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Abundance estimates of the Eastern Canada-West Greenland bowhead whale (*Balaena mysticetus*) population based on genetic mark-recapture analyses

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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ABSTRACT

We conducted Bayesian analyses of genetic capture-mark-recapture data to estimate abundance of the Eastern Canada-West Greenland (EC-WG) bowhead whale population. We employed two different analytical approaches, one that ignored location data and treated the entire data set as one large capture-mark-recapture data set, and another that used location-specific data to explicitly account for the presence of unsampled areas. For both approaches we conducted analyses based on two different data sets, one containing data from throughout the entire study period (19 years), and the other containing a 5-year subset of the data. The rationale was that the population size may have changed throughout the 19 years of sample collection, which would bias subsequent estimates. A total of 1,177 samples, from 9 locations throughout the distribution, were genotyped at 21 microsatellite loci. Of these, 992 unique genotypes were identified, with 49 recaptures occurring between years and/or locations. Both estimates for the 5-year data set were smaller than for the 19-year data set, which is consistent with a population increase throughout the study period. Although the estimates differ for each approach, our best estimate of total population abundance is 7,660 individuals (95% HDI 4,500-11,100). We also obtained location-specific estimate for four areas: Greenland (2,854, 95% HDI 1,230-6,460); Igloolik (2,760, 95% HDI 1,980-5,050); Pangnirtung (3,500, 95% HDI 1,700-4,960); and Repulse Bay (38, 95% HDI 20-124).

Estimations de l'abondance de la population de baleines boréales (*Balaena mysticetus*) de l'est du Canada et de l'ouest du Groenland d'après des analyses génétiques par marquage-recapture

RÉSUMÉ

Nous avons effectué des analyses bayésiennes de données génétiques obtenues par capture-marquage-recapture afin d'estimer l'abondance de la population de baleines boréales de l'est du Canada et de l'ouest du Groenland. Nous avons utilisé deux approches analytiques différentes : une qui ne tenait pas compte des données sur l'emplacement et considérait l'ensemble des données comme un seul grand ensemble de données de capture-marquage-recapture, et une autre qui utilisait les données d'un emplacement précis pour tenir compte explicitement de la présence des zones non échantillonnées. Dans le cadre des deux approches, nous avons effectué les analyses en fonction de deux ensembles de données différents. Le premier contenait des données obtenues pendant toute la période d'étude (19 ans) et le deuxième contenait un sous-ensemble de données recueillies sur cinq ans. Cette façon de faire se justifie par le fait que la taille de la population peut avoir changé au cours de la période d'échantillonnage de 19 ans et qu'un tel changement pourrait entraîner un biais dans les estimations subséquentes. Un total de 1 177 échantillons, prélevés dans neuf emplacements dans l'aire de répartition, ont été génotypés à 21 locus microsatellites. Parmi ceux-ci, 992 génotypes uniques ont été identifiés et on a procédé à 49 recaptures d'une année et d'un emplacement à l'autre. Les deux estimations obtenues pour l'ensemble de données sur cinq ans étaient inférieures à celles obtenues pour l'ensemble de données sur 19 ans, ce qui dénote une croissance de la population pendant la période d'étude. Bien que les estimations diffèrent dans chaque approche, notre meilleure estimation de l'abondance de la population totale est de 7 660 individus (intervalle de densité le plus élevé [IDE] à 95 % = de 4 500 à 11 100). Nous avons également obtenu des estimations pour des emplacements précis dans quatre zones : Groenland (2 854, IDE à 95 % = 1 230 à 6 460), Igloolik (2 760, IDE à 95% = 1 980 à 5 050), Pangnirtung (3 500, IDE à 95% = 1 700 à 4 960) et Repulse Bay (38, IDE à 95% = 20 à 124).

INTRODUCTION

Bowhead whales (*Balaena mysticetus*) are large arctic-adapted baleen whales that are listed as “special concern” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC 2009). Bowhead whales were heavily hunted between the 16th and 19th century with an estimate of more than 70 000 animals taken over a period of 350 years by commercial and Inuit whaling in the eastern Canadian Arctic and off West Greenland (Higdon 2010). This whaling pressure reduced the population to historic low levels in the 1800s (Mitchell and Reeves 1981). From this low point, populations have recovered to an unknown level and are now subject to limited hunting by Canadian Inuit and Greenlanders (Heide-Jørgensen et al. 2010).

Bowheads in the Canadian Arctic are currently considered a single population, the Eastern Canada-West Greenland (EC-WG) population (COSEWIC 2009). This designation was a change from the previous stock hypothesis that divided bowheads into two management units (Hudson Bay-Foxe Basin and Baffin Bay-Davis Strait) based largely on geographic discontinuities (Moore and Reeves 1993, Rugh et al. 2003). More recently, studies using satellite tracking data of whales tagged in both Canada and Greenland have shown that bowheads move rapidly and freely between the two hypothesized stock areas (Heide-Jørgensen et al. 2003, 2006; Ferguson et al. 2010). However, within this range there is evidence of segregation based on age, sex and reproductive status (Heide-Jørgensen et al. 2010). For example, female bowhead whales and their calves make up a large portion of the whales observed in northern Foxe Basin each spring (Cosens and Blouw 2003). It has been suggested that this area acts as a refuge from killer whales and reduces predation on calves as well as providing access through Fury and Hecla Strait to the central Arctic (Hay et al. 2000, Cosens and Blouw 2003).

