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Mitochondrial genetic variation in bowhead whales in the western Arctic

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ABSTRACT

Bowhead whales in the Western Arctic are managed as a single stock by the International Whaling Commission (IWC). In response to recent concerns about the potential existence of multiple stocks in the region, we examined genetic variation in the mitochondrial control region among various spatial, temporal and age-related strata. Sequences from 382 samples were used in the comparisons. No significant differences were detected in spatial comparisons or in temporal comparisons along Alaska's North Slope. However the $\chi\chi^2$ analysis showed evidence of genetic heterogeneity between some of the age cohorts, specifically between animals born prior to 1918 (n=8) and those born after 1979 (n=34) (p=0.030), between those born 1918-1949 (n=13) and those born after 1979 (p=0.050), and between the two aforementioned older cohorts and those born after 1979 (p=0.009). There was also a significant F_{st} difference between autumn (n=13) and spring (n=11) whales from St. Lawrence Island (p=0.049). The age data were insufficient to determine if this seasonal difference was due in part to the difference between age cohorts.

KEYWORDS: BOWHEAD WHALE; GENETICS; WHALING; ARCTIC; NORTHERN HEMISPHERE

INTRODUCTION

Bowhead whales (*Balaena mysticetus*) in the western Arctic were heavily exploited in the 19th century, their numbers reaching a nadir of approximately 1,500 whales early in the 20th century (Brandon and Wade, 2006). This population, which inhabits the Bering, Chukchi and Beaufort Seas (BCB), has since increased to about 10,000 whales (George *et al*., 2004; Zeh and Punt, 2005), and is estimated to be growing at about 3% per annum (George *et al*., 2004). Fig. 1, based on information presented in Moore and Reeves (1993), depicts the basic movements and seasonal ranges of bowhead whales in the western Arctic. Although the map reflects the basic pattern of known movements exhibited by the majority of the population, traditional knowledge, historical catch records (Bockstoce *et al*., 2005) and recent scientific observations indicate that there is considerable variation around this model. Although the commercial harvest has long ended, subsistence hunting by aboriginal communities continues in Alaska and along the Chukotka Peninsula in Russia, with an annual take of 30-40 whales per year over the past two decades (Braham, 1995; Suydam *et al*., 2006). Since 1977, the IWC has managed this population as a single stock (IWC, 2001; Rugh *et al*., 2003). However, in recent years, there have been questions raised regarding the possible presence of multiple stocks within the BCB population (Anon., 2005), which if true may necessitate a revision of management practices (e.g. IWC, 2006)[1].

Some multi-stock hypotheses involve spatial separation within the range of the population, while others invoke a temporal difference in the timing of migration. Another alternative is that there is only a single stock, but that genetic differences among age cohorts have arisen from the unusual demographic history of the population together with the unusual life history of bowhead whales, which live much longer than any other cetacean. A considerable amount of research, including the use of genetic markers, has been directed at examining these hypotheses (e.g. Jorde *et al*., 2007). Taylor *et al*. (2007) reviewed the different lines of evidence that bear upon the stock issue, including life history parameters, distribution and movements, catch records and genetic variability, concluding that the preponderance of evidence indicates the presence of a single stock. For genetic studies, it is reasonable to expect that most possible genetic subdivisions will be more easily detectable by the use of mitochondrial markers than nuclear genes; the haploid nature and maternal inheritance of the mitochondrial genome result in a smaller effective population size that is more strongly influenced by the effects of genetic drift (Avise, 1995). The magnitude of differentiation will be larger for mtDNA; however, mtDNA used alone will be unable to differentiate strata if the strata themselves contain samples from multiple stocks. Here, the results from an examination of genetic diversity are presented, both spatial and temporal, in BCB bowhead whales using mitochondrial control region sequences.

MATERIALS AND METHODS

Samples came primarily from whales taken in subsistence hunts, with additional samples taken from biopsies and stranded whales. The supplemental data contain a complete

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[1] Subsequent to the completion of this paper, the IWC Scientific Committee found that the bowhead *SLA* (*Strike limit algorithm*) used to provide management advice was robust to a wide range of stock structure hypotheses (IWC, 2008a).

