Stabilisation of the abundance of bowhead whales (*Balaena mysticetus*) in West Greenland

Mads Peter Heide-Jørgensen[1], Jonas Teilmann[2], Fredrik Christiansen[2] and Rikke Guldborg Hansen[1,2]

Contact email: mhj@ghsdk.dk

ABSTRACT

A proportion of the East Canada-West Greenland population of bowhead whales (*Balaena mysticetus*) spends January–June off West Greenland. Several aerial surveys conducted between 1998 and 2012 have estimated the abundance of bowhead whales on this winter feeding ground. Following identical methods, a visual aerial line-transect survey was conducted as a double-observer experiment with independent observation platforms covering the main distribution of the winter aggregation of bowhead whales in West Greenland between 26 March and 4 April 2022. The target region covered an area of 34,742 km^2 with six strata and a total of 3,667 km systematically placed transect lines. Abundance of bowhead whales was estimated using a Mark-Recapture Distance Sampling (MRDS) approach. The at-surface estimate was 208 (cv = 0.38, 95% CI: 99–436) whales. Availability correction incorporated data on diving behaviour, time-in-view, and the degree of diving synchrony. The mean time that whales were available for detection at the surface (23%, cv = 0.06), the mean duration of dives below 2 m (472 seconds), and the mean duration of surfacings (138 seconds), were estimated using high-resolution time-depth-recorders from 12 bowhead whales instrumented in the same area and season as the survey. Drone footage showed that small groups of bowhead whales (1–3) had highly synchronous surfacing patterns and long breathing periods at the surface (mean = 21 seconds). The MRDS abundance estimate, corrected for perception bias and availability bias, was 832 whales (cv = 0.39, 95% CI: 402–1,723) bowhead whales. The 2022 estimate is similar to an estimate from 2012 but lower than the estimate from 2006, suggesting that the abundance in winter in West Greenland has stabilised.

KEYWORDS: ABUNDANCE ESTIMATE; SURVEY-AERIAL; TRENDS; FEEDING GROUNDS; SATELLITE TAGGING; DIVING

INTRODUCTION

The bowhead whale (*Balaena mysticetus*) plays a vital role in the Arctic marine ecosystem off West Greenland. The shelf area, particularly Disko Bay, serves as a crucial feeding ground for these whales, which are significant predators of zooplankton, especially copepods, during the spring (Laidre *et al*., 2007; Heide-Jørgensen *et al*., 2013; Nielsen *et al*., 2015; Banas *et al*., 2021; Christiansen *et al*., 2024). Historically, bowhead whales were hunted by European whalers for centuries, but they gained protection under the League of Nations Convention in 1931 (Eschricht & Reinhardt, 1866; Woodby & Botkin, 1993).

Following new abundance estimates indicating a recovering population (Heide-Jørgensen *et al*., 2007), the International Whaling Commission's (IWC) Scientific Committee concluded in 2008 that the removal of five bowhead whales per year over a five-year period would be sustainable. In response, the Greenland government

[1] Greenland Institute of Natural Resources, PO Box-570, 3900 Nuuk, Greenland
[2] Department of Ecoscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

authorised the resumption of Inuit subsistence hunts, which began in 2009 (Heide-Jørgensen *et al*., 2012). Since then, nine bowhead whales have been harvested in West Greenland (IWC, 2023).

The bowhead whales wintering in West Greenland belong to a shared population spanning the Canadian Arctic Archipelago, Baffin Bay, Davis Strait, and West Greenland (Heide-Jørgensen *et al*., 2003, 2006). This population, known as the Eastern Canada-West Greenland (ECWG) bowhead population, was recently estimated at 6,446 individuals (cv = 0.26, 95% CI: 3,838–10,827) based on a 2013 aerial survey conducted in the Canadian Arctic Archipelago (Doniol-Valcroze *et al*., 2020). These whales undertake extensive migrations between the Canadian Arctic Archipelago and West Greenland, tracking seasonal changes in sea ice (Heide-Jørgensen *et al*., 2021), with a portion of the population spending January to June off the coast of West Greenland to feed.

Several aerial surveys have estimated the abundance of bowhead whales on their West Greenland winter ground (e.g., Rekdal *et al*., 2015). Past surveys indicated a rise in bowhead whale abundance from 246 individuals (95% CI: 62–978; Heide-Jørgensen & Acquarone, 2002) in 1998 to 1,229 individuals (95% CI: 495–2,939; Heide-Jørgensen *et al*., 2007) in 2006 and 744 whales in 2012 (cv = 0.34, 95% CI: 357–1,461; Rekdal *et al*., 2015).

In addition to aerial surveys, genetic mark-recapture studies have estimated the abundance of bowhead whales in the Canadian Arctic Archipelago at 11,747 individuals (95% CI: 8,169–20,043), based on 1,177 samples collected between 1995 and 2013 across their full range (Frasier, 2020). From a subset of these data (n = 292) from Disko Bay, it was estimated that 2,615 individuals (95% CI: 1,353–6,114) from this population visit West Greenland during the winter and spring, based on samples collected from 2001 to 2008. A separate genetic capture-recapture study using an extended sample size of 427 samples collected in Disko Bay between 1999 and 2013 estimated the local abundance at 1,538 whales (cv = 0.24, 95% CI: 827–2,249; Rekdal *et al*., 2015).

The present study provides an updated abundance estimate for bowhead whales in West Greenland in 2022, incorporating new data on availability bias and the synchrony of diving behaviour, further improving our understanding of bowhead whale population dynamics in the region.

