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Trends in bowhead whales in West Greenland: Aerial surveys *vs.* genetic capture-recapture analyses

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ABSTRACT

We contrast two methods for estimating the trends of bowhead whales (*Balaena mysticetus*) in West Greenland: (1) double platform visual aerial survey, corrected for missed sightings and the time the whales are available at the surface; and (2) a genetic capture-recapture approach based on a 14-yr-long biopsy sampling program in Disko Bay. The aerial survey covered 39,000 km^2 and resulted in 58 sightings, yielding an abundance estimate of 744 whales (CV = 0.34, 95% CI: 357–1,461). The genetic method relied on determining sex, mitochondrial haplotypes and genotypes of nine microsatellite markers. Based on samples from a total of 427 individuals, with 11 recaptures from previous years in 2013, this resulted in an estimate of 1,538 whales (CV = 0.24, 95% CI: 827–2,249). While the aerial survey is considered a *snapshot* of the local spring aggregation in Disko Bay, the genetic approach estimates the abundance of the *source* of this aggregation. As the whales in Disko Bay primarily are adult females that do not visit the bay annually, the genetic method would presumably yield higher estimates. The studies indicate that an increase in abundance observed between 1998 and 2006 has leveled off.

Key words: Hidden Markov Models, aerial surveys, capture-recapture, Arctic, genetics, bowhead whale, *Balaena mysticetus*, Disko Bay, abundance.

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Many baleen whale populations are recovering from significant declines due to past overexploitation (Best 1993, Wade *et al.* 2012). Nevertheless, there is a need to determine the rate of recovery to gain more detailed insight into the dynamics of the populations, which in turn provides the basis for stock management. One major problem with monitoring baleen whale populations is their ocean-wide distribution and the logistical difficulties associated with conducting informative surveys covering large areas. One approach is to monitor the abundance in restricted areas that are seasonally or periodically visited by whales. Conspicuous aggregations of whales gathered for feeding, breeding or other poorly understood activities may represent a reliable source for tracking population size and structure. One such area is Disko Bay in West Greenland with its seasonal occurrence of bowhead whales (*Balaena mysticetus*).

Bowhead whales are associated with polar pack ice, and inhabit waters at latitudes between about 54°N and 85°N (Moore and Reeves 1993). The International Whaling Commission (IWC) has recognized four mainly geographically defined stocks: (1) the Okhotsk Sea stock, (2) the Bering-Chukchi-Beaufort Seas (B-C-B) stock, (3) the Eastern Canada-West Greenland stock, and (4) the Spitsbergen stock (Heide-Jørgensen *et al.* 2006, Givens *et al.* 2010, IWC 2012). The Eastern Canada-West Greenland stock is estimated to consist of at least 7,000 animals, and is, like the B-C-B stock, substantially larger than the small Okhotsk Sea and Spitsbergen stocks (Reilly *et al.* 2012).

Bowhead whales between Greenland and Canada generally show annual migration patterns following the extent of the sea ice, with northwards movements as the ice recedes during spring and summer, and southwards migration with the expansion of seasonal ice in fall (Eschricht and Reinhardt 1861, Ferguson *et al.* 2010). Heide-Jørgensen *et al.* (2010) recently reviewed the sex and age-class segregation of Eastern Canada-West Greenland bowhead whales, and related the migration pattern of the eastern North American bowhead whales to their reproductive biology. In agreement with early whaling records (Southwell 1898), they hypothesized that primarily adult males and resting and pregnant females are found in Baffin Bay, while calves, subadults, and nursing females stay in Prince Regent Inlet, Gulf of Boothia, Foxe Basin, and northwestern Hudson Bay. Finley (2001) and Ferguson *et al.* (2010) argued that the main calving areas are in the Canadian High Arctic and the shallow waters of Foxe Basin, where sheltered areas may offer a refuge for young calves, minimizing the predation risk from killer whales as well as reducing the risk of ice entrapment.

Bowhead whales aggregate in Disko Bay during winter and spring (Eschricht and Reinhardt 1861) and are mainly observed in an area of about 25,000 km^2 southwest of Disko Island (Heide-Jørgensen *et al.* 2007). Stafford *et al.* (2008) concluded that Disko Bay serves as a mating ground, which is supported by recordings of singing whales in the area (Tervo *et al.* 2009) along with observations of other sexual activity such as copulations (Eschricht and Reinhardt 1861). There are few observations of whales less than 14 m long in the area (Heide-Jørgensen *et al.* 2007), the length at which the bowhead whales are thought to be sexually mature (George *et al.* 1999). It is thus assumed that the aggregation primarily consists of adult whales. A further peculiarity of this aggregation is the skewed sex ratio, with an estimated fraction of females of 78% (Heide-Jørgensen *et al.* 2010).

After almost a century of virtual absence from Greenlandic waters, bowhead whales started to reappear in Disko Bay around year 2000 and have appeared in increasing numbers for several years (Reeves and Heide-Jørgensen 1996, Heide-Jørgensen *et al.* 2007). In 2006, the abundance of bowhead whales in Disko Bay was estimated at 1,229 individuals (CV = 0.47, 95% CI: 495–2,939) based on sightings during an aerial survey (Heide-Jørgensen *et al.* 2007). A genetic capture-recapture estimate of 1,410 individuals (CV = 0.23, 95% CI: 783–2,038) was obtained by Wiig *et al.* (2011), based on samples collected locally in Disko Bay during the period 2000–2010. The estimates provided by this genetic method apply to some unknown portion of the Eastern Canada-West Greenland stock from which the bowhead whales in Disko Bay originate.

The combination of two independent approaches for estimating the abundance of bowhead whales in West Greenland provides two different estimates that can inform management decisions. The aerial surveys allow for independent but comparable estimates of the instantaneous abundance obtained at regular intervals or as frequently as needed. The capture-recapture technique requires estimation over longer sampling and/or resampling periods to avoid dependence. Because the Disko Bay aggregation mainly consist of adult females without calves, it is likely that the individual whales do not visit the bay annually (Heide-Jørgensen *et al.* 2010). Thus, the genetic approach provides a better representation of the fraction of the population that supplies the local spring aggregation of bowhead whales in Disko Bay over multiple years, while the aerial survey estimates the number of whales present in the surveyed area during the study.

The objectives of this study were to assess if the previously recorded increase in abundance in Disko Bay has been continued and to compare the applicability of two methods to estimate the abundance of bowhead whales in the area: (1) an aerial survey conducted along the west coast of Greenland in March–April 2012 and (2) an extended genetic capture-recapture approach utilizing data collected annually in Disko Bay between 2000 and 2013.

Materials and Methods

Aerial Survey

Visual aerial line-transect surveys of bowhead whales were conducted in coastal and offshore areas in West Greenland between 65°40′N and 75°30′N, in order to largely cover the area of the local spring aggregation in Disko Bay. The targeted region spanned an area of 242,650 km^2 and was divided into 16 strata based on previous information on expected densities of bowhead whales. In total, 7,836.5 km of east-west oriented systematically placed transect lines were searched between 24 March and 14 April 2012 (Fig. 1). The targeted altitude and speed was 213 m (700 ft) and 167 km/h (90 kn), respectively.

The aerial survey was conducted with two observation platforms on the survey plane, a DeHavilland Twin Otter equipped with four bubble windows. One participant was seated on each side in the front of the plane ("observer position 1") and operated independently of two other participants seated likewise in the rear ("observer position 2"). The Beaufort Sea State Code was used for assessing the survey conditions. The respective values were recorded at the start of each transect line and when conditions changed. Transects were only flown at Beaufort Sea States of 2 or less.

