Recaptures of genotyped bowhead whales *Balaena mysticetus* in eastern Canada and West Greenland

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ABSTRACT: Multi-locus genotype and sex were used to identify individual bowhead whales *Balaena mysticetus* from 710 samples collected between 1995 and 2010 at 4 localities in eastern Canada (Foxe Basin, Pelly Bay, Repulse Bay, and Cumberland Sound) and at 1 locality in West Greenland (Disko Bay). In total, 29 recaptures of the same individuals were identified between years, of which 26 individuals were recaptured within the same locality. The remaining 3 were recaptured between sampling localities, from 2 putative International Whaling Commission (IWC) stocks: the Hudson Bay–Foxe Basin stock and the Baffin Bay–Davis Strait stock. These recaptures agree with satellite tracking results that demonstrate movement between IWC stocks and question whether these stocks are true biological entities. The intervals between capture and recapture of females in Disko Bay ranged from 1 to 8 yr. The observed number of multi-year recaptures compared to the expected numbers of recaptures did not indicate any clear cyclicity in the use of Disko Bay consistent with the notion that the migration pattern of females to this area might be tied to their reproductive cycles. A mark–recapture estimate of whales identified in 2010 compared to all identifications between 2000 and 2009 resulted in an estimate of 1410 bowhead whales (SE = 320, 95% CI: 783–2038) constituting the spring aggregation in Disko Bay. The estimate for the female portion of the aggregation was 999 individuals (SE = 231, 95% CI: 546–1452). The multi-year cycle of appearance in Disko Bay emphasizes the necessity for identifying whales over multiple years for inclusion in mark–recapture estimation.

KEY WORDS: Bowhead whale · *Balaena mysticetus* · Genotyping · Recapture · Stock structure · Abundance · Mark–recapture

INTRODUCTION

Bowhead whales *Balaena mysticetus* are endemic to Arctic and sub-Arctic regions of the Atlantic, Bering, Beaufort, Chukchi, and Okhotsk Seas (Moore & Reeves 1993), where they live in close association with the sea ice edge. Exploitation over several centuries has dramatically reduced the population size of this once abundant species (Woodby & Botkin 1993). Commercial hunting for bowhead whales commenced in the early 1600s in the North Atlantic region around Svalbard, from where it expanded into other regions as the Svalbard stock became depleted. Five geographically separated stocks have been des-
igned: (1) the Bering/Chukchi/Beaufort Seas stock, (2) the Okhotsk Sea stock, (3) the Baffin Bay−Davis Strait stock, (4) the Hudson Bay−Foxe Basin stock, and (5) the Spitsbergen stock distributed in the Greenland, Barents, and Kara Seas (Moore & Reeves 1993).

In 1977, a 2-stock hypothesis for bowhead whales occupying East Canada and West Greenland waters was adopted as the working model by the International Whaling Commission (IWC 1978). The stocks were the Baffin Bay−Davis Strait (or Baffin Bay) stock and the Hudson Bay−Foxe Basin (or Hudson Bay) stock. The division was based on the disjunct summer distribution of bowhead whales in this region (see Reeves et al. 1983, Reeves & Mitchell 1990, Moore & Reeves 1993, Rugh et al. 2003). Bowhead whales are found in large numbers during the summer months at specific localities within Foxe Basin, northern Hudson Bay, and in fjords along the east coast of Baffin Island and in the Canadian high Arctic. During the winter, bowhead whales congregate in the Hudson Strait, at the mouth of Cumberland Sound, or along the West Greenland coast and in the North Water (Reeves et al. 1983, Reeves & Mitchell 1990). Although the IWC has designated the Hudson Bay−Foxe Basin and the Baffin Bay−Davis Strait as 2 different stocks separated to the north by Fury and Hecla Strait and to the east by the Hudson Strait, recent radio-satellite tagging data demonstrate that bowhead whales move freely around Baffin Island and between the hypothesized stocks (Heide-Jørgensen et al. 2003, 2006, Ferguson et al. 2010 Greenland Institute of Natural Resources [GINR] unpubl. data).