MATERIAL & METHODS

Survey design

Visual aerial line-transect surveys for bowhead whales were conducted using a double-platform, or double-observer, method, with independent teams of observers stationed at the front and rear of a De Havilland Twin Otter aircraft. The survey was a multispecies survey that also targeted beluga whales (*Delphinapterus leucas*) and walruses (*Odobenus rosmarus*). The target altitude was 213 m, and the cruising speed was 170 km/h. Only data collected during optimal conditions – sea states less than Beaufort 3 and visibility greater than 10 km – were included in the analysis. Two observers were positioned in the front seats just behind the cockpit, and two in the rear seats at the back of the aircraft. The front and rear observers were separated by approximately 4 m, with a long-range fuel tank and recording equipment between them to prevent any visual or acoustic cueing of sightings between platforms. Each observer had access to bubble windows, providing a clear view of the track line directly below the aircraft, ensuring effective detection of whales during the survey.

Declination angles (ω), measured with electronic inclinometers when animals were abeam, were converted to perpendicular distances (x) using the equation from Buckland *et al*. (2001): $x = v * \tan(90 - \omega)$ where v represents the altitude of the airplane (Hansen *et al*., 2020). Duplicate sightings, i.e., animals seen by both Observers 1 and 2, were identified based on the coincidence of timing and positions, as well as similarities in group size and direction of movement.

Survey area and timing

The aerial survey was conducted in coastal and offshore areas of West Greenland, between latitudes 65°40’N and 69°30’N, to cover the primary winter and spring aggregations of bowhead whales and beluga whales (*Delphinapterus leucas*). The survey region encompassed an area of 34,742 km², which was divided into six strata based on expected densities of bowhead from previous surveys (Heide-Jørgensen *et al*., 1993). A total of 3,667 km of east-west oriented, equally spaced transect lines were flown and searched between 26 March and 4 April 2022.

Availability bias

Twelve bowhead whales were equipped with Fastloc GPS retrievable data and dive loggers (Wildlife Computers, Redmond, WA, USA) to monitor their movement and diving behaviour in Disko Bay. The data collection periods ranged from 7 to 388 hours, capturing high-resolution spatial and temporal data between March and May from 2008 to 2018 (cf., Heide-Jørgensen *et al*., 2013). The tags recorded depths (± 0.5 m) at 1 Hz intervals and stored Fast GPS signal snapshots. The tag package was attached to a stainless-steel anchor, deployed on the whales using an 8 m fiberglass pole from a boat. The anchor penetrated the whale's blubber to a depth of approximately 15 cm, and the tag package was connected by a ~1 m wire, trailing behind the whale as it swam.

To retrieve the tags, approximate geographic locations were determined using Argos positions, and recovery was facilitated by tracking the VHF signal emitted by the tag. Dive data were processed using MultiTrace-Dive (Jensen Software Systems, Germany) with zero-offset corrections and filtering, as described by Heide-Jørgensen & Lage (2022). For each individual whale, the durations of surfacing periods (in seconds) spent above 2 m and diving periods below 2 m were computed and averaged. Both the duration of periods above and below 2 m were truncated at 600 and 1500 seconds, respectively, and periods shorter than 5 seconds were omitted. The overall proportion of time spent at or above 2 m was then estimated for each whale and a weighted average of these proportions was calculated across all individuals, using the total recording duration (in hours) as the weighting factor.

Bowhead whales are available for detection for a short period of time during aerial surveys (i.e., some whales may be seen ahead of the plane), and the probability that a whale was detectable at the surface was greater than the proportion of time it spends at depths at which it is assumed to be visible (0–2 m depth). A correction factor that includes data on both dive and surfacing periods and the frequency distribution of time-in-view observations was developed following the approach described in Richard *et al*. (2010) and Doniol-Valcroze (2010a, b).

Detection function estimation

The detections between observers were assumed to be independent only on the point immediately below the aircraft where the distance is zero. This involves estimating two models: a multiple covariate distance sampling (DS) detection function for combined platform detections, assuming a certain detection probability on the trackline, and a mark-recapture (MR) detection function (Burt *et al*., 2014).

Detection probability was estimated using the independent observer configuration implemented in *Distance 8.0* (Thomas *et al*., 2010). Hazard rate and half-normal detection function models were tested; the best performing model was selected.

Akaike's Information Criterion (AIC) and goodness of fit tests were used for model selection.

Synchrony of surfacings

The MRDS analysis utilises detections of groups at the surface for the density estimation. The individual-based availability correction factor assumes that an adjustment is applied if the whales in groups are diving independently of one another. To assess this assumption, drone footage of 11 whales in groups of two to three was analysed to observe the synchrony of surfacing behaviour. Specifically, the footage captured the whales' simultaneous appearances at the surface, the duration of their time at the surface, and the synchrony in their diving behaviour.

The aerial footage was recorded using a DJI Inspire 2 quadcopter drone equipped with a Lightware SF11/c laser range finder, flying at an altitude of 30–60 m. The videos were then reviewed to determine the degree of synchrony in the surfacing and diving times, providing insight into whether whales in groups behave independently when diving.

Estimating density and abundance

Group density $\hat{D}_{G_i}$ and at-surface abundance $\hat{N}_{G_i}$ of groups in stratum i were estimated as follows:

$$\hat{D}_{G_i} = \frac{1}{2wL_i}\sum_{j=1}^{n_i}\frac{1}{\hat{p}_{ij}} \quad \text{and} \quad \hat{N}_{G_i} = A_i\hat{D}_{G_i}$$

where A_i is the size of stratum *i*, *w* is the truncation distance, L_i is the total effort in stratum *i*, n_i is the total number of detections in the stratum *i*, and $\hat{p}_{ij}$ is the estimated probability of detecting group *j* in stratum *i*, obtained from the fitted detection models.

Individual animal abundance was estimated by:

$$\hat{N}'_i = \frac{A}{2wL_i}\sum_{j=1}^{n_i}\frac{s_i}{\hat{p}_{ij}}$$

where s_i is the size of the *i*th detected group.

