Further mitochondrial DNA analyses on stock structure in the B-C-B stock of bowhead whale

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ABSTRACT

Genetic analyses based on mtDNA control region sequences were conducted on samples of the B-C-B stock of bowhead whale collected from different villages engaged in aboriginal whaling. Laboratory work on mitochondrial DNA sequencing was carried out by US scientists and access to these data was possible under the Scientific Committee's data access protocol (Procedure A). The total number of sequences available was 380. A 68.2% of those come from a single locality (Point Barrow). An additional 24 sequences from the Okhotsk Sea bowhead whale stock and four from the Commander Island were used in the analysis for comparative purposes. Same as previously reported, the nucleotide diversity was smaller in whales from the Okhotsk Sea stock than in whales from the different localities of the B-C-B stock. The quantification of the temporal and geographical mtDNA differentiation was carried out using the Fst. In addition the genetic relationship was quantified using the chi-square statistics for heterogeneity of mtDNA haplotype frequencies. First temporal (seasonal) differentiation was examined in those localities with larger sample sizes (St. Lawrence Island and Point Barrow). Subsequently geographical mtDNA differentiation among four localities (Point Barrow, St. Lawrence Island, Chukotka and Okhotsk Sea), was examined. No significant mtDNA heterogeneity was found among B-C-B stock whales, apart of a significant seasonal heterogeneity for Fst found in St. Lawrence Island. In contrast with a previous mtDNA result, no significant heterogeneity was found at Barrow when the samples were grouped into spring and fall. Significant genetic heterogeneity was found between B-C-B stock localities and whales from the Okhotsk Sea stock. In general these mtDNA results provide no strong evidence for genetic population structure within the B-C-B stock. Sample sizes for several localities and months, however, remain low and therefore negative results in some comparison could just reflect the low statistical power of the analysis. Furthermore samples from Chukotka and St. Lawrence Island obtained in summer months, which are essential to investigate some of the multiple stock hypotheses, are still not available for analyses. At Barrow nuclear DNA markers have suggested structure. It is possible therefore that the mtDNA analysis could not identify structure if two stocks mix to each other in similar proportion when they pass through that locality.

INTRODUCTION

For management purposes the IWC has recognized five stocks of the bowhead whale (*Balaena mysticetus*) (Fig. 1). All these stocks, but the Bering-Chukchi-Beaufort (B-C-B) stock, are in the category of heavily depleted (in some cases perhaps extinguished e.g. the Spitsbergen stock). The B-C-B stock is the target of aboriginal whaling and the IWC manages this stock under the Aboriginal Whaling Management Procedure (AWMP). During the 2002 Scientific Committee Meeting an estimation of 9,860 animals was given for this stock (IWC, 2003). The estimation come from sighting data obtained during the spring migration at Point Barrow.

The B-C-B stock winters in central and western Bering Sea. From April to June whales migrate north and east until they pass Point Barrow where they travel east toward the south-eastern Beaufort Sea. Whales spend most of the summer through the Beaufort Sea. During the fall whales migrate west out the Beaufort Sea. From mid-September to mid October bowhead whales are seen in the northeast Chukchi Sea. Whales migrate from Point Barrow into the Chukchi Sea heading toward Wrangel Island. When they reach the Siberian coast, they follow it southeast to the Bering Sea. Fig. 2 is a modified version of Fig. 9.7 in Moore and Reeves (1993). This figure shows the generalized seasonal migration of the B-C-B stock and the locations of the villages where whales are hunted for aboriginal purpose.

Despite the limited availability of data and comparative analyses within the distribution area of the B-C-B stock, the Scientific Committee recommended in 2002 the single B-C-B stock scenario for management purpose (IWC, 2003). At that opportunity this was the only stock structure scenario considered by the AWMP. Recent genetic analyses conducted under the Scientific Committee data access protocol have showed substantial degree of heterogeneity within the B-C-B stock (e.g. Jorde *et al.*, 2004), and the possibility of additional stock structure has been considered. During the First Intersessional AWMP Workshop for the 2007 Bowhead *Implementation* Review, a total of nine stock structure hypotheses were considered. Four of these hypotheses involve single stock scenarios while five involve two stock scenarios (IWC, 2006a).

Previous mtDNA analysis showed a significant genetic heterogeneity when the samples in Point Barrow were grouped into spring (n= 98) and fall (n= 93) migrants (Fst= 0.007; p=0.0403) (Pastene *et al.*, 2004). LeDuc *et al.* (2006) conducted a mtDNA analysis using a large sample size. The comparison between spring (n= 135) and fall (n= 151) animals for North Slope resulted in no significant genetic heterogeneity (Fst= -0.0015; p=0.7302). They found a similar result for the comparison between spring and fall migrant in Point Barrow (Fst= 0.0003; p= 0.3574). The objective of this study is to conduct an update of the mitochondrial DNA (mtDNA) analysis using all availability data.