Fisheries and Oceans Canada (DFO) is developing an Integrated Fisheries Management Plan (IFMP) to identify the main objectives and requirements for the EC-WG Bowhead Whale fishery, and to summarize the management measures that will be used to achieve these objectives. This document communicates basic information about the fishery and its management to DFO and its co-management organizations in the Nunavut Settlement Area (NSA) and the Nunavik Marine Region (NMR), the Canadian public and other stakeholders. Co-management organizations in the NSA include the Nunavut Wildlife Management Board (NWMB), the three Regional Wildlife Organizations (RWO), and community Hunters and Trappers Organizations (HTO). Co-management organizations in the NMR include the Nunavik Marine Region Wildlife Board (NMRWB), the Regional Nunavimmi Umajulirijiit Katujjiqatigiinninga (RNUK) and the Local Nunavimmi Umajulirijiit Katujjiqatigiinninga (LNUK).

DFO has adopted a Sustainable Fisheries Framework for all Canadian fisheries to ensure that objectives for long-term sustainability, economic prosperity, and improved governance for Canadian fisheries are met. The Sustainable Fisheries Framework contains policies for adopting an ecosystem-based approach to fisheries management, including ‘A Fishery Decision-Making Framework Incorporating the Precautionary Approach’, and ‘Managing Impacts of Fishing on Benthic Habitat, Communities and Species’. This policy framework applies to the EC-WG Bowhead fishery in the Nunavut Settlement Area and the Nunavik Marine Region. Appropriate harvest levels for this population are based on abundance estimates derived from aerial surveys that can be logistically difficult and expensive to conduct.

In March 1981, aerial surveys of the EC-WG winter range provided an estimate of total population abundance of 1,349 (95% CI 402-4,529) (Koski et al 2006). During the 1990’s, aerial surveys, in combination with limited shore-based counts and photographic mark-recapture analyses, suggested that there were at least hundreds of Bowhead Whales in Eastern Canadian and West Greenland waters (Reeves and Mitchell 1990; Zeh et al. 1993; Reeves and Heide-Jørgensen 1996; Cosens et al. 1997; Cosens and Innes 2000; Finley 2001; Heide-Jørgensen and Acquarone 2002), but the surveys provided limited coverage of the range or missed important seasonal aggregations (COSEWIC 2009). The most recent aerial surveys of the EC-WG population were conducted by DFO in 2002, 2003 and 2004. However, there are no aerial surveys that have covered the full extent of the summer distribution in the Eastern Canadian Arctic. The available aerial survey data have undergone several analyses using different statistical approaches. The resulting abundance estimates are: 7,309 (95% CI = 3,161-16,900) (Cosens et al. 2006); 14,400 (95%CI = 4,811-43,105) (Dueck et al. 2008); 14,196 (95%CI = 5,935-33,956) (Heide-Jørgensen et al. 2008a); 8,187 (95%CI = 3,835-17,480) (Heide-Jørgensen et al. 2008b); 6,344 (95% CI = 3,119-12,906) (Givens et al. 2009); and 8,500 (90% CI = 3,900-17,000) (Witting 2011). Although relatively imprecise, all estimates indicate that the EC-WG population numbered in the thousands in the early 2000’s, and therefore has increased significantly since bowhead whales were first protected from commercial whaling the first half of the 20th century (COSEWIC 2009).

Capture-mark-recapture (CMR) techniques use marking or identification of individuals to estimate abundance and other population parameters, such as birth, death, immigration, and emigration rates (DeMaster et al. 1980, White and Burnham 1999). In a fashion similar to traditional capture-mark-recapture techniques, genetic CMR (gCMR) uses the unique genetic fingerprint of each animal as an identifying mark (Palsbøll et al. 1997, Petit and Valiere 2006). The use of genetic identifications to ‘mark’ animals have been used on a variety of taxa (e.g., bears (Mowat and Strobeck 2000) and North Atlantic right whales (Frasier et al. 2009)) and using a variety of samples sources (e.g., hair (Mowat and Strobeck 2000), scat (Kohn et al. 1999), and skin biopsies (Wiig et al. 2011)). General reviews of this methodology can be found in the literature (e.g., White and Burnham 1999, Lukacs and Burnham 2005). Genetic profiles have been successfully used to estimate population size in cetaceans (e.g., Stevick et al. 2001, Garrigue et al. 2004, Baker et al. 2012) including in bowhead whales (Wiig et al. 2010, Wiig et al. 2011). Wiig et al. (2011) used this approach to estimate bowhead whale abundance, with a result of 1,410 whales (95% CI 783-2038). However, they also identified a high degree of sex and reproductive class segregation and thus this estimate likely represents only a portion of the population (Koski and Ferguson 2012).

Preliminary work has been conducted by Petersen et al. (2014) to evaluate the potential of gCMR as a tool to estimate population abundance for EC-WG bowhead whales sampled in Canada. Results were encouraging and indicated that the collection of bowhead whale biopsy samples provides a promising source of data for estimating abundance of this population.

The research in this paper builds on the work of Petersen et al. (2014) with the addition of more samples and the development of a more sophisticated model to estimate population abundance. The objectives were to:

(a) develop and assess more rigorous statistical analyses for estimating abundance based on genetic capture-mark-recapture data when not all locations are sampled; and

(b) obtain abundance estimates for sampled locations, as well as for the total EC-WG population.