The time of first sighting as well as the time when the sighting passed abeam was recorded independently by the two observer positions. In addition, declination angle to each sighting of each group of bowhead whales as it came abeam was measured using inclinometers (Suunto). Decisions about duplicate detections, *i.e.*, animals recorded by both observer position 1 and 2, were made after completions of the surveys on the basis of coinciding time and location of the sightings. If declination angles or group size for duplicate sightings differed between the observer positions,

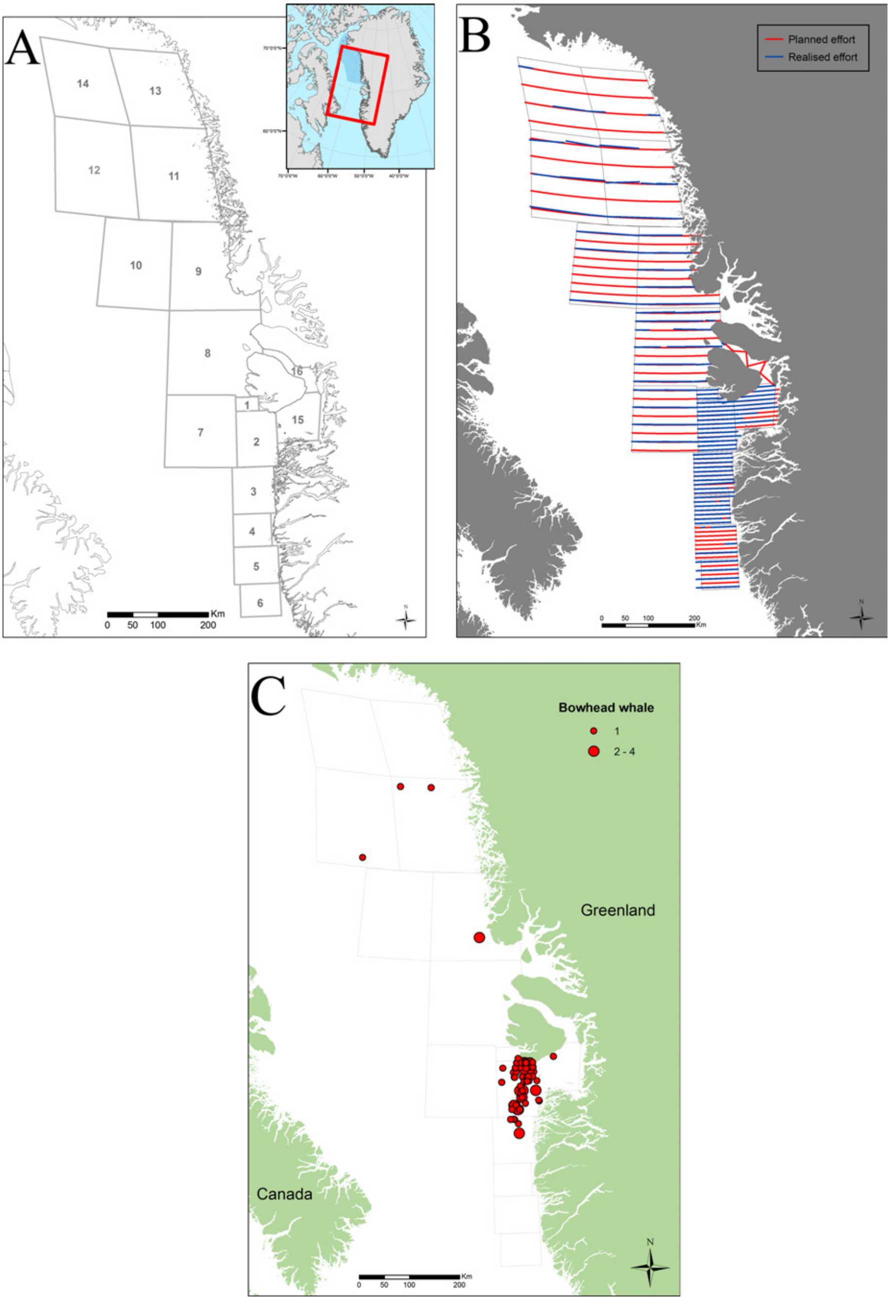

Figure 1. Stratification (A), planned transects (red) and realized transect lines (blue) in sea state <2 (B) and on-effort sightings of groups of bowhead whales (including uncertain and sightings with missing angle measurements; C) in West Greenland during aerial surveys in March–April 2012.

the mean values were used for downstream data analyses. Observations of mating behavior were registered whenever detected, and photographic documentation of whales involved in social activities was conducted by circling above.

Declination angles (ψ) measured when animals were abeam were converted to perpendicular distances (x) using the following equation from Buckland *et al.* (2001):

$$x = v \times \tan(90 - \psi)$$

where v is the altitude of the airplane. Forward distance (y) to each sighting was calculated based on time of first sighting, time when passing abeam and speed of aircraft.

The approach of Borchers *et al.* (2013) was used to estimate whale density and abundance. This involves first estimating the parameters of a hidden Markov model (HMM) for whale availability, using time-depth recorder data (see Heide-Jørgensen *et al.* 2007, Laidre *et al.* 2007, Borchers *et al.* 2013), and then integrating these HMMs with the aerial survey line transect data, using both perpendicular and forward distances to detected whales to estimate detection probability (see Borchers *et al.* 2013 for details).

Modeling whale availability—Eight separate HMMs were fitted to the individual time series of binary observations from eight whales instrumented with time-depth recorders. The R library HiddenMarkov Version 1.7.0 (Harte 2012) was used to fit the HMMs to the availability data after converting depths recorded every second to binary observations. For this purpose, whales at <2 m depth were considered available for observation (binary observation = 1), while unavailable when deeper than 2 m (binary observation = 0).

Hidden Markov models have two basic components: hidden states and observations whose probability density functions depend on the hidden states. The hidden states are notional and do not necessarily correspond to any real behavioral states. Nevertheless, in the case of HMMs for whale availability, the hidden states can conveniently be considered behavioral states, and are referred to as such in the Results section. The HMMs for availability are modeled using a two-state Markov model for the time series of states, and Bernoulli random variables with the parameters Pr(avail|state 1) and Pr(avail|state 2) for availability given the hidden states.

Detection probability estimation—Detection function parameters were estimated while accommodating individual availability random effects by maximizing a likelihood equation (eq. 5 of Borchers *et al.* 2013), conditional on the fitted HMMs for animal availability. In addition to perpendicular distance (x) and forward distance (y) for each detected group of whales, the Beaufort Sea State (bf) and group size (s) were available as explanatory variables for the detection process model. These variables were incorporated by allowing the x (perpendicular distance) and/or y (forward distance) scale parameters of the detection hazard function models (σ_x and σ_y) to depend on the covariates bf and/or s. For brevity, we refer to any covariates used in the hazard model as z, or z_x and z_y if different covariates were used for the x and the y scale parameters.

The following four forms of detection hazard function model, $h(x,y,z)$, were considered:

$$h(x, y, z) = \left(\frac{\sigma(z)}{\sqrt{\sigma(z) + x^2 + y^2}} \right)^{\gamma} \qquad \text{(Model IP)}$$

$$h(x, y, z) = \exp\left\{-\left(\frac{x}{\sigma(z)}\right)^{\gamma} - \left(\frac{y}{\sigma(z)}\right)^{\gamma}\right\} \qquad \text{(Model EP1)}$$

$$h(x, y, z) = \exp\left\{-\left(\frac{x}{\sigma(z)}\right)^{\gamma_x} - \left(\frac{y}{\sigma(z)}\right)^{\gamma_y}\right\} \qquad \text{(Model EP2)}$$

$$h(x, y, z) = \exp\left\{-\left(\frac{x}{\sigma_x(z)}\right)^{\gamma_x} - \left(\frac{y}{\sigma_y(z)}\right)^{\gamma_y}\right\} \qquad \text{(Model EP2x)}$$

The best model form among these was chosen on the basis of Akaike information criterion (AIC) after fitting each model with no covariates. The chosen model form was then fitted using each possible combination of covariates and the best among these was selected on the basis of AIC. The estimated parameters from this model were used to estimate detection probability, $p(x,z)$, which, from Equation (1) and the subsequent expression for $p(x)$ in Borchers *et al.* (2013), is as follows:

$$p(x, z) = 1 - \underline{\tau}\left[\prod_{t=1}^{T} \Gamma \begin{pmatrix} 1 - h(x, y_t, z) & 0 \\ 0 & 1 \end{pmatrix}\right] \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

where Γ is the 2×2 transition probability matrix governing the Markov availability process, $\underline{\tau}$ is a row vector giving the stationary distribution of this process (the average proportion of time spent available and unavailable), t indexes the T time intervals during which an animal at x is within detectable range and y_t is the forward distance of the animal at the midpoint of time interval t.