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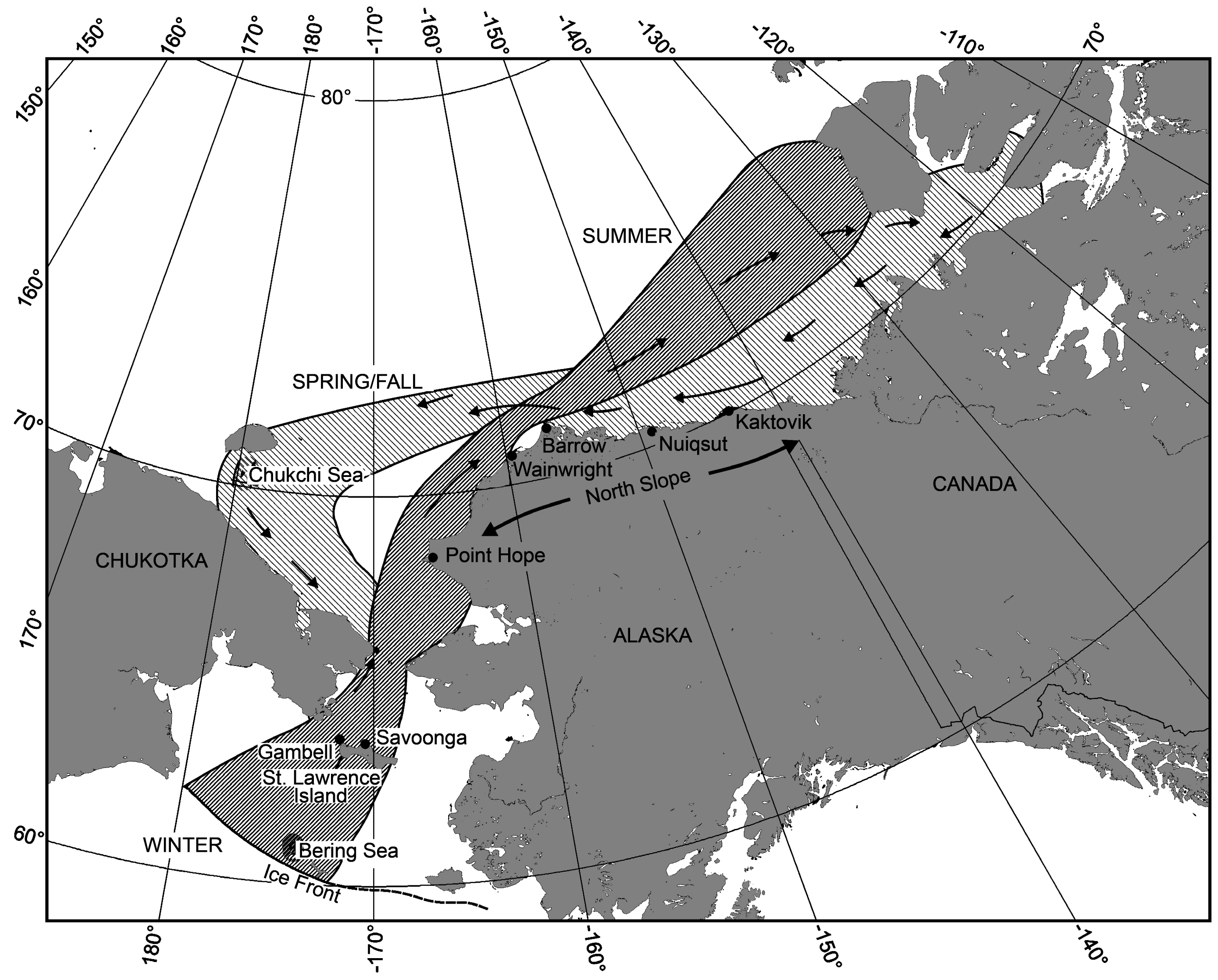

Fig. 1. Basic pattern of seasonal movements of bowhead whales in the western Arctic, based on information from Moore and Reeves (1993). The dark shading indicates spring migration (March to June), and the lighter shading is summer-autumn (July to November). The wintering area is Bering Sea south of the Bering Strait and north of 60°N; but mainly in the NW Bering Sea including Anadyr Gulf and within the seasonal sea ice.

list of samples, with their collection information, stratification and haplotype information. DNA extraction, amplification, and sequencing of skin samples were conducted using standard protocols (LeDuc *et al*., 2005) and also see additional material[2]). DNA was extracted from samples of bone and baleen as in Morin *et al.* (2006).