Satellite telemetry data demonstrate that bowhead whales are capable of travelling long distances over short periods of time, which prompted Heide-Jørgensen et al. (2006) to argue that there are no obvious reasons for bowhead whales to restrict their movement to only parts of the total potential range in eastern Canada and West Greenland waters. Further, Heide-Jørgensen et al. (2010) argued that based on patterns of sexual aggregation, bowhead whales summering in eastern Canada and wintering off the west coast of Greenland belong to the same stock. In light of these observations, the IWC has since 2007 revised the original 2-stock hypothesis of bowhead whales in this region to a single stock hypothesis as the main working hypothesis, while acknowledging remaining uncertainties regarding the stock structure of bowhead whales in the area (e.g. IWC 2010). In agreement with this, recent papers on satellite telemetry (Ferguson et al. 2010) and population genetics (Givens et al. 2010) have treated the bowhead whales in eastern Canada and West Greenland as a single stock.

Bowhead whales have for centuries arrived at specific wintering and summering sites with highly predictable timing. Therefore, a complex, perhaps cyclic movement pattern with long periods between returns to particular sampling localities has been assumed (Heide-Jørgensen et al. 2006, 2010). It is possible that the occurrence of individual female whales in Disko Bay may correlate to a multi-year reproductive cycle with years with calving and nursing spent in the Central Canadian Arctic Archipelago, whereas pregnant or post-lactating females feed intensively in Disko Bay (Laidre et al. 2007, Heide-Jørgensen et al. 2010). If this were true, one would assume that female bowhead whales appear in Disko Bay concomitantly with the assumed reproductive cycle of 3 to 4 yr (Shelden & Rugh 1995). Based on an aerial survey conducted in April 2006, Heide-Jørgensen et al. (2007) estimated that 1229 whales (95% CI: 495–2939) were present in Disko Bay at that time. The abundance was also shown to be increasing in West Greenland, which would require a large calf production not directly observable in the area. If the stock supplying Disko Bay makes periodical visits to the bay, a multi-year mark−recapture identification of whales would provide a more realistic estimate of the size of the aggregation occurring in Disko Bay than an aerial survey restricted in time to a single season.

In this paper we present and discuss genetic based mark−recapture data of bowhead whales sampled in eastern Canada and West Greenland between 1995 and 2010. The data were examined in light of the proposed stock structure in this area, and recapture patterns were investigated for Disko Bay with respect to the bowhead whale reproductive cycle and their local abundance in Disko Bay.

**MATERIALS AND METHODS**

Skin biopsies were collected from free-ranging bowhead whales using crossbows with biopsy darts (Palsbøll et al. 1991). Biopsies were collected in Pelly Bay, Cumberland Sound, Foxe Basin, and Repulse Bay in eastern Canada and in Disko Bay, West Greenland, between 1995 and 2010. The data were examined in light of the proposed stock structure in this area, and recapture patterns were investigated for Disko Bay with respect to the bowhead whale reproductive cycle and their local abundance in Disko Bay.
Basin and Repulse Bay fall within the Hudson Bay–Foxe Basin stock distribution area. The majority of samples were collected during field operations where bowhead whales were instrumented with satellite transmitters. In Pelly Bay, Repulse Bay, and Disko Bay, biopsies were also collected by local hunters who were asked to sample the whales. A few additional samples were collected from the subsistence hunt in eastern Canada and West Greenland. The majority of samples in Disko Bay were collected between March and June, while the samples from Canada were collected between June and September, corresponding to the timing of when bowhead whales are present in these areas (see Table 1). All samples were stored in saturated sodium chloride and 20% DMSO (Amos et al. 1992) and kept frozen at −20°C until genetic analysis.

Total genomic DNA was extracted from the skin biopsies using commercially available DNA extraction kits (Qiagen DNeasy™ Blood & Tissue Kit, Omega Bio-tek E.Z.N.A™. Tissue DNA kit, or Sigma-Aldrich GeneEluTe™) following the manufacturers’ instructions. Molecular sex determination of all samples was conducted using a PCR-based approach following the principle outlined by Palsbøll et al. (1992) and the primers published by Bérubé & Palsbøll (1996). In short, ZFX/ZFY PCR products were generated using the primers ZFYX582F 5′-ATA GGT CTG CAG ACT CTT CTA-3′ and ZFYX1204R 5′-CAT TAT GTG CTG GTT CTT TTC TG-3′ (Bérubé & Palsbøll 1996). Subsequently, the PCR products were digested using the restriction endonuclease Oli I (Fermentas) that cuts at nucleotide position 152 in the ZFX nucleotide sequences, thereby providing 2 fragments for females only. The sex-specific restriction fragment patterns were visualized by standard electrophoresis using 1% agarose gels and 0.5x Tris-Borate-EDTA (TBE) buffer.