The expected group size $\hat{E}[S_i]$ in stratum *i* was estimated by:

$$\hat{E}[S_i] = \frac{\hat{N}'_i}{\hat{N}_{G_i}}$$

It was assumed that bowhead whales were only available for detection when they were close to the surface (0–2 m) and that the proportion of time spent close to the surface was known from high-resolution dive data.

To account for availability bias ($\hat{a}$), corrected abundance ($\hat{N}'_c$) was estimated by:

$$\hat{N}'_{ci} = \frac{\hat{N}'_i}{\hat{a}}$$

The analytic variance of the density estimate, including the variance of encounter rate and group size, was estimated based on the empirical variance in estimated density between samples. The addition of variance for each component was estimated using the Delta method:

$$cv\left(\hat{N}'_{ci}\right) = \sqrt{cv^2\left(\hat{N}'_{ci}\right) + cv^2\left(\hat{a}\right)}$$

An estimate of abundance was computed for each stratum, and the total abundance was the sum of the stratum abundance estimates. Estimation of 95% confidence intervals for estimates of density and abundance were calculated following the derivation of Burnham *et al*. (1987).

RESULTS

Survey effort and distribution of sightings

The survey area spanning 34,742 km² was divided into six strata, with each transect treated as an independent sample. Observations of bowhead whales (n = 29) were recorded in Strata 1, 2, 3, and 5, with most sightings occurring in Stratum 2 (Fig. 1). The observed group sizes included 24 sightings of single individuals and five sightings of groups of two whales. The time-in-view (TIV) ranged from 0 to 60 seconds, but the observation with TIV = 60s and = 18° was considered unrealistic and was excluded (Fig. 2).

Availability bias

It was assumed that bowhead whales could be detected up to 2 m below the surface. For the 12 whales with detailed diving behaviour data, the mean duration of periods at the surface (0–2 m) was 138 seconds, while the mean time of the periods spent below 2 m was 472 seconds (Figs. 3 and 4, Table 1). The mean proportion of time spent within 0–2 m depth was 0.23 (cv = 0.06), which was used as the availability factor ($\hat{a} = 1/0.23$) for correcting the at-surface estimate of whale abundance. When incorporating the time-in-view observations and the time spent at the surface and diving, the availability correction factor adjusted to 0.25. Only the availability

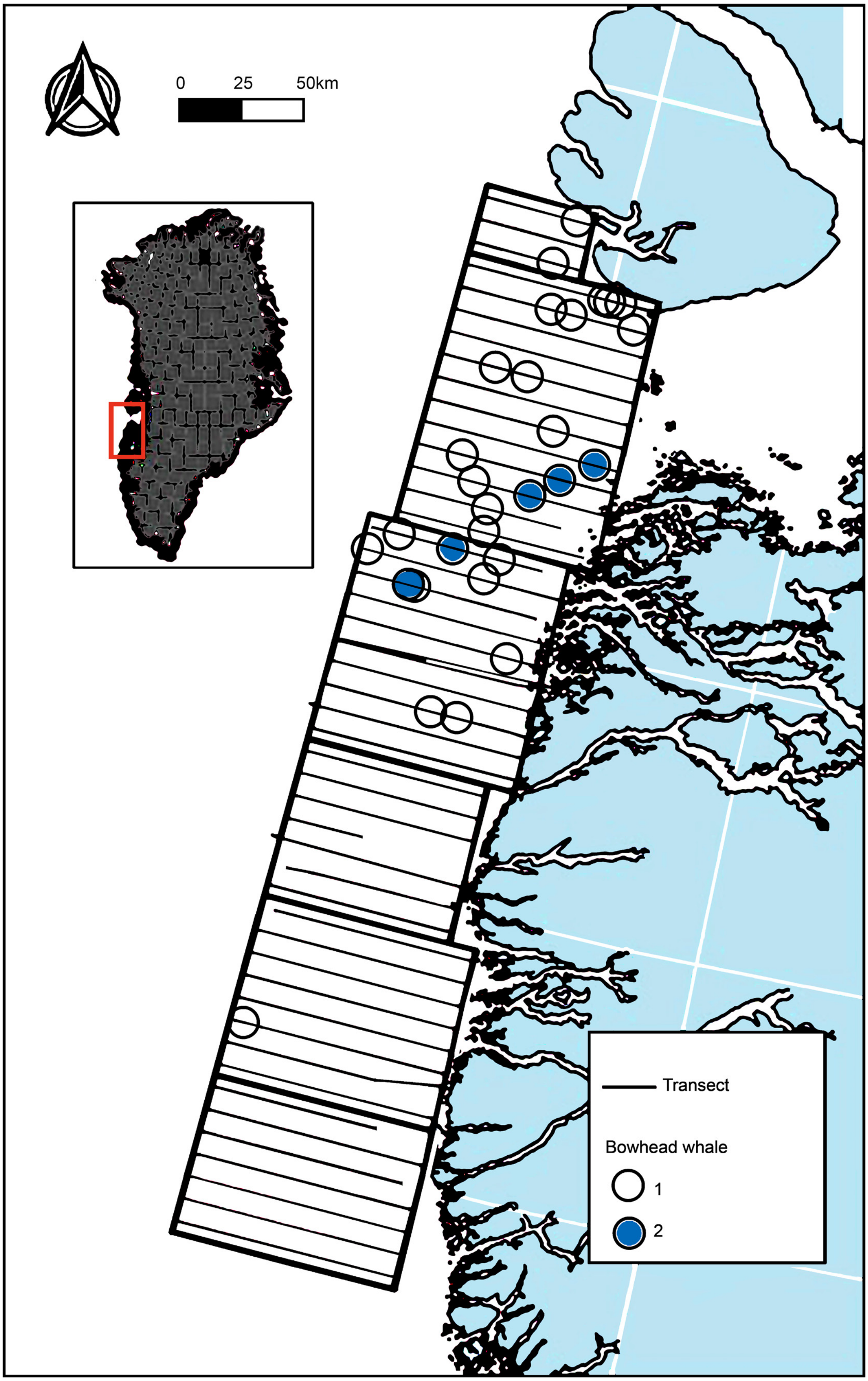

Figure 1. Transects on effort for the aerial survey off West Greenland in March/April 2022 with sightings of bowhead whales shown in white (group size = 1) and blue (group size = 2). Strata 1 (North) to 6 (South).