METHODS

SAMPLING

Teams searched for whales from boats or from along the floe edge near communities. During most years, one or two teams searched for bowhead whales based on local ice conditions and advice from local guides. When animals were located photos for photo ID were taken, satellite tags were deployed, and a biopsy was obtained. Additional biopsy samples from untagged individuals were also obtained using a 40- or 60mm biopsy dart (CETA-DART, Denmark) deployed with a 150lb crossbow (Excalibur Vixen, Ontario, Canada). Bolts were equipped with a fluorescent coloured float to facilitate retrieval. Samples were preserved either in a salt-saturated 20% DMSO solution (Seutin et al. 1991), flash frozen in liquid nitrogen, in RNAlater (Qiagen Inc., Valencia, CA, USA), or in Allprotect (Qiagen Inc., Valencia, CA) and frozen upon arrival at the lab. Field notes detailing the particulars of each animal sampled (e.g. approximate size, age or reproductive class, group size or composition, and other relevant notes) were recorded for most of the samples. All samples were transferred and archived in -80°C freezers at the Freshwater Institute (DFO, CA, Winnipeg) laboratories until further analysis.

Intensive biopsy sampling programs have been conducted based out of the communities of Igloolik and Pangnirtung in Canada and in Disko Bay, Greenland (hereafter referred to as Greenland). In addition, samples used here include smaller collections collected from Repulse Bay, Taloyoak, Kugaaruk, Cape Dorset and Arctic Bay (Figure 1). Sampling was conducted with community members as part of the sampling team. Combined, samples have been collected over a period of 19 years (1995-2013).

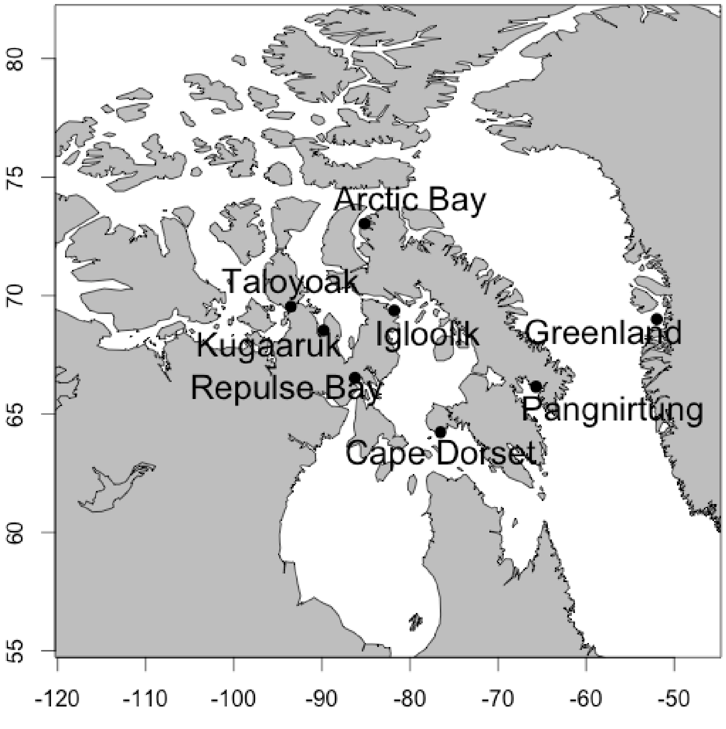

Figure 1. Map of sampling locations. Y-axis is longitude and X-axis is latitude

GENETIC ANALYSIS

DNA was extracted using a modified version of the standard Qiagen extraction protocol (Wang et al. 2008). This included extra steps to digest the tissue fully before extraction using Qiagen BioSprint 96 DNA Blood Kits (Qiagen Inc. Canada, Toronto, Ontario). DNA was quantified using a µQuant spectrophotometer (Bio-Tek US, Winooski, VT) or Nanodrop spectrophotometer UV-Vis Spectrophotometers (Thermo Fisher Scientific Inc., Wilmington, DE) and normalized to 10-100ng/µl. DNA was then used to amplify several genetic markers as briefly outlined below.

Sex was determined through amplification of a zinc finger gene intron using LGL331 and LGL335 primers (Shaw et al. 2003). PCR product was stained with GelRed (Biotium Inc., Hayward, CA) and visualized on a 1.5% agarose gel. The banding pattern of X (~975 bp) and Y (~1040 bp) fragments were used to infer sex.

Multiplex reactions were developed and used to amplify twenty-three microsatellite loci, and PCR products were size-separated and visualized on an ABI 3130xl Genetic Analyzer (Life Technologies Inc., Carlsbad, CA). Microsatellites were multiplexed as follows: multiplex 1 with Bmy1 (1.6µM), Bmy8 (0.2µM), Bmy16 (0.6µM), EV37 (0.16µM), and EV104 (0.4µM); multiplex 2 with Bmy10 (0.4µM), Bmy55 (0.6µM), EV76 (0.2µM), RW31 (1.2 µM), and FCB4 (0.3µM); multiplex 3 with Bmy19 (0.3µM), Bmy33 (0.4µM), Bmy36 (0.6µM), Bmy53 (1.6µM), and Bmy54 (0.4µM); multiplex 4 with Bmy49 (0.8µM), Bmy58 (1.0µM), and RW18 (0.3µM); and multiplex 5 with Bmy11 (0.3µM), Bmy57 (0.12µM), and EV1 (1.6µM). Three microsatellites were incompatible for multiplexing and were run individually. These were Bmy12, Bmy26, and GATA098 (0.5µM each). In addition to primers, the PCR cocktail included 10X AmpliTaq Gold Buffer (1X), $MgCl_2$ (2.0mM), dNTP mix (0.25mM), AmpliTaq Gold DNA Polymerase (0.5U)(Life Technologies Inc., Carlsbad, CA) and nuclease-free water to a final volume of 10µl, including 1.0µl of template DNA.