Density, abundance and mean group size estimation—Group abundance and animal abundance in each stratum with bowhead whale observation were estimated using the following Horvitz-Thompson-like estimators

$$\hat{N}_g = \frac{A}{a} \sum_{i=1}^{n} \frac{1}{\int_0^W \hat{p}_i(x, z_i) \frac{1}{W} dx}$$

and

$$\hat{N} = \frac{A}{a} \sum_{i=1}^{n} \frac{s_i}{\int_0^W \hat{p}_i(x, z_i) \frac{1}{W} dx}$$

where W is the perpendicular truncation distance, A is the stratum area, a is the covered area ($\alpha = 2WL$, where L is total transect length), s_i is the group size of the ith detected group, n is the total number of detections in the stratum and $\hat{p}_i(x, z_i)$ is the estimated detection probability of group i, with covariates z_i, evaluated at perpendicular distance x. Mean group size in each stratum was estimated by $\hat{E}[s] = \hat{N}_g/\hat{N}$. Group and animal density estimates ($\hat{D}_g$ and $\hat{D}$) were obtained by dividing respectively $\hat{N}_g$ and $\hat{N}$ by stratum area, A.

Variance and confidence interval estimation—Variances and 95% confidence intervals of density, abundance, mean group size and related parameters were estimated using a two-stage bootstrap procedure, in which each bootstrap iteration was as follows:

Stage 1: Resample parametrically from the eight fitted HMMs, generating new availability observations of length equal to the original availability time series; refit HMMs to each of these resampled availability observation time series.

Stage 2: Resample transects with replacement within each stratum, together with the sightings made on the resampled transects. Re-estimate detection hazard function parameters by maximizing the likelihood equation, conditional on the new fitted HMMs for animal availability; re-estimate group abundance, animal abundance, mean group size and related parameters, as described above.

A total of 999 bootstrap iterations were done. Variances were estimated by the variance of the 999 estimates of each of the quantities of interest. Confidence intervals were obtained from these 999 estimates using the percentile method.

Genetic Capture-recapture Approach

The genetic approach followed the methodology described by Wiig *et al.* (2011). The previously used data set (2000–2010) was extended with three further sampling years (2011–2013) and genotypes for three additional microsatellite loci.

Sampling and laboratory work—Skin biopsies were collected by crossbows equipped with biopsy darts (Palsbøll *et al.* 1991), from free-ranging bowhead whales in Disko Bay, close to Qeqertarsuaq, West Greenland. The sampling was carried out annually between year 2000 and 2013, mainly during March–May. All biopsies were stored in saturated sodium chloride and 20% dimethyl sulfoxide (DMSO), and kept at −20°C (Amos and Hoelzel 1991).

Extraction of total genomic DNA followed the Tissue DNA Spin Protocol of the E.Z.N.A. Tissue DNA Kit (Omega Bio-Tek Inc.) or other commercially available DNA extraction kits (Qiagen Dneasy Blood & Tissue Kit or Sigma-Aldrich GenElute).

Molecular sex determination was accomplished by amplifying parts of the ZFY/ZFX genes, which are located on the Y- and the X-chromosomes, respectively (Schneider-Gädicke *et al.* 1989). These X- and Y-chromosomal fragments have approximately the same length, but specific restriction patterns allow for sex differentiation through restriction digestion and subsequent separation of the restriction fragments by standard agarose gel electrophoresis (Palsbøll *et al.* 1992, Bérubé and Palsbøll 1996). Using the primers *ZFYX0582* and *ZFYX1204* (Table S1), 540 base pairs of the last exon of the ZFX/ZFY gene were amplified, and the obtained PCR products were digested with the restriction endonuclease *Oli*I (or the isoschizomer *Ale*I, PureExtreme [Fermentas]).

A 453 base pair fragment of the mitochondrial D-loop region (position 15,473–15,925) in the complete mitochondrial genome of the bowhead whale (Arnason *et al.* 1993; GenBank Accession no. AP006472, Sasaki *et al.* 2005), was amplified and sequenced for each sample (Table S1). The sequences were edited and aligned using the software BioEdit Sequence Alignment Editor v7.0.5.3 (Hall 1999) and MEGA v5.05 (Tamura *et al.* 2011). Haplotype frequencies and molecular diversity indices were computed using Arlequin v3.5.1.2 (see Excoffier and Lischer 2010 and references therein).

The samples were genotyped for nine microsatellite loci (Huebinger *et al.* 2008; Table S1). One of the locus specific primers was labeled fluorescently, in order to allow for allele detection using an ABI 3130 capillary sequencer. Allele calling was done using GeneMapper v4.0 (Applied Biosystems). In order to detect evidence of stutter or other sources of scoring errors (*i.e.*, large allele dropout and null alleles), the data set was analyzed with Micro-Checker v2.2.3 (van Oosterhout *et al.* 2004). GENEPOP v4.2 (Raymond and Rousset 1995, Rousset 2008) was used to execute the Hardy-Weinberg exact test and to test for linkage disequilibrium among the microsatellite loci.

Identification of recaptures—The probability of identity ($P_{(ID)}$; the probability that two individuals drawn at random will have the same genotype; Paetkau and Strobeck 1994) and the probability of identity among siblings ($P_{(ID)sibs}$; the probability that two full siblings will have the same genotype by chance; Waits *et al.* 2001) were calculated using GenAlEx v6.5b3 (Peakall and Smouse 2006, 2012), in order to determine the number of loci required for identification of individuals. Recaptures were initially identified manually utilizing the sort function in Excel (Microsoft). The sorting was conducted several times based on different criteria, such as mitochondrial haplotype or the most polymorphic microsatellite loci.

For automated identification of recaptures, CERVUS v3.0.3 (Kalinowski *et al.* 2007) was used to identify matching microsatellite genotypes within samples displaying the same sex. In these comparisons of pairs of genotypes, mismatches at up to three loci were allowed, in order to prevent overlooking recaptures due to genotyping errors and/or allelic drop out (Waits and Leberg 2000). Initial recaptures were compared by sex, microsatellite genotypes, and mitochondrial haplotypes to systematically determine the true recaptures.

Population size estimation—The size of the fraction of the bowhead whale population that supplies the Disko Bay aggregation with individuals was estimated for each year from 2009 to 2013 using the Chapman estimator (Chapman 1951, Chao and Huggins 2005, Wiig *et al.* 2011):

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

where n_1 is the number of unique individuals sampled in the years from 2000 to the year before the year of interest, n_2 is the number of individual whales sampled in the year of interest and m_2 is the number of recaptures in the year of interest, *i.e.*, the number of unique individuals first sampled in the period 2000 to the year before the year of interest, and subsequently resampled in the year of interest.

Population size estimations were restricted to the years with $n_1 > 150$, permitting estimates for the years 2009–2013. This was calculated for both sexes combined and for the females separately. The variance and 95% confidence intervals (95% CI) were computed as described in Wiig *et al.* (2011).