MATERIALS AND METHOD

Available data
Following the Procedure of Data Availability adopted by the Committee during the 2003 meeting (IWC, 2004), mtDNA data of the B-C-B stock was requested to and provided from US scientists. These included mtDNA control region sequences (397bp).

Table 1 shows the number of samples available for the mtDNA analysis by locality and month. Most of the available samples from the B-C-B stock localities come from Barrow (68.2%). A number of samples in St. Lawrence Island and Chukotka in the DNA data set were in the category of 'unknown', which mean that month or year allocation is uncertain. In the case of Gambell (St. Lawrence Island) some samples were assigned to month and year following the criteria provide in the DNA data set. The hypothesis testing analysis followed a step wise fashion. First temporal (seasonal) variation was examined in St. Lawrence Island and North Slope (the localities with larger sample sizes). Analysis of yearly variation was not possible due to the small sample sizes obtained when the samples were divided by year. However for the analysis of temporal (seasonal) variation the North Slope and Barrow samples were divided into two periods: 'Early Years' 1983-2000 and 'Late Years' 2001-2006. Next we conducted an examination of spatial differentiation among the main localities of the B-C-B stock: Barrow, St. Lawrence Island, Chukotka. For this analysis the total samples were used (included all samples in the 'unknown' category). Samples from the Okhotsk Sea were used as out-group.

mtDNA analysis
The evolutionary distance between two nucleotide sequences was calculated according to Kimura's two parameters method (Kimura, 1980). The degree of genetic diversity within each locality was estimated using the nucleotide diversity (Nei, 1987).

Following LeDuc *et al.* (2006) the Fst in AMOVA (Excoffier *et al.*, 1992) was used to investigate the temporal/spatial differentiation of mtDNA variation. In addition we used the randomized chi-square Test of Independence (Roff and Bentzen, 1989) to test genetic differences. In each test a total of 10,000 randomizations of the original data set were performed. A 'p' value below 5% was used as criteria for rejecting the null hypothesis of panmixia.

RESULTS

Variability of mtDNA control region sequences
A segment of 397bp of the mtDNA control region was determined in 408 animals. A total of 45 polymorphic sites defined 68 unique sequences (haplotypes) (Table 2). Nucleotide diversity by locality and stock is shown in Table 3. As reported by LeDuc *et al.* (2005) the diversity in the Okhotsk Sea samples was lower than in the B-C-B samples.

Geographical and temporal distribution of haplotypes
Table 2 shows the distribution of haplotypes among localities. Samples in Barrow were grouped into 'spring' and 'fall' groups. The samples from the Okhotsk Sea and Commander Island are included for comparison. The main haplotype in the B-C-B localities was haplotype '42' (24.2%) followed by haplotype '23' (7.9%). The main haplotype in the B-C-B localities was also the main haplotype in the Okhotsk Sea stock (54.2%). The four haplotypes in this stock were represented in the B-C-B localities. The Commander Island, which is located between Okhotsk Sea and Bering Sea, showed three haplotypes (n=4). All of them were represented in the B-C-B localities. One of them (n=2) was represented in the Okhotsk Sea samples.

Test for temporal differentiation
Table 4 shows the results of the heterogeneity test for temporal differentiation in St. Lawrence Island. The Fst showed significant differences when the samples were grouped into spring and winter seasons.

Tables 5 and 6 show the results of the heterogeneity test for temporal differentiation in North Slope and Barrow, respectively. The seasonal differentiation analysis was conducted for 'Early Years' and 'Late Years' periods as well for the all years of sampling. None of the comparisons by chi-square and Fst resulted in significant mtDNA differences.

Test for spatial differentiation
Table 7 shows the results of the heterogeneity test for spatial differentiation. No significant differences were found among the three localities of the B-C-B stock. However significant differences were found when these localities were compared with whales of the Okhotsk Sea Stock. This differentiation was more evident from the results of the Fst analysis.

DISCUSSION

The analysis of mtDNA on B-C-B stock of bowhead whales conducted in this study failed to find evidence of significant genetic heterogeneity within this stock. The only positive result was that found for St. Lawrence Island where a significant mtDNA heterogeneity for Fst was found when the samples were grouped into spring and winter. However the sample sizes in this comparison was small, 18 and 14, respectively, and it is possible that this result changes if sample size is increased. Also it is possible that the allocation of 'unknown' samples to month in Gambell might not be completely correct. Furthermore the problem of possible duplicate in bone and baleen samples in this locality has not been completely resolved (LeDuc *et al.*, 2006). The alternative explanation is that the sample in St. Lawrence Island contains animals from two different stocks and mtDNA differences were detected because the mixing proportion of these stocks was different in these two seasons. Further analysis with larger sample size is necessary for this locality.