The data set was stratified according to various temporal, spatial and age-related criteria. The spatial and temporal strata consisted of samples pooled over multiple years. The spatial strata applied were Barrow (the village on Alaska's North Slope with the largest hunt), the entire North Slope of Alaska (NS), St. Lawrence Island (SLI), Gambell and Savoonga (two villages on SLI), Alaska (comprised of NS plus SLI), and Chukotka, Russia. In addition, the Barrow and NS strata were divided into Fall (F; Aug-Oct) and Spring (S; Apr-Jun). Seasonal stratification for SLI was F (Nov-Jan) and S (Apr-May). For the age comparison, samples were divided into birth-year strata, based on the year of catch and the estimated ages of the samples based on baleen growth increments and aspartic acid racemisation (George *et al*., 1999; Lubetkin *et al*., In prep; Rosa *et al*., 2004). One stratum was comprised of animals born prior to the low point in the population's history (prior to 1918). The rest of the age-related strata were based on approximately 30-year increments after and including 1918 (i.e. 1918-49, 1950-79, and after 1979). In addition, a subsequent stratification was used wherein the two oldest cohorts were combined in order to increase the sample size of the oldest group. The sorting of individual samples into all the strata is given in the supplemental data. The calculation of Φ_{st} was performed using uncorrected pairwise differences in *Arlequin* 1.1. (Schneider *et al*., 1997). F_{st} and χ^2 (Roff and Bentzen, 1989) were calculated using a program written by KKM. For all analyses 10,000 permutations were used to calculate the *p*-value.

Due to the large number of samples obtained from skulls and baleen, there was some concern regarding some individual whales being duplicated in the dataset, either as multiple samples of hard tissue or as hard tissue and skin samples. Since the sample size from SLI is so limited, the potential effect of duplication of samples on the results is large. To address this, comparisons involving strata from SLI were reanalysed after incorporating putative matches into the dataset. To date, there have been two efforts to associate samples of bone and baleen with particular harvested whales. In the first, whale-ID numbers were assigned to the Gambell whale skulls used for the present study from the record of harvested whales going back to 1961, which included whale-ID number, body length, sex, date taken, and whaling captain. A whaling captain had been assigned to these skulls by one of the Gambell locals. Whale body length was then calculated using regression equations with skull length and skull width predicting body length.

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[2] *http://www.iwcoffice.org/_documents/publications/additions/mtDNA_sequences.xls*

These regression equations were derived using combined data for all whales with cranial measurements (e.g. male and female, data quality 1-3, 1974-2004); so they are NOT sex specific: (skull length (cm)2.3945+181.29)/100 = body length (m); (skull width (cm)5.7528+48.866)/100 = body length (m).

Using information from the whaling captain, the derived body length and any information in the comments mentioning if it was an old or recent skull, the skulls were matched to a whale-ID number from the harvest record. Those for which correct matches were fairly certain were considered as putative matches for the reanalysis. Less certain matches were not incorporated. These were usually due to uncertainty regarding the year of harvest for a particular skull, or the whaling record including multiple whales of a given size caught during the estimated time of harvest. In the second analysis, presented in Morin *et al.* (2007), nineteen single nucleotide polymorphisms (SNPs) were used to genotype samples and look for genetic matches. Although both methods produce equivocal results, they do provide some basis for detecting putative duplicates. All analyses involving SLI were therefore conducted twice; first with all samples treated as separate and independent and second incorporating SNP-based and 'fairly certain' matches from the aforementioned studies. These included matches within sample types (e.g. baleen – baleen) and between sample types (e.g. baleen – bone or bone – skin). The effect of incorporating theses matches was to reduce the sample size for most comparisons. However, since some of the matches were of skulls to previously unsampled whales, this meant that some of the skull samples now had collection dates associated with them. This allowed the seasonal comparison of SLI to have a greater sample size. Detailed sample information and stratifications used can be found on the IWC website[3]. The putative matches have been added to the table[3] in a separate column and the putative collection info (for whales not already represented by other samples) has been included in parentheses.