The quality of the obtained molecular data was assessed by several control experiments. The molecular sexing was performed in duplicate for 260 samples in the laboratories of the Natural History Museum, University of Oslo, Norway, and Fisheries and Oceans Canada, Winnipeg, Manitoba, Canada, respectively, and no incongruence was detected. Accordingly, the error rate for the molecular sexing was less than ~0.5%. The mitochondrial control region sequences were determined for 2 independent DNA extractions of 48 samples, and no sequence differences were detected, resulting in an error rate for the mt DNA sequencing of ~2% or less. For 7 microsatellite loci (Bmy26, Bmy29, Bmy33, Bmy41, Bmy42, Bmy53, Bmy58), a total of 460 genotypes were determined on independent extractions, which yielded 5 different genotypes and an error rate slightly above 1%, assuming that at least 1 of any 2 disaccording genotypes was correct. The probability of identity (PI), which is the probability that 2 unrelated individuals have identical genotypes, was calculated according
to Paetkau & Strobeck (1994). Single-locus PIs ranged between $7.09 \times 10^{-3}$ (Bmy29) and $9.07 \times 10^{-2}$ (Bmy33). The maximum PI (i.e. estimating at 4 microsatellite loci for individuals with identical sex and mitochondrial haplotype) was estimated at $6.85 \times 10^{-6}$ yielding an expected number of 1.74 pairs of unrelated individuals matching by chance.

In order to investigate possible cyclicity in recapture rates for females in Disko Bay, we estimated the probability of recapture ($p_{y+j}$) after $j$ number of years as:

$$p_{y+j} = \frac{n_y}{M_{y+j}} \times \left(\frac{r_{y+j}}{n_{y+j}}\right)$$

(1)

where $n_y$ is the number of whales sampled in year $y$, $M_{y+j}$ is the number of unique indentified whales sampled before year $y+j$, $r_{y+j}$ is the number of recaptures in year $y+j$, and $n_{y+j}$ is the number captured in year $y+j$. The total estimated probability for recapture after $j$ years is:

$$p_j = \sum (p_{y+j})$$

(2)

with summation over the years $y+j$. The observed number of recaptures after $j$ years was compared to the expected number of recaptures in order to evaluate possible cyclicity. The expected number of recaptures was estimated as:

$$\hat{r}_j = \sum (n_{y+j} \times p_{y+j})$$

(3)

A Chapman estimator with associated 95% CI (Chao & Huggins 2005) was used to make a mark–recapture estimate of the bowhead whales in Disko Bay in 2010.

The population size was estimated as:

$$\hat{N} = \left\{ \left[ (n_1 + 1) \times (n_2 + 1) / (m_2 + 1) \right] \right\} - 1$$

(4)

and its variance as:

$$\text{Var}(\hat{N}) = \left\{ [n_1 + 1] \times (n_2 + 1) \times \right.$$

$$\left. (n_1 - m_2)(n_2 - m_2) / [(m_2 + 1)^2 \times (m_2 + 2)] \right\}$$

(5)

where $n_1$ is the number of individuals captured in 2000 to 2009, $n_2$ is the number of individuals captured in 2010, and $m_2$ is the number of marked individuals captured in 2010. The 95% confidence interval (CI) was calculated as $\hat{N} \pm 1.96\text{Var}(\hat{N})^{-1/2}$.

We assumed a 0 mortality rate for all sampled individuals during the entire sampling period (2000 to 2010), which is unlikely to bias our results substantially given the lifespan of bowhead whales (George et al. 1999), so that all individuals identified in the period 2000 to 2009 were regarded as marked in the stock in 2010. Two females and 2 males (1 fetus) hunted in 2009 were not included in the estimation.