Thermal cycler profiles included a 5 minute incubation at 95°C followed by 35 cycles of 95°C for 30 seconds, annealing temperature for 30 seconds, and 72°C for 30 seconds. The final extension was at 72°C for 30 minutes. Multiplexes 1, 2, 3, and Bmy26 had an annealing temperature of 55°C; multiplexes 4, 5, and Bmy12 had an annealing temperature of 58°C; and GATA098 at 48°C. Samples were run on an Applied Biosystems 3130xl Genetic Analyzer (Life Technologies Inc., Carlsbad, CA) with GeneScan 600 LIZ size standard (Life Technologies Inc., Carlsbad, CA) and Hi-Di formamide (Life Technologies Inc., Carlsbad, CA). The program GeneMarker (SoftGenetics, State College, PA) was used to analyze and score the raw microsatellite data.

IDENTIFYING RECAPTURES

The crux in identifying genetic recaptures is developing appropriate criteria for defining when two genotypes can be considered “the same”, and thus representing the same individual. This problem has a long history, and has been most thoroughly dealt with in human forensic DNA typing (National Research Council 1996). The issues are two-fold. First, two genotypes may be the same at the typed loci, but represent different individuals if not enough resolution is available with the chosen markers, if individuals are related, or just by chance (a false inclusion). Second, two genotypes may be from the same individual but be scored differently due to genotyping errors or null alleles (a false exclusion). Thus, the key is identifying what criteria minimize the chances of each of these errors.

To identify recaptures, or samples likely originating from the same individual, we used the R package ALLELEMATCH (Galpern et al. 2012). This package deals with these issues by calculating the genetic similarity of all genotypes and then creating clusters based on genetic similarity. It then re-creates these clusters by sequentially allowing an incremental number of mismatches, while keeping track of how many “unique” genotypes are present under each number of allowed mismatches. The appropriate number of allowed mismatches is then identified as the point when each genotype associates with only one cluster.

ESTIMATING POPULATION SIZE

We used Bayesian methods to estimate population size from the genetic mark-recapture data, based on the general approaches described in Kéry and Schaub (2011) and Kruschke (2011). We tried two general strategies, each with their own strengths and weaknesses. The first and most simple approach involved ignoring the location information and treating the data as one large capture-mark-recapture study. The main benefit of this approach is that it allows all samples to be used, regardless of whether recaptures were found within each location. The main weakness of this approach is that it does not explicitly account for the fact that not all locations have been sampled, and therefore makes the assumption that individuals move throughout sampled and unsampled locations, and thus information from whales utilizing the unsampled locations is included in the capture history data in sampled locations. Our second strategy was modeled after that of Durban et al. (2005). Here, location-specific estimates of population size and movement rates were obtained and used to explicitly infer the number of individuals in unsampled locations. The strength of this approach is that it provides a quantitative means to infer the number of individuals using unsampled locations. The main weakness is that it requires dividing the data by locations, with the result that many locations did not have enough samples to be included in the analyses, and thus some information was lost. Both of these methods are described in more detail below. For both strategies, we estimated population sizes based on two data sets: the full data set, and a subset containing only five years of data. The rationale is that the population may have changed throughout the 19 years throughout which samples were collected. Therefore, abundance estimates based on the entire study period may be biased. The 5 year data set contains less data, but is also expected to be less biased by changes in population size. Combined, this resulted in four estimates of abundance based on:

1) location-independent full data set (LI-FD);
2) location-independent 5 year data set (LI-5Y);
3) location-specific full data set (LS-FD); and
4) location-specific 5 year data set (LS-5Y).

For all analyses, the recaptures identified by ALLELEMATCH were filtered to *exclude* recaptures from the same location in the same year. Bowhead whales are known to vary their migration and habitat use patterns depending on age, sex, and life-history stage (e.g., Moore and Reeves 1993; Heide-Jørgensen et al. 2010). Additionally, once in an area, whales are likely to remain there for some period of “residency” (e.g., Finley 1990). Thus, we thought that within-year recaptures would be artificially high and would not be representative of general capture probabilities for the entire population throughout the study period.

Location-Independent Full Data Set (LI-FD)

To estimate population sizes for each sampled location, the recapture data from ALLELEMATCH were first converted to typical sighting histories consisting of ones and zeros for each sampling period where individuals were, or were not, captured, respectively. These sighting histories were augmented by 60,000 to ensure that considered probabilities covered a wide enough range to ensure adequate sampling of the posterior distribution (Tanner and Wong 1987, Royle et al. 2007). The parameters of interest are the sighting probability (*p*), and the inclusion probability (*omega*), which is the probability that a member of the augmented data set is part of the “true” population size (*N*). Population size estimates were then obtained for a closed population model (model M_0 from Otis et al. (1978)) using the approach described in Royle et al. (2007) and Kéry and Schaub (2011). The priors for both the sighting probability (*p*) and the inclusion probability (*omega*) were uniform distributions ranging from 0 to 1. Although it is unrealistic to assume that the population was closed throughout the sampling period, the recaptures were so few and far between that we did not think there was enough information to estimate parameters for models that relax this assumption. All Bayesian analyses were conducted using a combination of R (R Core Team 2014), rjags (Plummer 2014), and JAGS (Plummer 2003); and the performance of chains for all analyses were assessed based on examination of trace plots, autocorrelation plots, the Gelman and Rubin diagnostic (Gelman and Rubin 1992), and the effective sample size, using the coda package (Plummer et al. 2006).