Results

Aerial Survey

The effort was less than originally planned due to unfavorable weather conditions with Beaufort Sea States >2 and horizontal visibility <1 km. A total of 60 groups of a total of 74 bowhead whales were sighted; most were from strata 2 and 3 in the southwestern entrance to Disko Bay with only a few sightings further north

Table 1. Estimated parameters of the availability hidden Markov models for each of eight bowhead whales tagged by satellite transmitters (see Heide-Jørgensen *et al.* 2007). %avail and %unavail are the long-run percentages of the time animals are available and unavailable; Pr (avail|state1) and Pr(avail|state2) are the probabilities that animals are available given that they are in hidden behavioral states 1 and 2; E[time avail] and E[time unavail] are the mean times in seconds that animals are available and unavailable in a single dive cycle.

	Whale							
Parameter	1	2	3	4	5	6	7	8
%unavail	78	77	86	80	59	77	75	53
%avail	22	23	14	20	41	23	25	47
Pr(avail|state1)	5.8e–4	4.6e–4	8.0e–5	3.0e–8	1.2e–2	5.1e–4	1.9e–4	1.6e–3
Pr(avail|state2)	0.9942	0.9965	0.9906	0.9801	0.9801	0.9958	0.9996	0.9930
E[time unavail]	269	290	213	145	31	175	414	52
E[time avail]	65	80	33	37	21	54	123	48

(Fig. 1, S1). Five additional sightings were excluded from further analyses due to observations not being confirmed by the other observers (n = 2) or missing declination angles and associated perpendicular distances (n = 3). The percentage of time the whales were available for detection varied between 14% and 47% and the mean times that animals are available in a single dive cycle varied between 21 s and 123 s (Table 1).

The maximum perpendicular distance considered (W) was set to 2,500 m for density and abundance estimation. The perpendicular distance distribution of detections showed a slight reduction in detection frequency close to the transect line, suggesting a somewhat obscured view close to the transect line. Detections were therefore left-truncated at 100 m. The left-truncation resulted in two further detections being discarded from the analyses. The final data set thus comprised 58 sightings, and all remaining perpendicular and forward distances were used in estimation of detection functions. The majority of sightings were of single animals (n = 46), but nine sightings had a group size of two whales and three sightings were of three or four whales.

Detection hazard model form EP2x was chosen on the basis of AIC. This form allows different shape parameters (γ_x and γ_y) in the perpendicular (x) and forward (y) distance dimensions, as well as different scale parameters in each of these dimensions, with dependence of scale parameters on possibly different sets of covariates ($\sigma_x(z_x)$ and $\sigma_y(z_y)$, where z_x and z_y are the covariates affecting the perpendicular distance and forward distance scale parameters, respectively). Table 2 shows the AIC differences for each fitted EP2x model, together with Kolmogorov-Smirnov (KS) goodness-of-fit test P-values for the perpendicular and forward distance distributions of detections. (see Borchers *et al.* 2013 for details).

The best model was found to be model EP2x with the scale parameter in the forward direction depending on group size (Table 2). Fits of this model to the data are shown in Figure 2. Total bowhead whale abundance was estimated to be 744 animals (CV = 0.34, 95% CI: 357–1,461; Table 3). Standard error, CV and confidence interval estimates of density, abundance, and group size estimates in each stratum are given in Table S3.

Table 2. AIC differences: AIC differences (ΔAIC=difference between AIC for given model and lowest AIC across models) for fits of detection hazard model with various covariate combinations for the perpendicular distance scale parameter ("x-covariate") and forward distance scale parameter ("y-covariate") from an aerial survey of bowhead whales in West Greenland. Covariates are Beaufort sea state (*bf*) and group size (*s*) as well as their interaction. Also shown are Kolmogarov-Smirnov goodness-of-fit statistic *P*-values: "KS (x) *P*-value" for perpendicular distance fit, "KS (y) *P*-value" for forward distance fit. For the models with ΔAIC < 2, point estimates are given in the column "$\hat{N}$" followed by %CV and lower and upper 95% confidence bounds from percentile method with 200 bootstrap replicates.

x-covariate model	y-covariate model	ΔAIC	KS(x) P-value	KS(y) P-value	$\hat{N}$	%CV	Lower 95% CI	Upper 95% CI
–	*s*	0.00	0.992	0.368	744	34	357	1,461
s	*s*	0.27	0.943	0.404	746	37	369	1,363
–	*s+bf*	1.24	0.992	0.435	735	31	328	1,251
–	–	1.28	0.965	0.228	758	34	377	1,371
s	*s+bf*	1.40	0.961	0.497	661	35	331	1,424
bf	*s*	1.65	0.986	0.380	739	27	434	1,211
–	*bf*	1.93	0.971	0.270	744	30	328	1,374
bf	*s+bf*	2.35	0.971	0.412				
s+bf	*s*	2.54	0.947	0.428				
bf	*bf*	2.97	0.913	0.270				
bf	–	3.10	0.976	0.210				
s	–	3.22	0.993	0.245				
s+bf	*s+bf*	3.34	0.668	0.466				
s	*bf*	4.05	0.980	0.340				
s+bf	*bf*	4.37	0.869	0.326				
s+bf	–	4.79	0.974	0.235				

Genetic Capture-recapture Approach

A total of 648 samples obtained from free-ranging bowhead whales in Disko Bay (Fig. S1) were included in the analyses. All were sexed and genotyped using mitochondrial control region sequences and microsatellite data. The error rates were assumed to be similar to those given by Wiig *et al.* (2011; molecular sexing: <0.5%, mitochondrial sequencing: <2%, microsatellite genotyping: ~1%).

Fifty-two distinct mitochondrial haplotypes were recognized, of which 15 were found in one individual only. In the samples collected in 2011–2013, seven haplotypes were detected that were not reported by Wiig *et al.* (2011). The haplotype diversity (h) and nucleotide diversity (π) over all sampling years were computed as 0.9231 ± 0.0073 and 0.0122 ± 0.0065, respectively.

Genotypes at nine microsatellite loci were determined for all bowhead whale individuals. There was no evidence of stutter related problems in allele calling, large allele dropout, or null alleles. However, loci Bmy33 and Bmy58 were not in Hardy Weinberg equilibrium, and multiple-locus pairs were in linkage disequilibrium (Table S2).

Recaptures—For the microsatellite loci, $P_{(ID)}$ ranged between 0.0066 (Bmy29) and 0.1091 (Bmy16), yielding a probability of identity between two individuals of <0.01 when combining any two loci. A more conservative estimate was given by $P_{(ID)sibs}$, where the corresponding locus-specific probabilities of identity between siblings ranged from 0.2812 (Bmy29) to 0.4083 (Bmy16), requiring at least five loci to achieve a