RESULTS

Genotype and sex were determined for 710 samples collected between 1995 and 2010. A total of 104 samples collected from Foxe Basin, Disko Bay, and Cumberland Sound were removed from the data set, as they were determined to represent recaptures within the same sampling season. Thus, 606 individuals were identified (209 males and 397 females; Table 1).

There were 29 between-year recaptures of individual whales, of which 26 were within the same sampling locality and 3 were between different localities (Table 1, Fig. 1). One individual was recaptured twice (a male from Repulse Bay recaptured the first time at the same locality and the second time in Cumberland Sound), while the others were recaptured only once. In Disko Bay ($n = 346$, 57% of all individuals), 21 (6%) were recaptured after 1 to 9 yr (4 males and 17 females). In Foxe Basin ($n = 160$; 26% of all individuals), 3 individuals (2%) were recaptured after 1 to 7 yr (1 male and 2 females). In Repulse Bay ($n = 15$; 2% of all individuals), 2 individuals (13%) were recaptured after 2 and 3 yr (1 male and 1 female, respectively).

Three recaptures were identified between areas (1 male and 2 females). All 3 individuals were recaptured in Cumberland Sound between June and August 2006 ($n = 29$, 5% of all individuals sampled, Table 1, Fig. 1). One female was first sampled in Foxe Basin in August 2003, while the other female was first sampled in Repulse Bay in September 1998. The male was previously sampled in Repulse Bay both in September 1998 and September 2000. Thus, 2 out of 4 individuals sampled in Repulse Bay in 1998 were sampled in Cumberland Sound 8 yr later. The low sample size does not cover the heterogeneity of the samples (different years and proportion of sex); it is therefore impossible to estimate the variance of the between-area recapture rate.

The observed number of recaptures in relation to number of years after first capture seems to be higher than expected for 1 and 4 yr, similar to that expected for 5 to 8 yr, and lower than expected for 2 and 3 yr (Table 2).

A mark–recapture estimate of the abundance in Disko Bay was calculated for whales identified between 2000 and 2009 (259) and re-identified in the sample of 75 with 13 recaptures collected in 2010 (Table 3). The resultant abundance estimate was 1410 bowhead whales (SE = 320, 95% CI: 783–2038) in the Disko Bay aggregation. We also calculated the
The resultant abundance estimate was 999 female bowhead whales (SE = 231, 95% CI: 546–1452) in the Disko Bay aggregation.
DISCUSSION

It was noted by European whalers operating in Baffin Bay and adjacent waters that bowhead whales occurred in a population segregated by age and sex with different migratory schedules for the different segments (Southwell 1898). Old whales were thought to overwinter off the entrance to Hudson Strait, move to Disko Bay in April and May, and then cross Baffin Bay to join the immature whales at Lancaster Sound (Southwell 1898). Small whales, as well as cows and calves, were taken in Prince Regent Inlet in July, August, and early September. Southwell (1898) maintained that females and young whales migrated south from Prince Regent Inlet through Fury and Hecla Strait through Foxe Basin to Hudson Strait in the fall. Females and young whales were thought to overwinter near the entrance of Hudson Strait as far south as the Labrador coast near the 57th parallel.

The 3 whales that were identified between localities were first sampled within the range of the presumed Hudson Bay–Foxe Basin stock and then recaptured in Cumberland Sound, or within what is hypothesized to be the Baffin Bay–Davis Strait stock
area. The sampling effort was relatively low before 2007 in most areas but increased substantially from 2007 in Disko Bay within the putative Baffin Bay−Davis Strait stock (2007 to 2010 = 264 individuals), while no individuals were sampled in the Hudson Bay−Foxe Basin putative stock area after 2006. Consequently, it is likely that the movements of bowhead whales between the 2 stock areas are underestimated because the identified individuals from the Baffin Bay−Davis Strait stock after 2007 were not available for re-identification in the Hudson Bay−Foxe Basin stock area.

Studies of exchange between individuals across presumed stocks are limited by the fact that several important aggregations of bowhead whales have not been sampled. This includes Prince Regent Inlet (estimated at 6344 bowhead whales in 2002, 95% CI: 3119−12,906, IWC 2009) and Isabella Bay on the east coast of Baffin Island (estimated at 1105 in 2009, 95% CI: 532−2294, Hansen et al. in press). These population estimates are from aggregations within the distribution area of the presumed Baffin Bay−Davis Strait stock. Bowhead whales also winter in Hudson Strait, at the mouth of Cumberland Sound and in the North Water (Heide-Jørgensen et al. 2007).