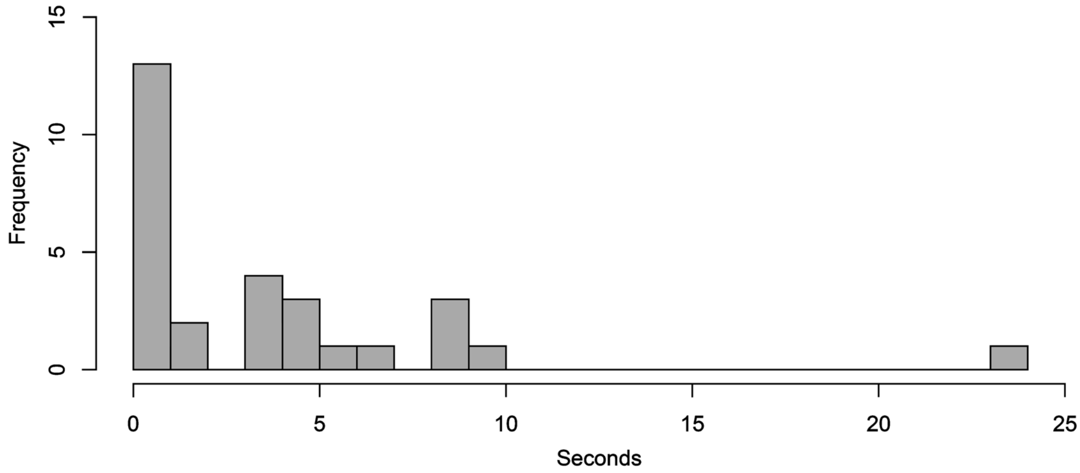

Figure 2. Frequency distribution of time-in-view of 29 observations (both platforms) of bowhead whales during the aerial survey in West Greenland in March/April 2022. One observation with a time-in-view of 60 s was excluded from further analyses as it was considered unrealistic (~3 km distance).

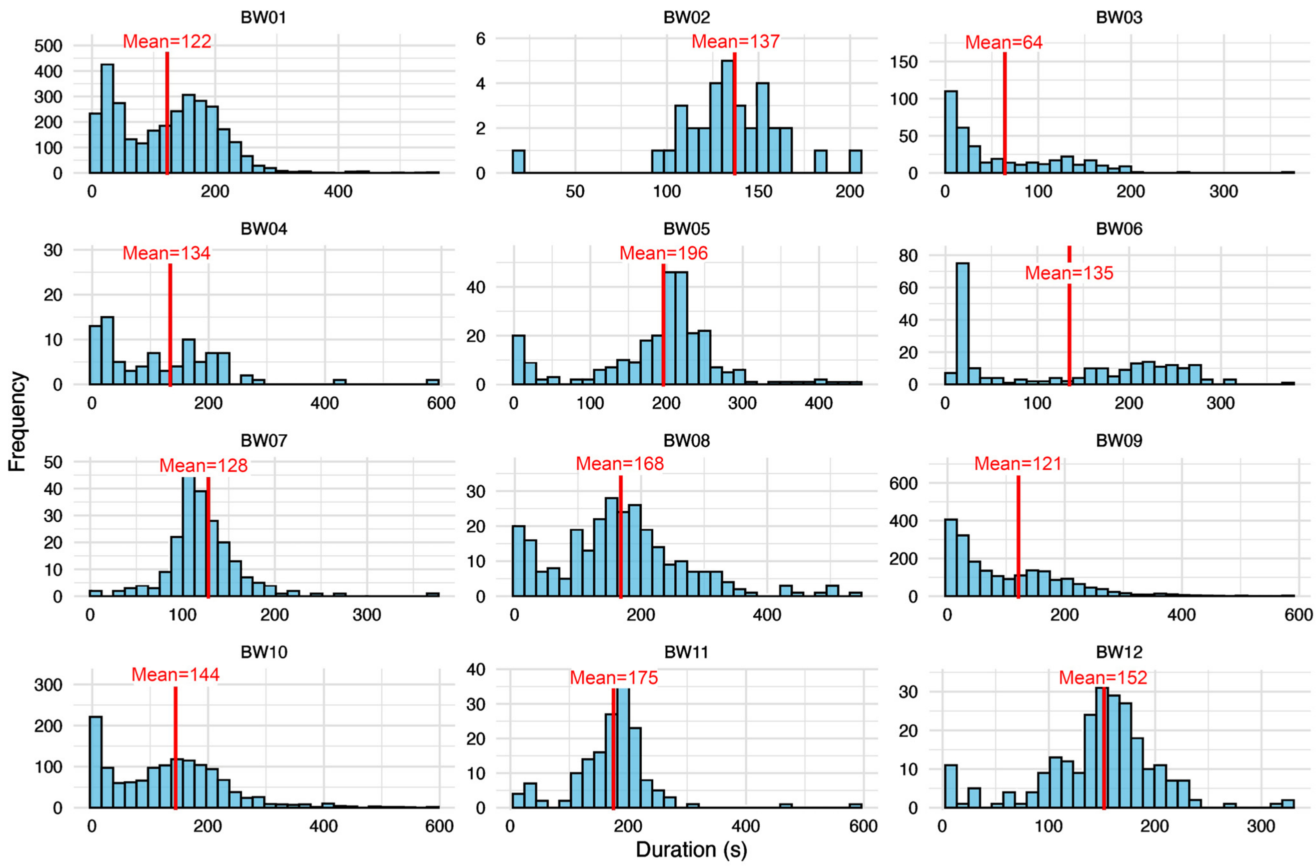

Figure 3. Frequency distributions of the durations of surfacings above 2 m for 12 bowhead whales instrumented with time-depth-recorders in Disko Bay, West Greenland, in March–May 2008–2018.

factor was assumed to contribute to the variance of the correction. Other options for availability bias with different selections of TIV values were also considered, but it appeared that the availability bias was relatively insensitive to the TIV values (Table 2).