Location-Independent 5-Year Data Set (LI-5Y)

Although it would make intuitive sense to select the most recent 5-year period for these analyses, we did not do this because most locations did not have data for the most recent year (2013). Instead, we queried the data to identify which 5-year subset would contain the most sampling events. This turned out to be years 2008-2012, and therefore represents a very recent sampling period. Once this subset of data had been identified, estimates of abundance were obtained using the same approach as described for the full data set.

Location-Specific Full Data Set (LS-FD)

Our location-specific approach for estimating population size was modeled after that used by Durban et al. (2005). The general idea is that location-specific estimates of population size can be used in association with estimated migration rates between locations, to identify (and/or infer) the number of individuals with different sighting histories. For example, for three locations there are eight possible sighting histories: individuals seen in locations

a) 1, 2 and 3;
b) 1 and 2 but not 3;
c) 1 and 3 but not 2;
d) 2 and 3 but not 1;
e) 1 but not 2 or 3;
f) 2 but not 1 or 3;
g) 3, but not 1 or 2; and
h) not seen in any location (Table 1).

When some areas are unsampled, the goal is to estimate the number of individuals in category (h), who were not seen in any sampled location. This number can then be added to those from sighting histories (a) through (g) to obtain an estimate of total population size even when some areas remain unsampled.

Table 1. Examples of different sighting history categories, and example numbers, when data are available for three locations. The example data are from Durban et al. (2005). The row marked by the asterisk indicates a pattern inferred from previous data.

Sighting History	Number	Location 1	Location 2	Location 3
a	1	YES	YES	YES
b	16	YES	YES	NO
c	3	YES	NO	YES
d	35	NO	YES	YES
e	2	YES	NO	NO
f	2	NO	YES	NO
g	16	NO	NO	YES
h*	??	NO	NO	NO

Durban et al. (2005) recognized that this number could be inferred using standard multiple regression techniques. Briefly, the data from the first seven sighting histories (a through g) are used in a multiple regression analysis to estimate the coefficients of the regression equation. Once these coefficients have been estimated, they can be used to predict values for new conditions, which in this case is the number of individuals with sighting history (h). In this way, data on location-specific population sizes can be used to infer the number of individuals who do not use the sampled areas. This is exactly what is needed for estimating population size for Eastern Canada-West Greenland (EC-WG) Arctic bowhead whales, were it is unlikely that all important areas can be adequately sampled.

The first step in this process was to estimate the migration rates between all pairs of sampled locations. We made the assumption that migration rates were symmetrical, largely because the number of cross-location recaptures was very low (see Results), and therefore there were few data available from which to estimate migration rates, and we did not want to further divide these sparse data into direction-specific types. The number of recaptures within and between each pair of locations was converted into a string of zeros and ones, where ones represented recaptures across locations. The mean migration rates, and associated 95% highest density intervals (HDIs), were then estimated using a Bernoulli likelihood function and a beta prior with a uniform (flat) distribution. An estimate of the symmetrical migration rate with the unsampled location(s) was then obtained by taking the average of the pairwise migration rates between sampled locations. This approach makes the explicit assumption that the rate at which individuals move from sampled to unsampled locations is within the same range as the migration rates among sampled locations. We felt that this assumption was valid, and simulations showed that our overall method performed well even when this assumption was violated (data not shown).

To estimate population sizes for each sampled location, the recapture data from ALLELEMATCH were first converted to typical sighting histories consisting of ones and zeros for each sampling period where individuals were, or were not, captured, respectively. However, these sighting histories were biased due to individuals moving to and from the unsampled location(s). Individuals marked in the sampled location could move to an unsampled location, and therefore not be available for recapture, artificially reducing the number of recaptures. In the opposite direction, unmarked individuals from the unsampled location(s) could move into the sampled location, which would also artificially reduce the proportion of recaptures. Both of these processes reduce the proportion of individuals available for recapture, and would therefore bias population size estimates upwards. To correct for this, for each sampled location we estimated the number of whales moving to and from the unsampled location(s) and randomly added these to the sighting history data. For example, suppose at one location there were 300 marked individuals and 68 recaptures. Suppose that the estimated migration rate to and from the unsampled location(s) is 0.12. This means that we have “lost” 12% of marked individuals to unsampled locations, and our number of unmarked individuals is also artificially inflated by 12% due to movement of unmarked individuals from unsampled areas into this area. This means that our proportion of recaptures is underestimated by two times the movement rate (24%). Thus, our original 68 recaptures only represent (1 – 0.24 = 0.76) 76% of the recaptures we “should” have had, if individuals did not move to and from unsampled locations (i.e., we should have had 68 / 0.76 = 89 recaptures). To account for this, these (89 – 68 = 21) additional recaptures were randomly added to the sighting histories for this location.

Once the sighting histories had been corrected, population sizes were estimated for each location using the same techniques as described for the location-independent approach. Note that although the model assumed a closed population, movement to and from other locations was already taken into account in the development of the capture history tables, and therefore “closed” in this sense just refers to births and deaths. Because we assumed migrations were symmetrical, the whales that were recaptured within each area that were originally marked elsewhere, were still counted as recaptures for that area. This works because with symmetrical movements the number of marked and unmarked individuals emigrating from an area should be equal to the number of marked and unmarked individuals immigrating into an area. Thus, including recaptures that were originally marked elsewhere corrects for the marked individuals that emigrated.

