust the availability correction factor. Unfortunately we lack sufficiently detailed data on the dive cycle of bowhead whales in their Eastern Arctic summering areas to derive an appropriate correction for this survey. Würsig et al. (1984) estimated the availability of bowhead whales feeding in the Beaufort Sea to observers in a circling aircraft, finding a mean surface time of 1.3 minutes and a mean dive duration (during which time the whales were not visible) of 6.3 minutes. Instantaneous availability was therefore 0.17 (or C_I of 5.85), which is substantially lower than the Watt et al. (2015) estimates for HACS. To illustrate the potential magnitude of the bias caused by non-instantaneous availability to observers, we applied the Beaufort Sea data to the mean time in view during HACS of 10.6 seconds. The resulting availability correction factors would be adjusted by a factor of 0.894, which in turn would reduce the abundance estimates of each stratum by 10.6%. However, this approach assumes that bowhead whale diving behaviour is similar across populations within the Arctic and across strata within the HACS study area. Würsig et al. (1984) found considerable variability in surface and dive times across years, age-classes, feeding behaviours, and between areas with and without ice. Moreover, it would be inconsistent to use the Beaufort Sea surface and dive times to calculate the correction for non-instantaneous availability C_M but not to calculate C_I (which is 5.85 in the Beaufort Sea data but ranges from 3.44 to 5.68 in the HACS strata). Our estimates can be better corrected for non-instantaneous availability once more information on the diving behaviour of bowhead whales in the area becomes available.

Comparison to previous estimates

Our total bowhead abundance estimate is similar to a previous aerial survey estimate of 6,344 (95% CI: 3,119–12,906) based on 14 unique observations made during a partial survey conducted in 2002 (IWC, 2009). The latter surveys did not include any areas north of Lancaster Sound, which were covered in 2013 but produced no bowhead whale sightings. More importantly, the 2002–2004 surveys did not cover Cumberland Sound, an area that accounts for 42% of our total summer estimate and 30% of the genetic mark-recapture population estimate (Frasier et al., 2015). The earlier survey did cover parts of Foxe Basin, Fury and Hecla Strait and northern Hudson Bay which were not covered in our survey. However, deriving an acceptable estimate from the 2002–2004 survey has proven problematic (Cosens, Cleator, & Richard, 2006; Dueck et al., 2007; Hiede-Jørgensen, Laidre, & Fossette, 2008; IWC, 2009), primarily because relatively few bowhead whales were detected, there were few duplicate detections, and the flat windows in the survey aircraft limited detections close to the track line. In addition, the conduct of the earlier surveys over 3 years raises the possibility of bias due to inter-annual shifts in the distribution of bowhead whales between strata. We therefore consider our estimate to be the most complete and reliable survey estimate available for the EC-WG stock of bowhead whales

An alternate estimate of abundance from roughly the same period as our study is available. Frasier et al. (2015) used genetic mark-recapture methods to estimate the abundance of bowhead whales in the EC-WG population. Biopsy samples from several locations in Nunavut as well as Disko Bay in West Greenland, from the period 1995–2013 were used in the analysis. The best estimate for the present population, using only samples collected in the last 5 years of the period, was 7,660 (95% High Density Interval 4,500–11,100), only 19% higher and was thus similar to our aerial survey estimate for 2013. Use of data from the full 19 years of sample collection suggests that the population has grown over the period. This estimate is completely independent from ours both in source data and methodology, and their close correspondence increases our confidence in the results of our survey.

The EC-WG bowhead whale stock was reduced to a very low level by a prolonged period of commercial exploitation which ended early in the 20th century (Hay et al., 2000; Higdon, 2010). Population modelling using known takes and estimates of population dynamics suggest a pre-exploitation population of about 18,500 whales (Higdon & Ferguson, 2016). As recently as the 1970s the population was thought to number only in the low hundreds (Davis & Koski, 1980). While we cannot know the present carrying capacity for the stock, recent estimates from our survey and others (Dueck et al., 2006; Frasier et al., 2015; Koski, Heide-Jørgensen, & Laidre, 2006) suggest that the population is recovering.

ADHERENCE TO ANIMAL WELFARE PROTOCOLS

The research presented in this article has been done in accordance with the institutional and national animal welfare laws and protocols applicable in the jurisdictions in which the work was conducted.

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