RESULTS AND DISCUSSION

There were 68 different haplotypes recorded, defined by 44 variable sites. For details about the frequencies and specific sequences, see Appendix 1 and additional data[3]. Complete sequences are available on Gen Bank, accession numbers FJ744425-FS744492. Results of the pairwise comparisons are summarised in Table 1. None of the spatial comparisons yielded significant differences. Significant differences were seen in χ^2 analyses between the animals born before 1918 and those after 1979, between those born 1918-1949 and those after 1979, as well as between the two oldest cohorts combined and the youngest. There was near significance (p=0.088) when the youngest cohort was compared to those born 1950-1979. It may be that the historical population dynamics of the BCB bowhead whales – extreme reduction followed by rapid recovery – have led to changes in haplotype frequencies across generations, at least between those generations on either side of the population's nadir (Martien *et al*., 2007; Ripley *et al*., 2006). Shifting haplotype frequencies over time have also been found for a recovering population of humpback whales (Rosenbaum *et al*., 2002). For the bowhead whales, additional samples from aged whales are desirable to further assess the variability between cohorts.

There have been several multi-stock hypotheses proposed for this population in recent years (IWC, 2008b). In some of those hypotheses, the stocks are spatially segregated, with one stock migrating past and being hunted along the North Slope, and the other predominating around either St. Lawrence Island or the Chukotka Peninsula. The results presented here do not support these multi-stock hypotheses, as all the comparisons were non-significant at the 0.05 level. In comparison, LeDuc *et al*. (2005) found that BCB and Okhotsk Sea bowhead whales were different in their mitochondrial sequences in an F_{st} analysis (p=0.026), and that the Okhotsk Sea population had a much lower level of haplotypic diversity (0.61 vs. 0.93). However, there is a caveat attached to the comparisons involving Chukotka. Available samples do not allow adequate testing for a resident stock of bowhead whales off the Chukotka Peninsula because samples for Chukotka were only available in the autumn, which is a period when some whales that migrate to the Canadian arctic are known to move to Chukotka for autumn feeding (Krutzikowsky and Mate, 2000; Mate *et al*., 2000; Moore and Reeves, 1993). To test for the potential of a resident Chukotka group, samples need to be collected there in spring or early summer when all the whales that migrate along the North Slope are thought to be in Alaskan and Canadian waters.

Other multi-stock hypotheses that have been suggested postulate the existence of temporally segregated stocks. Under these hypotheses, the animals migrating past Barrow in the spring constitute a single, pure stock, while those passing Barrow in the autumn represent a mixed-stock assemblage. This hypothesis would predict some level of genetic differentiation between Barrow animals hunted in the spring and autumn. No such differentiation was found.

There was a significant difference found between autumn and spring whales from SLI when putative matches were incorporated into the dataset. Although intriguing, this may not necessarily be indicative of the presence of multiple stocks. Given that one season (fall) occurs just before the mating season, the whales caught in this season may include a higher proportion of older whales than those caught in spring, and the difference may therefore be age-related. At present there are not enough data to test this hypothesis because only one SLI sample came from an animal that had been aged.

For all the comparisons, the results should not be considered conclusive. Many of the strata had small samples sizes, and non-significant p-values may reflect low power (Type II error) – the addition of more samples may lead to different results. On the other hand, Type I errors are also possible. In seasonal comparisons (F v S) for Barrow and the North Slope, there were significant and near significant differences that were found in earlier studies (Taylor *et al*., 2004) that have disappeared with the addition of more samples (present results). Although an explicit calculation of statistical power would provide readers with a stronger ability to interpret the data, specific alternate hypotheses regarding the magnitude of expected differentiation between strata are needed for such calculations. It had been hoped that such specific alternate hypotheses could have been obtained from analyses of nuclear DNA data together with reviews of other data relevant to population structure (reviewed in Taylor *et al*., 2007). However no specific alternate hypotheses with specific hypothesised abundances and levels of dispersal arose from those other data sources.

In addition to the statistical considerations discussed above, interpretation of genetic data for bowhead whales is further complicated by various factors: a population known

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[3] *http://www.iwcoffice.org/_documents/publications/additions/mtdnaSTRATAnew.xls*

Table 1

Results of the analyses of mitochondrial sequence data. Note: Data set includes two stranded whales that were used in large-scale spatial analyses (e.g., NS v SLI) but were omitted from temporal analyses or those strata specific to a village.