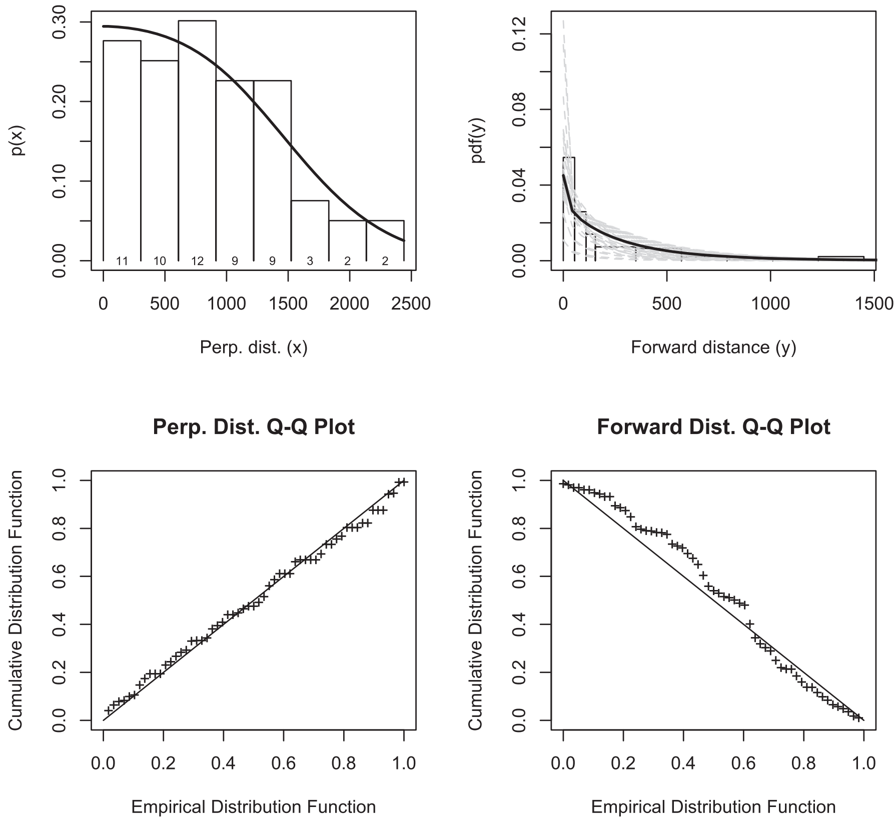

Figure 2. Detection functions superimposed on detection frequencies and Q-Q-plots. Top left: Fitted perpendicular detection function superimposed on histogram of detection frequencies (shown at the base of each histogram bar). Top right: Fitted forward distance detection function superimposed on histogram of detection frequencies; gray lines are detection functions for each observed perpendicular distance; black line is the average of the gray lines. Bottom left: Q-Q plot of perpendicular distances. Bottom right: Q-Q plot of forward distances (shown with increasing x-axis value corresponding to increasing forward distance).

Table 3. Density, abundance and related estimates of bowhead whales in Disko Bay, obtained through an aerial survey. Number of sightings is n; L is effort (in km); a is covered area (km^2), A is stratum area (km^2), $\hat{D}_g$ and $\hat{D}$ are estimated group and animal density (numbers per 100 km^2), $\hat{N}_g$ and $\hat{N}$ are estimated group and animal abundance; $\hat{E}[s]$ is estimated mean group size.

Stratum	n	L	a	A	$\hat{D}_g$	$\hat{N}_g$	$\hat{E}[s]$	$\hat{D}$	$\hat{N}$
2	50	1,481.4	7,407.0	8,941	3.810	340	1.34	5.110	457
3	4	977.6	4,888.0	7,813	0.447	35	1.00	0.447	35
9	1	618.7	3,093.3	22,461	0.195	44	2.00	0.391	88
11	1	408.1	2,040.4	29,437	0.268	79	1.00	0.268	79
12	1	467.0	2,334.9	29,466	0.234	69	1.00	0.234	69
15	1	493.3	2,466.6	7,142	0.222	16	1.00	0.222	16
All	58	4,446.1	22,230.3	105,260	0.554	583	1.28	0.707	744

probability of identity <0.01. When comparing the sex, mitochondrial haplotype and microsatellite genotype of the samples, 164 of the 648 samples were considered within-year recaptures and were excluded from further analyses. In addition, there were 59 between-year recaptures; of which one male and one female were captured in three different years (see Table 4). Thus, 427 unique individuals were recognized, of which 337 (79%) were females.

Population size estimate—The 2013 capture-recapture abundance estimate of the source of the Disko Bay aggregation was 1,538 bowhead whales (CV = 0.24, 95% CI: 827–2,249), with a corresponding estimate of 1,212 females (CV = 0.27, 95% CI: 574–1,851). The respective estimates for the years 2009–2012 were similar to that obtained for 2013, and are summarized in Table 4 and illustrated in Figure 3.

There is no indication that bowhead whale stocks deviate from a 1:1 sex ratio (Nerini *et al.* 1984, Heide-Jørgensen *et al.* 2010). If it is assumed that all mature females in the stock visit Disko Bay as part of their reproductive cycle, the female source population size estimate can be used for an approximation of the total stock size. Using the calculated percent of mature bowhead whales of 39% at a population growth rate of 0.03 as obtained by Taylor *et al.* (2007), the population size of the Eastern Canada-West Greenland population in 2013 can accordingly be approximated as $(1,212 + 1,212)/0.39 = 6,215$.

Discussion

There are only few cases where both line transect and capture-recapture techniques for estimating abundance of large whales have been conducted on the same aggregation of whales. Although ocean-wide studies of humpback whales (*Megaptera novaeangliae*) have been conducted using both genetic and photographic capture-recapture techniques (*e.g.*, Palsbøll *et al.* 1997, Smith *et al.* 1999) comparisons between sighting survey and capture-recapture estimates have only been reported on smaller regional scales (*e.g.*, Calambokidis and Barlow 2004). Calambokidis and Barlow (2004) highlighted that capture-recapture techniques estimate the population regardless if all individuals are present within the study area at a particular moment, while line transect methodology estimates the density and abundance of the animals present in the given area at the time of the study. Given that not all bowhead whales visit Disko Bay annually, the genetic capture-recapture approach in the present study estimates the size of the fraction of the total population that supplies this local spring aggregation with whales. In contrast, the aerial survey provides an instantaneous abundance estimate of the aggregation itself. Therefore, the estimates from the two methods give different kinds of information and are not directly comparable.

Aerial Survey

The 2012 aerial survey of bowhead whales along the coast of West Greenland indicated that most individuals were found within a relatively restricted area southwest of Disko Island (strata 2 and 3 of the survey scheme). This survey largely covered the same areas covered in earlier surveys in 1981 and 2006 (Heide-Jørgensen *et al.* 2007) and is the core area used by bowhead whales in spring as determined by satellite telemetry (Heide-Jørgensen *et al.* 2003, Laidre and Heide-Jørgensen 2012). For the 2012 survey the combined sighting rate for strata 1 and 2 was 0.023 (CV = 0.31), which is similar to the estimate of 0.023 in 2006 for the same area.

Table 4. The number of free-ranging male and female bowhead whales sampled each year in Disko Bay, West Greenland, from year 2000 to 2013. Within-year recaptures are removed, while the number of male (M) and female (F) between-year recaptures are given with the year the individuals were first sampled in parentheses. The pertaining abundance estimates for the part of the population that supplies the Disko Bay spring aggregation with individuals are listed to the right.

Year	Males	Females	Recaptures between years		Abundance estimate
2000	5	2	0		
2001	5	7	0		
2002	4	6	0		
2003	0	10	0		
2004	0	1	0		
2005	6	17	1F (2001)		
2006	0	20	0		
2007	17	73	1M(2000) 1F(2005)	One male recaptured twice (captured 2000, 2007, 2011)	
2008	10	37	1F(2007)		
2009	18	31	1M(2008) 1F(2001) 1F(2007) 2F(2008)	One female recaptured twice (captured 2008, 2009, 2013)	Both sexes: 1,087 (CV = 0.35, 95% CI: 568–3,047) Females: 1,093 (CV = 0.37, 95% CI: 301–1,886)
2010	11	74	1M(2001) 1F(2001) 1F(2002) 1F(2003) 2F(2005) 3F(2006) 5F(2007) 4F(2009)		Both sexes: 1,180 (CV = 0.19, 95% CI: 740–1,620) Females: 824 (CV = 0.19, 95% CI: 516–1,132)
2011	7	38	1M(2000) 2M(2007) 2F(2003) 3F(2007) 1F(2010)	One male recaptured twice (captured 2000, 2007, 2011)	Both sexes: 1,675 (CV = 0.28, 95% CI: 756–2,594) Females: 1,420 (CV = 0.32, 95% CI: 540–2,299)

(Continued)

Table 4. (*Continued*)