Once population size estimates were available for each sampled location, these were used in combination with the estimated migration rates to infer the number of individuals with different sighting histories, as shown in Table 2. Note that we had four locations with adequate data, whereas Durban et al. (2005) had three, and therefore our table is slightly different than Table 1, which was used as an example. We then used the approach of Durban et al. (2005) to use these data to infer the number of individuals in unsampled locations. Considering all variables, this equation has 16 potential coefficients to estimate (β_{0-15}), and here the x values refer to each of the four locations. Because we had 15 different sighting histories, only 11 of which had non-zero estimates, we did not consider three- or four-way effects, and instead only estimated and used coefficients β_{0-10}.

$$y=\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \beta_5 x_1 x_2 + \beta_6 x_1 x_3 + \beta_7 x_1 x_4 + \beta_8 x_2 x_3 + \beta_9 x_2 x_4 + \beta_{10} x_3 x_4 + \beta_{11} x_1 x_2 x_3 + \beta_{12} x_1 x_2 x_4 + \beta_{13} x_1 x_3 x_4 + \beta_{14} x_2 x_3 x_4 + \beta_{15} x_1 x_2 x_3 x_4)$$

Estimates of total population size can then be obtained by adding the data from column 2 in Table 2, including the estimated number of individuals in unsampled areas, obtained above.

Table 2. Location use categories, and number of individuals in each category, for the four locations containing adequate recapture data for analyses. The values in the "Number" column were inferred based on a combination of population size and migration rate estimates for each location. For example, the estimated number of individuals that only use Igloolik (row m) represents our abundance estimate for Igloolik minus the estimated number of individuals that moved to other locations as well. The row marked by the asterisk indicates a pattern inferred from previous data.

Location Use Pattern	Number	Greenland	Igloolik	Pangnirtung	Repulse Bay
a	0	YES	YES	YES	YES
b	0	YES	YES	YES	NO
c	0	YES	YES	NO	YES
d	0	YES	NO	YES	YES
e	1	NO	YES	YES	YES
f	11	YES	YES	NO	NO
g	31	YES	NO	YES	NO
h	10	YES	NO	NO	YES
i	72	NO	YES	YES	NO
j	10	NO	YES	NO	YES
k	72	NO	NO	YES	YES
l	3268	YES	NO	NO	NO
m	5906	NO	YES	NO	NO
n	2844	NO	NO	YES	NO
o	37	NO	NO	NO	YES
p*	??	NO	NO	NO	NO

Location-Specific 5-Year Data Set (LS-5Y)

To limit our analyses to just the most recent five years of data, we first checked to see if all locations had recaptures within the same time frames. They did not, and therefore we had to choose different years for the analyses of each location, although all time frames used were close together. While this process may make combining the data a bit tenuous, we felt that it was still appropriate given the long life spans and generally slow life histories of bowhead whales. Only three locations had adequate recaptures within a 5-year period to be used in subsequent analyses. These included Greenland, Igloolik, and Pangnirtung. Specifically, the timeframes used for each were: Greenland – 2004-2008, Igloolik – 2008-2012; Pangnirtung – 2008-2012. All analyses were conducted as described above for the full data set, except here they were based on these three locations alone.

RESULTS

SAMPLES, GENOTYPES, AND RECAPTURES

A total of 1,177 samples were genotyped. Table 3 shows how these were divided among locations. The final microsatellite data set contained 21 loci since two loci were dropped due to a significant portion of the samples missing data that were profiled before 2008. Furthermore, a sample was only included in the analysis if it had at least 10 of the 21 loci scored. This provided an overall probability of identity of 1.16×10^{-9}, which corresponds to a 1 in 8.62×10^{8} chance that the match identified was due to two random animal matching at all loci. Appendix 1 shows how these samples are divided by year, location, and sex.

The ALLELEMATCH analysis suggested that the best fit for the data was to allow 3 mismatches. Based on this criterion, 992 unique genotypes were identified, along with 185 recaptures. However, 136 of these recaptures represented whales recaptured within the same area and year in which they were marked, and were therefore removed from the analyses. This left 49 recaptures for subsequent analyses. Table 4 summarizes the recaptures by location. Based on the number of recaptures, only Greenland, Igloolik, Pangnirtung, and Repulse Bay were used for estimating population size based on the full data set.

Table 3. Genotyped samples by location.

Location	Count
Arctic Bay	9
Cape Dorset	1
Greenland	295
Igloolik	546
Iqaluit	1
Kugaaruk	8
Pangnirtung	293
Repulse Bay	23
Taloyoak	1
Total	**1177**

Table 4. Identified recaptures by location. Only locations with recaptures are included.

	Greenland	Igloolik	Kugaaruk	Pangnirtung	Repulse Bay
Greenland	5	0	0	2	0
Igloolik	-	23	1	6	0
Kugaaruk	-	-	0	0	0
Pangnirtung	-	-	-	3	3
Repulse Bay	-	-	-	-	1

Estimates of Population Size

Location-Independent Analyses

The location-independent abundance estimates based on the full data set and the 5-year data set were 12,220 whales (95% HDI = 8,680 – 16,200) and 7,660 whales (95% HDI = 4,500 – 11,100), respectively (Table 5, row 7).

Table 5. Estimates of population size for each location, as well as for the total population. Included are the estimate and 95% highest density interval (HDI). Total-LS refers to the estimate for total population size based on inference from the location-specific analyses and Total-LI refers to estimates based on the location-independent analyse.