The drone footage revealed that the average duration of simultaneous breathing at the surface for groups of whales was 21 seconds (cv = 0.13), which is slightly less than the time spent at 0–2 m depth but still significantly longer than the median time-in-view (Table 2). Additionally, all whales within the filmes groups were observed to dive and surface synchronously.

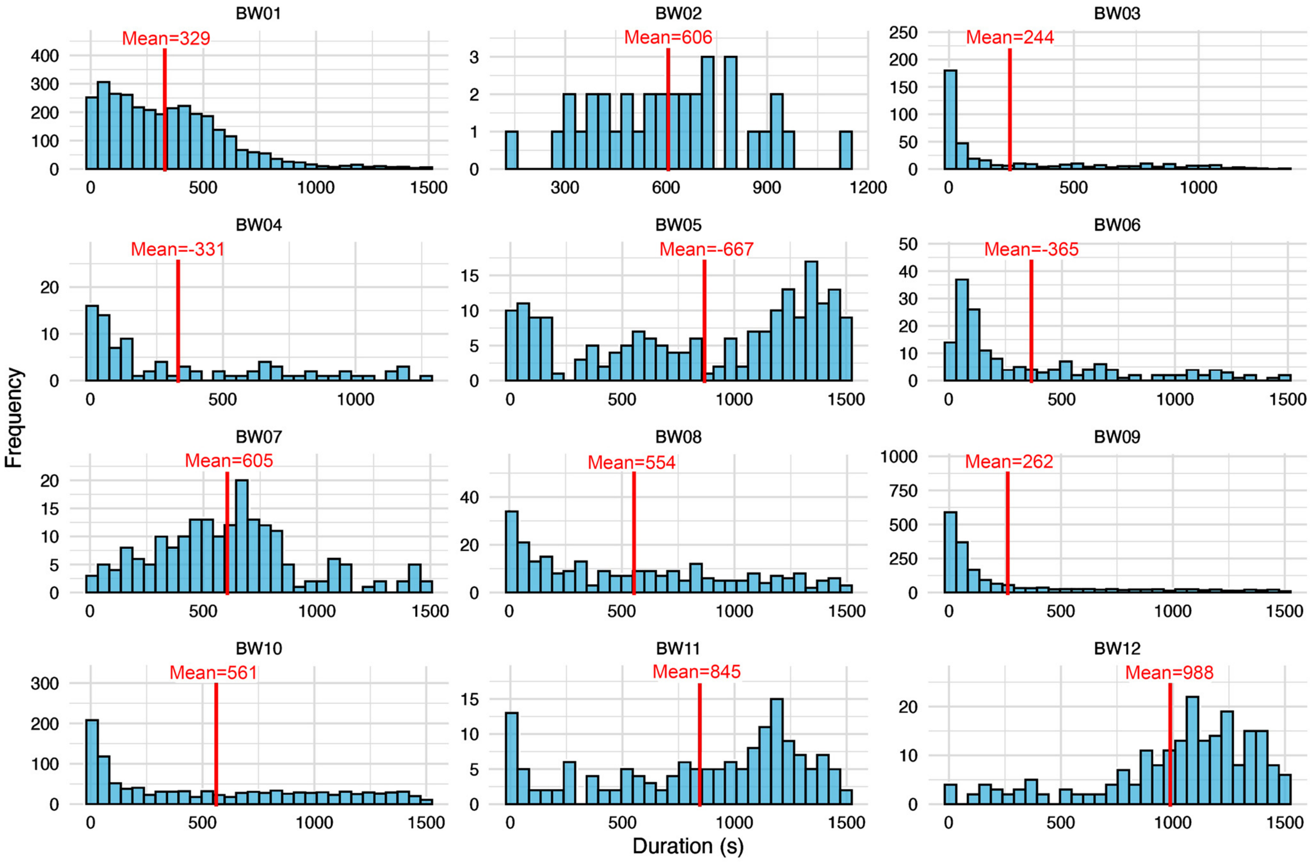

Figure 4. Frequency distributions of the durations of dives below 2 m for 12 bowhead whales instrumented with time-depth-recorders in Disko Bay, West Greenland, in March–May 2008–2018.

Table 1

Surface time and time spent above and below 2 m depth for 12 bowhead whales instrumented with time-depth recorders in Disko Bay during March–May 2008–18. The original data were zero-offset corrected following the procedure described by Heide-Jørgensen & Lage (2022). Surface time was calculated for the 0–2 m depth interval and weighted by individual sample sizes.

Whale ID	Sex	Tag attachment period	Above 2m (s)	Below 2m (s)	Surface time (0–2 m)	Sample size (hrs)
BW1	F	28.4.08–31.5.08	122	329	0.29	388
BW2	F	12.5.09–13.5.09	137	606	0.18	7
BW3	M	6.5.09–8.5.09	64	244	0.21	31
BW4	F	2.5.09–2.5.09	134	331	0.28	11
BW5	F	31.3.10–8.4.10	196	867	0.17	93
BW6	?	7.3.10–12.3.10	135	365	0.17	60
BW7	M	19.4.10–23.4.10	128	605	0.16	45
BW8	?	14.3.10–21.3.10	168	554	0.29	85
BW9	?	23.3.11–19.4.11	121	262	0.25	320
BW10	?	31.3.10–28.4.10	144	561	0.21	338
BW11	?	4.5.18–9.5.18	175	845	0.21	48
BW12	?	6.5.18–12.5.18	152	988	0.12	76
Weighted mean			138	472	0.23 (cv = 0.06)	

Table 2

The effects of changes in time-in-view (TIV) thresholds on availability bias ($\hat{a}$) used for the abundance estimates of bowhead whales.