Year	Males	Females	Recaptures between years		Abundance estimate
2012	6	33	1M(2000) 2M(2008) 1F(2003) 1F(2005) 5F(2007) 1F(2010)		Both sexes: 1,216 (CV = 0.23, 95% CI: 671–-1,760) Females: 1,083 (CV = 0.27, 95% CI: 516–1,650)
2013	12	34	1M(2002) 2M(2007) 1F(2005) 1F(2008) 3F(2009) 1F(2010) 3F(2012)	One female recaptured twice (captured 2008, 2009, 2013)	Both sexes: 1,538 (CV = 0.24, 95% CI: 827–2,249) Females: 1,212 (CV = 0.27, 95% CI: 574–1,851)
Total	101	383	59		

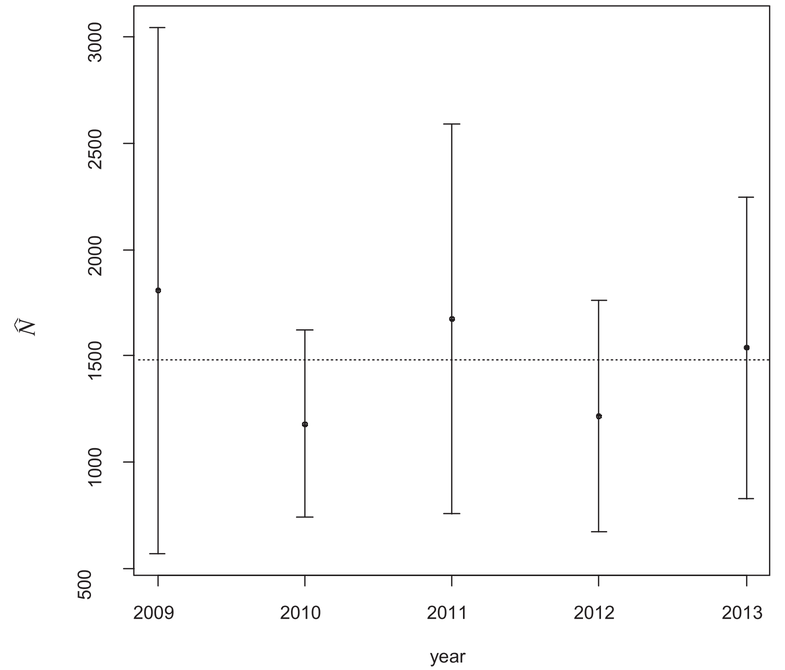

Figure 3. Population size of the source of the Disko Bay bowhead whale aggregation ($\hat{N}$), estimated for both sexes in each sampling year in the period 2009–2013 by a genetic capture-recapture approach, with 95% confidence intervals. Dotted line is mean value over these years.

However, the 2006 (1,229 individuals CV = 0.47, 95% CI: 495–2,939; Heide-Jørgensen *et al.* 2007) and the 2012 (744 individuals; CV = 0.34, 95% CI: 357–1,461) abundance estimates rely on slightly different analysis methods. The 2012 estimate was corrected for both the time animals are available to be detected and the time the whales are in view of the observers, whereas the 2006 survey was not corrected for the latter. Accordingly, the 2006 estimate was positively biased as compared to the 2012 estimate. The 2012 data can, however, be processed 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, and the range of the 2012 estimate is largely within the confidence interval of the 2006 estimate. The 2006 data suggested a significant increase in sighting rates of bowhead whales in West Greenlandic waters as compared to surveys conducted before year 2000 (Heide-Jørgensen *et al.* 2007), but further increase in sighting rates could not be detected in the 2012 survey.

Genetic Capture-recapture Approach

The genetic capture-recapture approach was used earlier for the Disko Bay spring aggregation in 2010 by Wiig *et al.* (2011), who estimated the source population size as 1,410 bowhead whales (CV = 0.23, 95% CI: 783–2,038) and 999 (CV = 0.23, 95% CI: 546–1,452) when analyzing the females only. As the confidence ranges of these estimates are largely overlapping with the estimates obtained in this study, we have not detected any change in source population size during the period 2009–2013 based on the genetic capture-recapture result alone (Table 4). This was not statistically tested due to possible dependence between the estimates (Fig. 3).

One of the major assumptions of the Chapman capture-recapture method is a closed population, *i.e.*, that the effects of mortality, recruitment and migration are insignificant, and that N thus remains constant over the sampling period (Seber 1973). The longevity of bowhead whales of over 100 yr (George *et al.* 1999) makes an impact of mortality effects on the estimated size of the source population likely to be negligible, and as long as the marked and unmarked individuals have the same average probability of surviving until the second sampling occasion, the population size estimate is unaffected (Seber 1973). Earlier sighting rates of bowhead whales in the area indicated an increasing population (Heide-Jørgensen *et al.* 2007), and accordingly, N cannot be considered constant. In an increasing source population the proportion of marked individuals at the time of the second sampling will be lowered. Even though the initial population size thus would be overestimated, $\hat{N}$ will be applicable to the stock at the time of the second sampling (Seber 1973). However, there might be a significant effect of migration, as discussed below.

A further assumption of the capture-recapture analysis is that all individuals have the same probability of being sampled and resampled. As the resampling was conducted in one year only, a possible multi-year cyclical pattern linked to female reproductive biology, in which the females may not visit the bay annually (Heide-Jørgensen *et al.* 2010, Wiig *et al.* 2011), must be considered. The analysis can be modified to overcome this bias to include the females' cyclic returns, *i.e.*, letting the resampling interval cover four years, while excluding within-period recaptures. Using the years between 2000 and 2009 as the initial sampling period and treating the sampling years of 2010–2013 as the resampling period, a similar yet more precise abundance estimate was obtained (for both sexes: 1,274 (CV = 0.12, 95% CI: 967–1,581), for females only: 1,012 (CV = 0.14, 95% CI: 738–1,286)). This approach maintains large sample sizes (>150) for both sampling and resampling. These estimates are within the range of the 2013 genetic abundance estimates, and the consistency of the results may indicate that the estimates of the population size of the source of the Disko Bay aggregation are reliable.

Temporal Changes in the Disko Bay Bowhead Aggregation

While the aerial surveys offer a temporary *snapshot* of the local spring aggregation in West Greenland, the genetic capture-recapture approach relates to the size of the *source* population based on a 14 yr sampling period. If not all individuals of the source population visit Disko Bay annually, the genetic estimate of the source population is expected to be higher than the aerial survey abundance estimate, which is valid only for the surveyed area in a single year. This fits well with our findings; the genetic capture-recapture estimate ($\hat{N}$ = 1,538) was about two-fold of the aerial survey estimate ($\hat{N}$ = 744).

Both approaches, however, provide information on only a fraction of the entire stock in the waters between eastern Canada and West Greenland. Calves are rarely seen in Disko Bay. The first confirmed observation of a bowhead whale calf in Disko Bay since the 1840s (Eschricht and Reinhardt 1861) occurred in Disko Bay on 20 April 2012 during the aerial survey. Given the absence of calves and a strongly skewed sex ratio, the aggregation presumably consists primarily of pregnant or postlactating females (Heide-Jørgensen *et al.* 2007). Applying the sex ratio to the aerial abundance estimate (744 × 0.789), we roughly estimated 590 of the whales in the 2012 Disko Bay spring aggregation were females. This corresponds to ~50% of the adult female part of the source population, based on the genetic abundance estimate (1,212 females (CV = 0.27, 95% CI: 574–1,851)). If the occurrence in the bay is tied to the reproductive cycle of the females, cyclic returns of the females may be expected (Heide-Jørgensen *et al.* 2010, Wiig *et al.* 2011). Assuming a 3 or 4 yr reproductive cycle (Koski *et al.* 1993), this pattern may arise if adult female bowhead whales visit the bay in resting and gestation years, while giving birth and spending the lactation period elsewhere. Some of the mature females in the area are indeed reproductively active as newly pregnant females and a near-term pregnancy were found among the animals taken during the subsistence hunt in Disko Bay since 2009 (Heide-Jørgensen *et al.* 2012*a*). During the aerial survey in March–April 2012, six possible mating events with three or more closely interacting whales were observed (Fig. S1). Because Disko Bay is a region of high productivity (Laidre *et al.* 2007), it is likely that the area is used both as a mating and as a feeding ground (Heide-Jørgensen *et al.* 2010).