		Full Data Set		5 Years of Data	
Row #	Location	Estimate	95% HDI	Estimate	95% HDI
1	**Greenland**	3,317	1,620 – 9,760	2,854	1,230 – 6,460
2	**Igloolik**	6,005	3,600 – 8,280	2,760	1,980 – 5,050
3	**Pangnirtung**	2,935	1,750 – 6,350	3,500	1,700 – 4,960
4	**Repulse Bay**	38	20 - 124	NA	NA
5	**“Missing”**	6,831	44 – 28,700	0	0 - 1,720,000
6	**Total-LS**	19,093	12,300 – 41,000	11,800	7,190 – 17,100
7	**Total–LI**	12,220	8,680 – 16,200	7,660	4,500 – 11,100

Location-Dependent Analyses

The estimated movement rates between locations are shown in Table 6. All were quite low, which is not surprising given the recapture data.

Table 6. Estimates of movement rates between pairs of locations. Included is the mean and 95% highest density interval (HDI). Locations are abbreviated as follows: Greenland = G,

Igloolik = I, Pangnirtung = P, and Repulse Bay = RB. The movement rate to unsampled locations is shown as m_u.

	Full Data Set		5 Years of Data	
Movement Type	**Mean**	**95% HDI**	**Mean**	**95% HDI**
mGI	0.00119	5.79x10-8 – 0.00356	0.00151	1.19x10-7 – 0.00453
mGP	0.00506	5.05x10-4 – 0.0107	0.0105	0.00261 – 0.0196
mGRB	0.00312	5.66x10-8 – 0.00929	NA	NA
mIP	0.00824	0.00286 – 0.0146	0.0032	6.30x10-5 – 0.00776
mIRB	0.00176	2.71x10-8 – 0.00525	NA	NA
mPRB	0.0124	0.00259 – 0.0249	NA	NA
mu	0.0053	0.00278 – 0.00807	0.00506	0.00184 – 0.00853

The estimates of population size for each location, and inferred for the unsampled location(s), are shown in Table 5 (rows 1 – 6). Note that the mode was used instead of the mean because the posterior probability distributions for all population size estimates had heavy right-hand tails (e.g., Figure 2), and therefore the mode represented the most likely estimate better than the mean. For the 5-year data set the mode for the number of inferred individuals was 0, suggesting that no individuals are "missing", but with a wide 95% highest density interval (Figure 3). Because of this, we obtained the estimate of total population size by taking the sum of the data from the three locations. These estimates are inclusive, meaning, for example, that the estimate for Igloolik represents all whales that use Igloolik (and may also be sighted elsewhere), rather than representing whales that only use Igloolik (and no other sampled locations).

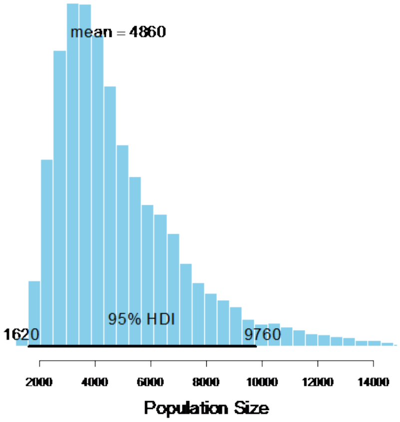

Figure 2. Posterior probability distribution for Greenland population size estimate. Note that the distribution has a heavy right-hand tail, resulting in the mean not representing the most likely value.

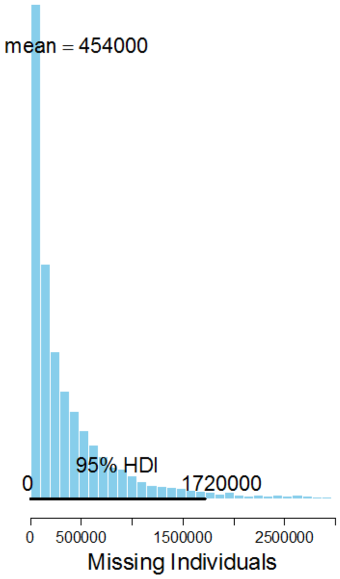

Figure 3. Posterior probability distribution for the "missing locations" for the 5-year data set. Note that the mode is zero, showing that the most likely number of "missing" individuals is zero.

DISCUSSION

Overall, the number of recaptures was very low, despite the substantial effort in sample collection across a wide range of areas. This fact alone indicates that the population size is quite large, and demonstrates the inherent difficulties in estimating population size for EC-WG bowhead whales. Given their movement dynamics and heterogeneity, it seems that any estimate of population size is going to have its shortcomings, and have to be taken with a fairly large grain of salt. However, here we have tried to be comprehensive in our analyses to try to make the most of the data that are available.

For both analysis approaches, abundance estimates were lower for the 5-year data set than for the full data set. This would be expected if the population was increasing during the time in which samples were collected, which would decrease the proportion of marked individuals throughout the study and inflate abundance estimates. Given that other data suggest that the population is in fact increasing, we think that using the results from the 5-year analyses are appropriate. Our results of this time period from the two analysis approaches are similar to each other, as well as to other estimates obtained for this population (location-independent estimate = 7,660, 95% HDI 4,500-11,100; location-specific estimate = 11,800, 95% HDI 7,190-17,100). Although the locus-specific estimate explicitly accounts for the presence of unsampled locations, in this case the inferred number of individuals was 0, thus limiting the benefits of this approach. Combining this result with the fact that the location-independent estimate was based on more samples and recaptures (because it was not limited to specific locations), we think that our location-independent 5-year results represent the best estimate of abundance for this population (7,660 whales, 95% HDI 4,500-11,100) (Table 5, row 7).