Threshold	TIV (s)	$1/\hat{a}$
No TIV correction	–	0.23
Maximum observed TIV	24	0.26
Observed TIV	Mean = 4.0	0.25
Cut off at 95% observed values	0–10	0.24
Cut off at 90% observed values	0–9	0.24
Cut off at 85% observed values	0–7	0.24
Maximum possible TIV	60	0.26

Table 3

Drone footage of 11 groups of bowhead whales observed in March–April 2023 in Disko Bay, West Greenland.

Date	Video duration hh:mm:ss	Composition	Duration of synchronized breathing (s)
2023/03/28	00:01:25	Pair	10
2023/03/28	00:03:05	Pair	10
2023/04/06	00:02:32	Pair	13
2023/03/26	00:01:48	Pair	16
2023/03/30	00:00:53	Pair	20
2023/04/06	00:01:25	Pair	21
2023/04/05	00:01:32	3 Adults	22
2023/03/28	00:01:12	Pair	24
2023/03/28	00:03:12	Pair	25
2023/04/06	00:00:53	Pair	28
2023/03/28	00:01:47	Pair	44

Table 4

Summary information of survey data; *k* is the number of transects searched in a stratum. Sightings used in the MRDS analysis are all sightings between 0–2,000 m.

Stratum	Size (km²)	*k*	Effort (km)	Sightings	Density of groups $\hat{D}_{G_i}$	At-surface abundance of groups $\hat{N}_{G_i}$	Expected group size $\hat{E}[S_i]$	Individual abundance $\hat{N}'_i$
1	1,275	3	138	1	0.0048 (1.05)	6 (1.05)	1 (0)	6 (1.05)
2	8,941	11	865	15	0.0115 (0.41)	103 (0.41)	1.2 (0.09)	123 (0.40)
3	7,813	10	866	10	0.0077 (0.49)	60 (0.49)	1.2 (0.09)	72 (0.51)
4	4,928	7	483	0	0	0	0	0
5	6,605	8	703	1	0.0009 (1.05)	6 (1.05)	1 (0)	6 (1.05)
6	5,180	7	609	0	0	0	0	0
Total	34,742	47	3664	27	0.0071 (0.38)	175 (0.38)	1.19 (0.06)	208 (0.38)

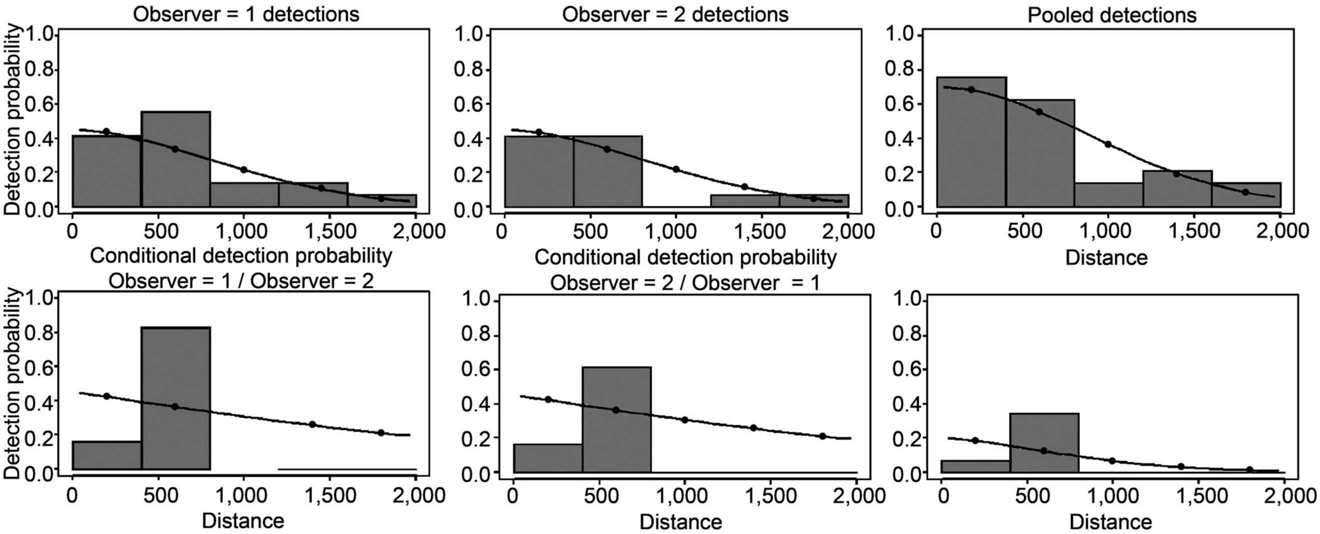

Figure 5. Scaled histograms of perpendicular distances and the predicted detection probability functions for bowhead whales with sightings fitted to a half-normal model where each observation prediction is shown as a circle. Observer 1 = front observers. Observer 2 = rear observers and distance is measured in meters from the track line directly below the aircraft.

Estimates of abundance

The probability of detecting a bowhead whale, as estimated from the MRDS model, was 0.62 (cv = 0.35) for the combined observer effort. The probability of detection for each observer was 0.38 (cv = 0.46). After truncating the data at 2,000 m, 27 sightings remained for analysis (Table 3).

To simplify the MRDS model, a half-normal detection function with no covariates other than distance was used (Fig. 5). The estimated abundance of bowhead whales, corrected for perception bias, was 208 whales (cv = 0.38, 95% CI: 99–436; Table 3). When further corrected for both perception and availability bias, the estimated abundance increased to 770 whales (cv = 0.39, 95% CI: 372–1,596).