It is generally accepted that commercial whaling prior to 1815 greatly reduced the bowhead whale stock, and that termination of industrial whaling enabled restoration of prewhaling stock sizes (Zeh *et al.* 1993, Finley 2001). Even though ecosystem shifts could pose limitations on the exploited bowhead whale stocks and may lead to a time lag in the recovery (Hacquebord 1999, Clapham *et al.* 2008), the estimated population size implies that the stock has expanded from the assumed low abundance in the 20th century. The abundance estimates obtained since year 2000 are in sharp contrast to those obtained in earlier attempts to estimate abundance of bowhead whales in West Greenland. Reeves *et al.* (1983) and Zeh *et al.* (1993) indicated that the former Baffin Bay-Davis Strait stock consisted of only "a few hundred" whales. However, we now assume that bowhead whales in eastern Canada and West Greenland belong to one stock, with an estimate of over 7,000 whales (Reilly *et al*. 2012). The predicted population growth rates for the species (*i.e.*, 3.4%; George *et al.* 2004) are too low to explain the increase observed in Disko Bay at the turn of this century, which may also be caused by immigration. A persistent retreat of sea ice could facilitate an influx of individuals to Disko Bay from the expanding B-C-B stock through the opening of the Northwest Passage (George *et al.* 2004, Heide-Jørgensen *et al.* 2012*b*). Whether site-fidelity (Reeves *et al.* 1983; Finley 1990, 2001) or a "cultural memory" (see Clapham *et al.* 2008) could prevent such movements is not known, but improved access to Arctic straits would likely lead to increased migration between the stocks.

Because all estimates of population size are based on geographically restricted sampling, they are sensitive to changes in migration patterns of the stock. Reduced sea ice and thus extended access to coastal foraging areas and changes in the primary production could be alternative reasons for the increased sightings of bowhead whales in certain areas since the turn of this century (Heide-Jørgensen *et al.* 2007). Plasticity in the migration of bowhead whales (Heide-Jørgensen *et al.* 2006) may thus be responsible for the sudden increase in abundance in Disko Bay.

The result of the capture-recapture study compared to the stock size in 2002–2004 (*i.e.*, over 7,000 bowhead whales (Reilly *et al.* 2012)) indicates that the size of the Eastern Canada-West Greenland stock of bowhead whales has been high during the whole period 2002–2013. The latest estimate from the aerial surveys in West Greenland indicates that the abundance of bowhead whales has stabilized in Disko Bay after the dramatic increase in numbers documented in the early 2000s (Heide-Jørgensen *et al.* 2007). The cause for the sudden appearance of large numbers of bowhead whales by the turn of the century remains unknown. One reason may be the availability of prey. Laidre *et al.* (2007) concluded that the total biomass of zooplankton in the upper 50 m of the water column in Disko Bay theoretically could support the predation level of bowhead whales in the area. However, bowhead whales leave the Disko Bay area before the peak in the zooplankton bloom, and we therefore believe that limited food availability is not the main explanation for variability in abundance. Future monitoring of bowhead whales in West Greenland may help answer this question.

The present study is one of few studies of large whales with two independent abundance estimates for the same population. The two abundance estimates are complementary as the aerial survey provides snapshots that are useful for examining local trends without dependence between years, whereas the genetic capture-recapture approach allows for estimating the size of the actual source population. However, it is less suited for time series estimates as it requires samples over many years in both the marked and recaptured samples. The two approaches have different merits and do not necessarily lead to identical estimates, but when used in combination give valuable insight into trends affecting abundance and the fraction of the population that is present within the surveyed area.

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Literature Cited

Amos, B., and A. R. Hoelzel. 1991. Long-term preservation of whale skin for DNA analysis. Report of the International Whaling Commission 13:99–103.

Arnason, U., A. Gullberg and B. Widegren. 1993. Cetacean mitochondrial DNA control region: Sequences of all extant baleen whales and two sperm whale species. Molecular Biology and Evolution 10:960–970.

Bérubé, M., and P. Palsbøll. 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. Molecular Ecology 5:283–287.

Best, P. B. 1993. Increase rates in severely depleted stocks of baleen whales. ICES Journal of Marine Science: Journal du Conseil 50:169–186.

Borchers, D. L., W. Zucchini, M. P. Heide Jørgensen, A. Cañadas and R. Langrock. 2013. Using hidden markov models to deal with availability bias on line transect surveys. Biometrics.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, U.K.

Calambokidis, J., and J. Barlow. 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. Marine Mammal Science 20:63–85.

Chao, A., and R. M. Huggins. 2005. Classical closed-population capture-recapture models. Pages 22–35 *in* S. C. Amstrup, T. L. McDonald and B. F. J. Manly, eds. Handbook of capture-recapture analysis. Princeton University Press, Princeton, NJ.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. University of California Publications in Statistics 1 (7):131–160.

Clapham, P. J., A. Aguilar and L. T. Hatch. 2008. Determining spatial and temporal scales for management: Lessons from whaling. Marine Mammal Science 24:183–201.

Eschricht, D. F., and J. Reinhardt. 1861. Om nordhvalen (*Balæna mysticetus* L.) navnlig med hensyn til dens udbredning i fortiden og nutiden og til dens ydre og indre særkjender. [About the northwhale (*Balaena mysticetus* L.) namely with regard to its distribution in the past and the present and on its external and internal characteristics.] Copenhagen, Det Kongelige Danske Videnskapernes Selskabs Skrifter, naturvidenskabelig og mathematisk Afdeling 5. 158 pp.

Excoffier, L., and H. E. L. Lischer. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10:564–567.

Ferguson, S. H., L. Dueck, L. L. Loseto and S. P. Luque. 2010. Bowhead whale *Balaena mysticetus* seasonal selection of sea ice. Marine Ecology Progress Series 411:285–297.

Finley, K. 1990. Isabella Bay, Baffin Island: An important historical and present-day concentration area for the endangered bowhead whale (*Balaena mysticetus*) of the eastern Canadian Arctic. Arctic 43:137–152.

Finley, K. 2001. Natural history and conservation of the Greenland whale, or bowhead, in the Northwest Atlantic. Arctic 54:55–76.

George, J. C., J. Bada, J. Zeh, L. Scott, S. E. Brown, T. O'Hara and R. Suydam. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. Canadian Journal of Zoology 77:571–580.

George, J. C., J. Zeh, R. Suydam and C. Clark. 2004. Abundance and population trend (1978–2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20:755–773.

Givens, G. H., R. M. Huebinger, J. C. Patton, *et al*. 2010. Population genetics of bowhead whales (*Balaena mysticetus*) in the western Arctic. Arctic 63:1–12.

Hacquebord, L. 1999. The hunting of the Greenland right whale in Svalbard, its interaction with climate and its impact on the marine ecosystem. Polar Research 18:375–382.

Hall, T. A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41:95–98.

Harte, D. 2012. HiddenMarkov Version 1.7.0: Hidden Markov Models. Available at http://cran.at.r-project.org/web/packages/HiddenMarkov.

Heide-Jørgensen, M. P., K. L. Laidre, Ø. Wiig, *et al*. 2003. From Greenland to Canada in ten days: Tracks of bowhead whales, *Balaena mysticetus*, across Baffin Bay. Arctic 56:21–31.