Strata (sample size)	F_{st}	*p*	χ^2 (per df)	*p*	Φ_{st}	*p*
Spatial						
Barrow (258) v SLI (63) I	-0.0006	0.469	0.995	0.493	0.006	0.122
Barrow (258) v SLI (52) II	-0.003	0.820	0.865	0.772	0.0003	0.357
Barrow (258) v Savoonga (21) I	-0.002	0.495	0.856	0.688	-0.002	0.464
Barrow (258) v Savoonga (20) II	-0.004	0.587	0.857	0.687	-0.003	0.494
Barrow (258) v Gambell (42) I	0.002	0.218	1.133	0.243	0.012	0.069
Barrow (258) v Gambell (32) II	-0.004	0.731	0.935	0.597	0.001	0.342
Barrow (258) v Chukotka (22)	-0.009	0.919	0.707	0.877	-0.009	0.764
AK (360) v Chukotka (22) I	-0.008	0.856	0.752	0.792	-0.006	0.605
AK (349) v Chukotka (22) II	-0.008	0.879	0.750	0.799	-0.007	0.631
NS (297) v SLI (63) I	0.0004	0.359	1.026	0.429	0.005	0.147
NS (297) v SLI (52) II	-0.003	0.728	0.895	0.709	-0.0001	0.390
NS (297) v Savoonga (21) I	0.00003	0.394	0.883	0.643	-0.0009	0.409
NS (297) v Savoonga (20) II	-0.002	0.506	0.880	0.637	-0.002	0.436
NS (297) v Gambell (42) I	0.003	0.211	1.150	0.226	0.011	0.082
NS (297) v Gambell (32) II	-0.004	0.714	0.955	0.563	-0.0001	0.382
NS (297) v Chukotka (22)	-0.009	0.913	0.711	0.860	-0.008	0.695
Temporal						
Barrow F (133) v S (125)	0.0003	0.357	0.984	0.546	0.002	0.210
NS F (154) v S (141)	-0.001	0.640	1.026	0.421	0.0003	0.346
SLI F (13) v S (11) I	0.054	0.070	1.180	0.176	-0.013	0.481
SLI F (14) v S (17) II	0.056	0.024	1.193	0.154	0.011	0.268
Age cohort						
Birth-year <1918 (8) v 1918-1949 (13)	-0.010	0.513	1.102	0.320	-0.035	0.714
Birth-year <1918 (8) v 1950-1979 (25)	-0.013	0.680	1.001	0.686	-0.027	0.698
Birth-year <1918 (8) v >1979 (33)	0.003	0.357	1.519	0.030	0.005	0.361
Birth-year 1918-1949 (13) v 1950-1979 (25)	-0.010	0.652	0.745	0.981	0.006	0.315
Birth-year 1918-1949 (13) v >1979 (33)	0.010	0.230	1.390	0.050	0.007	0.294
Birth-year 1950-1979 (25) v >1979 (33)	0.008	0.182	1.194	0.088	-0.009	0.566
Birth-year <1950 (21) v 1950-1979 (25)	-0.007	0.652	0.910	0.829	0.004	0.322
Birth-year <1950 (21) v >1979 (33)	0.009	0.204	1.386	0.009	0.010	0.236

to be out of demographic equilibrium because of recent population dynamics, sampling that is known to be non-random with respect to the age structure of the population and limited sample sizes outside of the migratory corridor that includes Barrow. The unusual longevity of bowhead whales means that the sample set contains both whales born during the commercial whaling era over 100 years ago, who represent a relatively pristine population, and whales born in recent decades, representing a population in the process of increasing from around 1,500 whales to the current 10,000. The genetic sample set has the potential to exaggerate the patterns of disequilibrium by disproportionately selecting the oldest and youngest individuals. Bowhead whales are known to migrate according to age and reproductive condition (Moore and Reeves, 1993). Some of the smaller villages prefer the largest whales, while Barrow whalers prefer smaller whales. The present mtDNA results are consistent with a single stock with genetic heterogeneity related to age cohorts, and patterns of genetic heterogeneity found in other markers (e.g. Jorde *et al*., 2007) could also result from similar age-related processes as those that were suggested here. However, samples sizes for many strata are small, and some hypotheses of stock structure do not lend themselves to testing with the present dataset. Ideally, samples would be obtained from breeding grounds and season to directly test for the presence of multiple stocks.

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