For the location-specific analyses, we think that the location-specific estimates for sampled locations are reliable, and that it was in the inference of missing individuals where the model had trouble (note the very wide highest density intervals for the number of missing individuals Table 5, row 5). This is likely due to the very low movement rates between locations, which meant that there was very little information in the sampled location data on which inferences could be made about the unsampled locations. However, the estimates for each included location should represent appropriate abundance estimates.

With respect to location-specific estimates, there are two areas for which comparable information is available. Cosens and Innes (2000) report estimates for a larger area centered around Repulse Bay. Their estimate was 75 individuals, with a 95% confidence interval of 17 – 133. This agrees well with our estimate of 38 (20 – 124), particularly when considering that they covered a larger area than was available here.

Rekdal et al. (2015) report aerial survey and genetic estimates of population size for West Greenland. The estimates from these methods were 744 whales (95% CI: 357 – 1,461) and 1,538 whales (827 – 2,249), respectively. However, the aerial surveys were conducted in a single year, and therefore the resulting estimates do not include whales that may use the area, but did not in the year of the survey, which may represent a substantial number. Additionally, the genetic estimates were obtained on a per-year basis, and therefore whales that use the area, but not on an annual basis, would not be included in their estimates. Based on these differences, it is not surprising that our estimate for West Greenland (2,854, 95% HDI: 1,230 – 6,460) is larger than those reported in Rekdal et al. (2015). Given the heterogeneity in bowhead movement patterns we think that basing estimates on a longer-term data set increases the chances of including all whales that use specific areas, and therefore results in more accurate estimates.

UNCERTAINTIES AND RECOMMENDATIONS FOR THE FUTURE

The methods used here are very promising, but there are a number of uncertainties and/or assumptions that require further attention. First, due to the shortage of recaptures, we had to assume a closed population, and equal sighting probabilities across locations and individuals. Models exist to relax these assumptions, and it would be worthwhile:

(a) to conduct a sensitivity analysis to assess how making these assumptions influence population size estimates on simulated bowhead whale populations with biologically realistic data on birth and death rates, and sighting heterogeneity; and

(b) to assess (perhaps in the same analyses) how many recaptures would be needed to obtain informative estimates using the less restrictive models.

Despite these uncertainties, the cost and logistics of this approach make it attractive for obtaining abundance estimates in the future. First, genetic analyses of samples are inexpensive relative to aerial surveys, and thus may be a more efficient means to obtain such estimates over time. Second, increasing sample collection collaborations with local groups makes the increase of sampling effort and expansion to new sampling locations realistic and inexpensive possibilities. In addition to increasing the data on which abundance estimates are based, such work will also increase the collaboration between DFO and local communities.

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APPENDIX. SAMPLE NUMBERS BY YEAR, LOCATION, AND SEX.

Year	Location	Sex	Count
1995	Igloolik	Unknown	10
1996	Igloolik	Unknown	17
1997	Igloolik	Unknown	1
1997	Pangnirtung	Unknown	17
1997	Repulse Bay	Unknown	5
1998	Repulse Bay	Unknown	3
2000	Repulse Bay	Unknown	4
2001	Greenland	Unknown	13
2001	Igloolik	Unknown	34
2001	Kugaaruk	Unknown	2
2001	Repulse Bay	Unknown	3
2002	Greenland	Unknown	13
2002	Igloolik	Unknown	53
2002	Kugaaruk	Unknown	5
2002	Pangnirtung	Unknown	10
2003	Greenland	Unknown	10
2003	Igloolik	Unknown	27
2004	Pangnirtung	Unknown	6
2005	Greenland	Unknown	17
2005	Pangnirtung	Unknown	15
2005	Repulse Bay	Female	1
2006	Greenland	Unknown	22
2006	Pangnirtung	Unknown	31

Year	Location	Sex	Count
2007	Greenland	Female	130
2007	Greenland	Male	26
2008	Arctic Bay	Female	2
2008	Greenland	Female	45
2008	Greenland	Male	8
2008	Greenland	Unknown	8
2008	Igloolik	Female	4
2008	Igloolik	Male	2
2008	Pangnirtung	Female	1
2008	Pangnirtung	Male	1
2008	Pangnirtung	Unknown	1
2008	Repulse Bay	Female	1
2008	Repulse Bay	Unknown	4
2009	Arctic Bay	Female	5
2009	Arctic Bay	Male	1
2009	Cape Dorset	Male	1
2009	Igloolik	Female	42
2009	Igloolik	Male	40
2009	Repulse Bay	Female	1
2009	Repulse Bay	Male	1
2011	Igloolik	Female	17
2011	Igloolik	Male	24
2011	Iqaluit	Male	1
2011	Kugaaruk	Female	1

Year	Location	Sex	Count
2011	Pangnirtung	Female	28
2011	Pangnirtung	Male	25
2012	Arctic Bay	Male	1
2012	Igloolik	Female	58
2012	Igloolik	Male	53
2012	Igloolik	Unknown	4
2012	Pangnirtung	Female	38
2012	Pangnirtung	Male	66
2012	Pangnirtung	Unknown	5
2012	Taloyoak	Female	1
2013	Igloolik	Unknown	160
2013	Pangnirtung	Female	14
2013	Pangnirtung	Male	34
2013	Pangnirtung	Unknown	1
Unknown	Greenland	Unknown	6