DISCUSSION

Correction for availability significantly extrapolates the at-surface abundance estimates of whales. This study provides new data for estimating the availability correction and its variance, as well as insight into the synchrony of bowhead whale diving behaviour. Bowhead whales in West Greenland are observed in small groups, with a high degree of synchrony within groups; even groups that are geographically distant may dive synchronously (Podolskiy *et al.*, 2023). The observed bowhead whales appeared to dive in synchrony, suggesting that group availability and individual availability could be treated as equivalent. No additional adjustments were deemed necessary for the individual-based availability correction factor given the relatively long mean duration spent at the surface (138 seconds) when compared with the brief time-in-view during aerial surveys (mean = 4.5 seconds) and the pronounced coordination in diving behaviour.

In West Greenland, aerial surveys of bowhead whales are conducted in March and April. The aerial survey in 2012 estimated the abundance at 744 whales (cv = 0.34, 95% CI: 357–1,461; Rekdal *et al*., 2014). The 2012 survey was analysed with a Hidden Markov Line Transect technique (Borchers *et al*., 2013) that included both time-in-view and availability bias. The survey in 2012 was close to identical to the 2022 aerial survey that, corrected for perception and availability bias using MRDS methods, estimated an abundance of 770 whales (cv = 0.39, 95% CI: 372–1,596).

A survey in 2006 (1,229 individuals CV = 0.47, 95% CI: 495–2,939; Heide-Jørgensen *et al*., 2007) used different analysis methods as it did not include correction for the time-in-view. Accordingly, the 2006 estimate was positively biased compared with the later estimates. Rekdal *et al*. (2015) processed the 2012 data following the same analytical approach used for the 2006 estimate, generating comparable estimates. Doing so yields an abundance estimate in 2012 of 829 individuals (CV = 0.35; 95% CI: 425–1,618). This is 33% lower than the 2006 abundance estimate. The 2006 data suggested a significant increase in sighting rates of bowhead whales in West Greenland waters compared with surveys conducted before 2000 (Heide-Jørgensen et al., 2007), but further increase in sighting rates could not be detected in the 2012 and 2022 surveys.

After a rapid increase in bowhead whale abundance in the 2000s (Heide-Jørgensen *et al*., 2007), the increase appears to have levelled off after 2012. It is unclear whether the stabilisation of bowhead whale abundance in West Greenland reflects a situation where the local aggregation has reached its carrying capacity or if the entire population across Greenland and Canada is nearing its carrying capacity.

REFERENCES

Banas, N.S., Møller, E.F., Laidre, K.L., Simon, M., Ellingsen, I.H., & Nielsen, T.G. (2021). Reconciling behavioural, bioenergetic, and oceanographic views of bowhead whale predation on overwintering copepods at an Arctic hotspot (Disko Bay, Greenland). *Front. Mar. Sci.* 8: 614582. [Available at: *https://doi.org/10.3389/fmars.2021.614582*]

Biddlecombe, B.A., Ferguson, S.H., Heide-Jørgensen, M.P., Gillis, D.M., & Watt, C.A. (2023). Estimating abundance of Eastern Canada-West Greenland bowhead whales using genetic mark-recapture analyses. *Glob. Ecol. Conserv.* 45: e02524. [Available at: *https://doi.org/10.1016/j.gecco.2023.e02524*]

Borchers, D.L., Zucchini, W., Heide-Jørgensen, M.P., Cañadas, A., & Langrock, R. (2013). Using hidden Markov models to deal with availability bias on line transect surveys. *Biometrics* 69(3): 703–713. [Available at: *https://doi.org/10.1111/biom.12049*]

Buckland, S.T., Anderson, D., Burnham, K., Laake, J., Borchers, D., & Thomas, L. (2001) *Introduction to Distance Sampling Estimating Abundance of Biological Populations*. Oxford University Press.

Burnham, K. P., Anderson, D.R., White, G.C., Brownie, C., & Pollock, K.H. (1987). Design and analysis methods for fish survival experiments based on release–recapture. *American Fisheries Society* Monograph No. 5.

Christiansen, F., Tervo, O.M., Heide-Jørgensen, M.P., & Teilmann, J. (2024). Prey consumption of bowhead whales in West Greenland estimated from drone measurements of body size and condition. *Polar Biology* 47: 17–39. [Available at: *https://doi.org/10.1007/s00300-023-03207-8*]

Doniol-Valcroze, T., Gosselin, J.-F., Pike, D.G., Lawson, J.W., Asselin, N.C., Hedges, K.J., & Ferguson, S.H. (2020a). Distribution and Abundance of the Eastern Canada-West Greenland Bowhead Whale Population Based on the 2013 High Arctic Cetacean Survey. *NAMMCO Scientific Publications* 11. [Available at: *https://doi.org/10.7557/3.5315*]

Doniol-Valcroze, T., Gosselin, J.-F., Pike, D.G., Lawson, J.W., Asselin, N.C., Hedges, K., & Ferguson S.H. (2020b). Narwhal Abundance in the Eastern Canadian High Arctic in 2013. *NAMMCO Scientific Publications 11*. [Available at: *https://doi.org/10.7557/3.5100*]

Eschricht, D.F., & Reinhardt, J. (1866). Om nordhvalen (*Balaena mysticetus* L.): navnlig med Hensyn til dens Udbredning i Fortiden og Nutiden og til dens ydre og indre Saerkjender. K. *Danske Videnskabernes Selskabs Skrifter* Series 5. Naturvidensk. Math. Afdel. 5: 433–590.