Our analysis was conducted for both sexes combined. An analysis by sexes in Barrow (locality with the larger sample size) had shown no differences between female and male samples (data not shown). A strict analysis of yearly variation in the different localities was not possible due to the small sample size obtained when the samples were grouped by year. The analysis in Barrow was conducted for two year periods and no significant differences were found between these two periods. In both of these periods samples obtained in several years were combined. This required the assumption that the pattern of migration in each year is the same.

In general results of our mtDNA analysis provide no strong evidence for population structure within the B-C-B stock of bowhead whale. However the sample sizes for several localities and months remain low (see Table 1). Therefore the negative results of some of the tests could just reflect the low statistical power of the analysis. A sample size of n=24 in Chukotka was large enough to detect significant differences with the sample of the Okhotsk Sea stock. However the degree of genetic differentiation among putative stocks within the area of distribution of the B-C-B stock is expected to be smaller than that between B-C-B and Okhotsk Sea stocks, therefore larger sample sizes will be necessary to detect mtDNA differences among putative stocks within the B-C-B stock.

The Scientific Committee has recognized that the interpretation of the results of hypothesis tests when the null hypothesis is not rejected is difficult because failure to reject the null hypothesis may occur not only if the null hypothesis is true but also if the null hypothesis is false but the data are insufficient to identify this (i.e. the statistical test has low power). The Committee has recommended that the power of the statistical techniques should be explored in these cases. In the case of the North Pacific Bryde's whale RMP *Implementation* the

genetic analysis involved the use of the same genetic markers but larger sample sizes by locality than in the case of the bowhead whale. No significant genetic differences among localities were found. Kitakado *et al.* (2005) evaluated power under an island model and the Workshop where the results were presented believed that the approach used in that study provided a defensible means of identifying the power of the hypothesis test (IWC, 2006b). A similar approach could be used to examine the power of the hypothesis test in the case of the bowhead mtDNA analysis.

Apart from the issue of the number of samples the attainment of samples in particular months is important to test different hypotheses on stock structure. For example summer samples from the St. Lawrence Island and Chukotka are essential to test Hypotheses 7 and 8 listed during the First Intersessional Workshop. Such samples are still not available for the genetic analysis (see Table 1) and further effort should be made to attain such samples.

Previous mtDNA analysis showed a significant genetic heterogeneity when the samples in Barrow were grouped into spring (n= 98) and fall (n= 93) migrants (Fst= 0.007; p=0.0403) (Pastene *et al.*, 2004). In the present analysis comparison between the spring (n=123) and fall (n=134) produced dramatic differences in comparison with the results of the pervious mtDNA analysis, not only in p value but also in Fst (Fst=0.001, p=0.2930). The present results are similar to those obtained by LeDuc *et al.* (2006). One explanation for these results is that there is no genetic structure of bowhead whale at Barrow. An alternative explanation for the negative results found is that whales from two different stocks are present in the spring and fall migrant groups but they mix in similar proportion in both seasons. The implication of this is that the occurrence of multiple stocks at that locality is not detected by the mtDNA analysis. A similar rationale has been presented in the case of the North Pacific Bryde's whale *Implementation* to explain negative results. In the case of bowhead whale, analyses of nuclear DNA markers in Barrow suggested structure (see Kitakado *et al.* in this meeting) and the possibility of mixing can not be discarded. Apart from further analysis of nuclear markers during migration, the attainment of genetic samples from breeding grounds will help in resolving the issue of possible mixing of stocks during migration in the case of the bowhead whale.