The movement of bowhead whales between the 2 presumed stock areas using genetic recapture is in good agreement with the results of satellite tracking data. Recent satellite tracking studies have shown that bowhead whales wintering off the west coast of Greenland summer in the eastern Canadian Arctic later swim to Hudson Strait where they overwinter (Heide-Jørgensen et al. 2003, 2006). In 2009, 27 bowhead whales were tagged in Disko Bay. One of these whales circumnavigated Baffin Island and 2 moved through Hudson Strait into the Repulse Bay area (GINR unpubl. data). In 2010, 2 of 40 tagged whales from Disko Bay went into the Repulse Bay area (GINR unpubl. data). Two out of 27 bowhead whales tagged with satellite transmitters in Foxe Basin and Cumberland Sound circumnavigated Baffin Island, and several whales moved from Foxe Basin to Prince Regent Inlet during the summer (Ferguson et al. 2010). All of these findings call into question the stock delineation in the area.

Primarily adult females without calves visit Disko Bay in the spring, suggesting that a multi-year movement pattern may be linked to their reproductive cycle (Heide-Jørgensen et al. 2010). However, the observed number of multi-year recaptures compared to the expected numbers of recaptures did not indicate any clear cyclicity consistent with the notion that the migration pattern of females to Disko Bay might be tied to their reproductive cycle. We have to some degree underestimated the recapture probabilities and the number of expected recaptures since estimates in years with 0 recaptures are 0. The underestimates are small and have no effect on the conclusion in relation to cyclicity. Some bowhead whales live more than 100 yr (George et al. 1999), and it is possible that the area in Disko Bay frequented by bowhead whales during the spring is revisited by individual whales over longer intervals than the 10 yr period covered by the sampling at this locality. Samples collected during the coming years might shed more light onto this question.

The mark−recapture estimate of the bowhead whale abundance in Disko Bay in 2010 was 1410 (SE = 320, 95% CI: 783−2038). This is similar to but more precise than the estimate of 1229 whales (95% CI: 495−2939) derived from an aerial survey conducted in April 2006 (Heide-Jørgensen et al. 2007). It is important to note that the aerial survey covered a single snapshot in time, whereas the mark−recapture estimate is based on 11 yr of genetic identification of the whale abundance that supplies the aggregation of whales in Disko Bay.

The Chapman mark−recapture estimator is based on a closed population model. The local aggregation of bowhead whales in Disko Bay constitutes a fraction of the entire population of bowhead whales inhabiting eastern Canada and West Greenland; however, the mark−recapture method with genetic markers still provides a valid estimate of the local spring abundance of bowhead whales in Disko Bay. One assumption under this model is that all whales supplying the aggregation must have an equal probability of being sampled in at least the period with the initial identifications or in the sampling for re-identifications. The long-term (10 yr) sampling for initial identification covers the likely reproductive cycle with cyclical returns to Disko Bay.

Another assumption of the closed model is that the stock size is constant over the study period. In our case, the stock was likely increasing (Heide-Jørgensen et al. 2007). This would negatively affect the abundance estimate of the aggregation in Disko Bay that consists of mostly mature females (Heide-Jørgensen et al. 2010). Few calves have been observed in Disko, and the increase is facilitated through calf production in other areas (e.g. Foxe Basin). This is also why the females are assumed to have a cyclical presence in Disko Bay that spans several years. In our study, the estimated female abundance was 71% of the estimated abundance for both sexes combined. Most of the male part of the total stock is distributed in other
areas (Heide-Jørgensen et al. 2010). Given that individual whales do not visit Disko Bay annually and that they are part of a larger stock, the mark–recapture estimate given here cannot be viewed as an abundance estimate for the total stock.

This study confirms that Disko Bay is an important area for female bowhead whales in spring and that the aggregation is part of a larger stock that ranges across eastern Canada and Baffin Bay. The study also demonstrates that long-term studies are required to understand the dynamics of this long-lived species.

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