Frasier, T., Petersen, S., Postma, L., Johnson, L., Heide-Jørgensen, M.P., & Ferguson, S. (2020). Abundance estimation from genetic mark-recapture data when not all sites are sampled: An example with the bowhead whale. *Conserv. Ecol*. 22: e00903. [Available at: *https://doi.org/10.1016/j.gecco. 2020.e00903*]

Givens, G.H., & Heide-Jørgensen, M.P. (2020). Abundance. In: J.C. George & J.G.M. Thewissen (eds.) *The Bowhead Whale:* Balaena mysticetus*: Biology and Human Interactions* (pp.77–86). Academic Press.

Hansen, R.G., Pike, D.G., Thorgilsson, B., Gunnlaugsson, T., & Lawson, J. (2020). The Geometer: A New Device for Recording Angles in Visual Surveys. *NAMMCO Scientific Publications* 11. [Available at: *https://doi.org/10.7557/3.5585*]

Heide-Jørgensen, M.-P., & Acquarone, M. (2002). Size and trends of the bowhead whale, beluga and narwhal stocks wintering off West Greenland. *NAMMCO Scientific Publications* 4: 191–210. [Available at: *https://doi.org/10.7557/3.2844*]

Heide-Jørgensen, M.P., & Lage, J. (2022). On the availability bias in narwhal abundance estimates. *NAMMCO Scientific Publications* 12. [Available at: *https://doi.org/10.7557/3.6518*]

Heide-Jørgensen, M.-P., Lassen, H., Teilmann, J., & Davis, R.A. (1993). An index of the relative abundance of wintering belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, off West Greenland. *Can. J. Fish. Aquat. Sci.* 50: 2323–2335.

Heide-Jørgensen, M.-P., Laidre, K.L., Wiig, Ø., Jensen, M.V., Dueck, L., Schmidt, H.C., & Hobbs, R.C. (2003). From Greenland to Canada in ten days: Tracks of bowhead whales, *Balaena mysticetus*, across Baffin Bay. *Arctic* 56: 21–31. [Available at: *https://doi.org/10.14430/arctic599*]

Heide-Jørgensen, M.-P., Laidre, K.L., Jensen, M.V., Dueck, L., & Postma, L.D. (2006). Dissolving stock discreteness with satellite tracking: bowhead whales in Baffin Bay. *Mar. Mam. Sci.* 22: 34–45. [Available at: *https://doi.org/10.1111/j.1748-7692.2006.00004.x*]

Heide-Jørgensen, M.-P., Laidre, K., Borchers, D., Samarrra, F., & Stern, H. (2007). Increasing abundance of bowhead whales in West Greenland. *Biol. Lett.* 3: 577–580. [Available at: *https://doi.org/10.1098/rsbl.2007.0310*]

Heide-Jørgensen, M.-P., Laidre, K.L., Nielsen, N.H., Hansen, R.G., & Røstad, A. (2013). Winter and spring feeding behavior of bowhead whales. *Anim. Biotelem.* 1–15. [Available at: *http://www.animalbiotelemetry.com/content/1/1/15*]

Heide-Jørgensen, M.-P., Hansen, R.G., & Shpak, O.V. (2021). Distribution, migrations, and ecology of the Atlantic and the Okhotsk Sea populations. In: J.C. George & J.G.M. Thewissen (eds). *The Bowhead Whale:* Balaena Mysticetus*: Biology and Human Interactions* (pp.57–76). Academic Press.

International Whaling Commission (IWC) (2023). Aboriginal subsistence whaling catches since 1985. [Webpage, accessed November 2025]. [Available at: *https://iwc.int/table_aboriginal*]

Laake, J.L., Calambokidis, J., Osmek, S.D., & Rugh, D.J. (1997). Probability of detecting harbour porpoise from aerial surveys: Estimating g(0). *J. Wildl.Manag.* 61(1). 63–75. [Available at: *https://doi.org/10.2307/3802415*]

Laidre, K.L., Heide-Jørgensen M.P., & Nielsen, T.G. (2007). Role of bowhead whale as a predator in West Greenland. *Mar. Ecol.Prog. Ser.* 346: 285–297. [Available at: *https://doi.org/10.3354/meps06995*]

Nielsen, N.H., Laidre, K., Larsen, R.S., & Heide-Jørgensen, M.P. (2015). Identification of potential foraging areas for bowhead whales in Baffin Bay and adjacent waters. *Arctic* 68(2): 169–179. [Available at: *https://doi.org/10.14430/arctic4488*]

Podolskiy, E.A., Teilmann, J., & Heide-Jørgensen, M.P. (2024). Synchronization of bowhead whales. *Phys. Rev. Research* 6: 033174. [Available at: *https://doi.org/10.1103/PhysRevResearch.6.033174*]

Rekdal, S.L., Hansen, R.G., Borchers, D., Bachmann, L., Laidre, K.L., Wiig, Ø., Nielsen, N.H., Fossette, S., Tervo, O., & Heide-Jørgensen, M.P. (2015). Trends in bowhead whales in West Greenland: Aerial surveys *vs*. genetic capture-recapture analyses. *Mar. Mam. Sci.* 31: 133–154. [Available at: *https://doi.org/10.1111/mms.12150*]

Richard, P.R., Laake, J.L., Hobbs, R.C., Heide-Jørgensen, M.P., Asselin, N., & Cleator, H. (2010). Baffin Bay narwhal population distribution and numbers: Aerial surveys in the Canadian High Arctic, 2002–04. *Arctic* 63: 85–99. [Available at: *https://doi.org/10.14430/arctic649*]

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques T.A., & Burnham, K.P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol*. 47(1): 5–14. [Available at: *https://doi.org/10.1111/j.1365-2664.2009.01737*.x]

Woodby, D.A., & Botkin D.B. (1993). Stock sizes prior to commercial whaling. In: J.J. Burns, J.J. Montague & C.J. Cowles (eds.) *The Bowhead Whale* (pp.387–407). Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS, USA.