Heide-Jørgensen, M. P., K. L. Laidre, M. V. Jensen, L. Dueck and L. Postma. 2006. Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay. Marine Mammal Science 22:34–45.

Heide-Jørgensen, M. P., K. L. Laidre, D. Borchers, F. Samarra and H. Stern. 2007. Increasing abundance of bowhead whales in West Greenland. Biology Letters 3:577–580.

Heide-Jørgensen, M. P., K. L. Laidre, Ø. Wiig, L. Postma, L. Dueck and L. Bachmann. 2010. Large-scale sexual segregation of bowhead whales. Endangered Species Research 13: 73–78.

Heide-Jørgensen, M. P., E. Garde, N. H. Nielsen, O. N. Andersen and S. H. Hansen. 2012*a*. A Note on biological data from the hunt of bowhead whales in West Greenland 2009–2011. The Journal of Cetacean Research and Management 12:329–333.

Heide-Jørgensen, M. P., K. L. Laidre, L. T. Quakenbush and J. J. Citta. 2012*b*. The Northwest Passage opens for bowhead whales. Biology Letters 8:270–273.

Huebinger, R. M., J. C. Patton, J. C. George, R. Suydam, E. E. Louis and J. W. Bickham. 2008. Characterization of 25 microsatellite loci in bowhead whales (*Balaena mysticetus*). Molecular Ecology Resources 8:612–615.

IWC. 2012. Report of the Scientific Committee. Available at https://archive.iwc.int/pages/search.php?search=!collection2&k=.

Kalinowski, S. T., M. L. Taper and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16:1099–1106.

Koski, W. R., R. A. Davis, G. W. Miller and D. E. Withrow. 1993. Reproduction. Pages 239–274 *in* J. J. Burns, J. J. Montague and C. J. Cowles, eds. The bowhead whale. Special Publication Number 2. The Society for Marine Mammalogy.

Laidre, K. L., M. P. Heide-Jørgensen and T. G. Nielsen. 2007. The role of the bowhead whale as a predator in West Greenland. Marine Ecology Progress Series 346:285–297.

Laidre, K. L., and M. P. Heide-Jørgensen. 2012. Spring partitioning of Disko Bay, West Greenland, by Arctic and Subarctic baleen whales. ICES Journal of Marine Science: Journal du Conseil 69:1226–1233.

Moore, S. E., and R. R. Reeves. 1993. Distribution and movement. Pages 313–386 *in* J. J. Burns, J. J. Montague, and C. J. Cowles, eds. The bowhead whale. Special Publication Number 2. The Society for Marine Mammalogy.

Nerini, M. K., H. W. Braham, W. M. Marquette and D. J. Rugh. 1984. Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). Journal of Zoology 204:443–468.

Paetkau, D., and C. Strobeck. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489–495.

Palsbøll, P. J., F. Larsen and E. S. Hansen. 1991. Sampling of skin biopsies from free-ranging large cetaceans in West Greenland: Development of new biopsy tips and bolt designs. Report of the International Whaling Commission (Special Issue 13):71–79.

Palsbøll, P. J., A. Vader, I. Bakke and M. R. El-Gewely. 1992. Determination of gender in cetaceans by the polymerase chain reaction. Canadian Journal of Zoology 70:2166–2170.

Palsbøll, P. J., J. Allen, M. Berube, P. J. Clapham, *et al*. 1997. Genetic tagging of humpback whales. Nature 388:767–769.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: Genetic analysis in EXCEL. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research—an update. Bioinformatics 28:2537–2539.

Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Reeves, R. R., E. Mitchell, A. Mansfield and M. McLaughlin. 1983. Distribution and migration of the bowhead whale, *Balaena mysticetus*, in the eastern North American Arctic. Arctic 36:5–64.

Reeves, R. R., and M. P. Heide-Jørgensen. 1996. Recent status of bowhead whales, *Balaena mysticetus*, in the wintering grounds off West Greenland. Polar Research 15:115–125.

Reilly, S. B., J. L. Bannister and P. B. Best, *et al*. 2012. *Balaena mysticetus*. IUCN 2013, IUCN Red List of Threatened Species. Version 2013.2. Available at http://www.iucnredlist.org.

Rousset, F. 2008. GENEPOP'007: A complete re-implementation of the genepop software for Windows and Linux. Molecular Ecology Resources 8:103–106.

Sasaki, T., M. Nikaido, H. Hamilton, *et al*. 2005. Mitochondrial phylogenetics and evolution of mysticete whales. Systematic biology 54:77–90.

Schneider-Gädicke, A., P. Beer-Romero, L. G. Brown, R. Nussbaum and D. C. Page. 1989. ZFX has a gene structure similar to ZFY, the putative human sex determinant, and escapes X inactivation. Cell 57:1247–1258.

Seber, G. 1973. The estimation of animal abundance and related parameters. J. W. Arrowsmith Ltd., Bristol, U.K.

Smith, T. D., J. Allen, P. J. Clapham, *et al*. 1999. An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). Marine Mammal Science 15:1–32.

Southwell, T. 1898. The migration of the right whale (*Balaena mysticetus*). Natural Science 12:397–414.

Stafford, K. M., S. E. Moore, K. L. Laidre and M. P. Heide-Jørgensen. 2008. Bowhead whale springtime song off West Greenland. Journal of the Acoustical Society of America 124:3315–3323.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei and S. Kumar. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28:2731–2739.

Taylor, B. L., S. J. Chivers, J. Larese and W. F. Perrin. 2007. Generation length and percent mature estimates for IUCN assessments of cetaceans. Administrative Report LJ-07-01, Southwest Fisheries Science Center, La Jolla, CA.

Tervo, O. M., S. E. Parks and L. A. Miller. 2009. Seasonal changes in the vocal behavior of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western-Greenland. Journal of the Acoustical Society of America 126:1570–1580.

van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills and P. Shipley. 2004. Micro-Checker: Software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4:535–538.

Wade, P. R., R. R. Reeves and S. L. Mesnick. 2012. Social and behavioural factors in cetacean responses to overexploitation: Are odontocetes less "resilient" than mysticetes? Journal of Marine Biology 2012.

Waits, J. L., and P. L. Leberg. 2000. Biases associated with population estimation using molecular tagging. Animal Conservation 3:191–199.

Waits, L. P., G. Luikart and P. Taberlet. 2001. Estimating the probability of identity among genotypes in natural populations: Cautions and guidelines. Molecular Ecology 10:249–256.

Wiig, Ø., M. P. Heide-Jørgensen, C. Lindqvist, *et al*. 2011. Recaptures of genotyped bowhead whales *Balaena mysticetus* in eastern Canada and West Greenland. Endangered Species Research 14:235–242.

Zeh, J. E., C. W. Clark, J. C. George, D. Withrow, G. M. Carroll and W. R. Koski. 1993. Current population size and dynamics. Pages 409–489 *in* J. J. Burns, J. J. Montague and C. J. Cowles, eds. The bowhead whale. Special Publication Number 2, The Society for Marine Mammalogy.

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Supporting Information

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12150/suppinfo.

Figure S1. Disko Bay as part of survey area. Locations where mating incidents were observed (red dots), sightings from the aerial survey (yellow dots) and locations for collection of biopsies (blue dots).

Table S1. Primers used during this study of bowhead whales sampled in Disko Bay, West Greenland, between year 2000 and 2013.

Table S2. The microsatellite loci. General information on the microsatellite loci used in this study, when analyzing bowhead whales sampled in Disko Bay, West Greenland, between 2000 and 2013.

Table S3. Bootstrap estimates of the aerial survey. $\hat{D}_g$ and $\hat{D}$ are estimated group and animal density (numbers per 100 km^2), $\hat{N}_g$ and $\hat{N}$ are estimated group and animal abundance; $\hat{E}[s]$ is estimated mean group size.