ACKNOWLEDGMENTS

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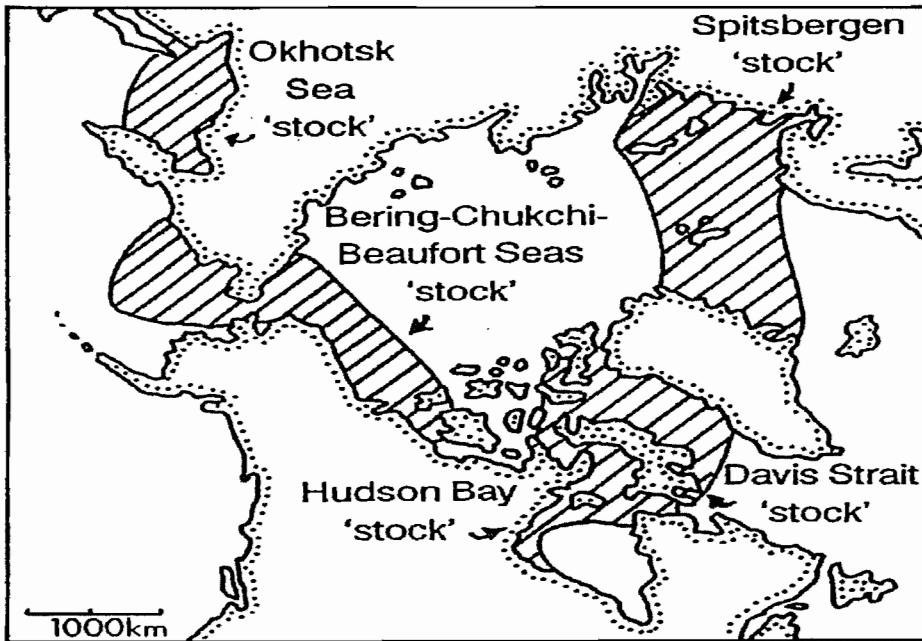
Fig. 1: Putative stocks of the bowhead whale (modified from IWC, 1992).
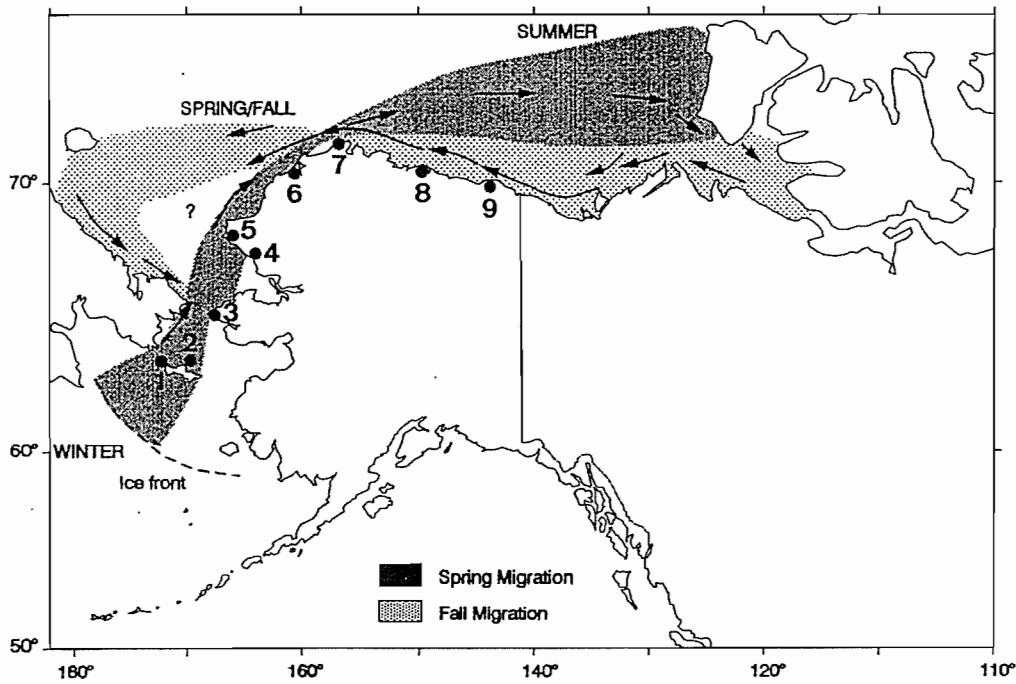
Fig. 2: Generalized seasonal occurrence and migration corridor for the B-C-B bowhead whale stock depicting spring and fall pathways. The figure also shows the villages where whales are taken by aboriginal whaling: 1= Gambell (Lawrence Island, Bering Sea), 2=Savoonga (Lawrence Island, Bering Sea), 3= Wales (Bering Sea), 4=Kivalina (Chuckchi Sea), 5= Pt. Hope (Chuckchi Sea), 6= Wainwright (Chuckchi Sea), 7= Barrow (Chuckchi Sea), 8= Nuiqsut (Beaufort Sea), 9= Kaktovik (Beaufort Sea) (modified from Moore and Reeves, 1993).

Table 1: Number of samples of bowhead whale used in the mtDNA analysis, by locality and month. All fetus samples except 99B6F are excluded from this Table. UK: sampled month or year is unknown.

Strata	Village	Year	1	2	3	4	5	6	7	8	9	10	11	12	UK	Total
	Barrow	1983					1									
		1984					3									
		1986				2	3									
		1987					1									
		1988									1					
		1989					2					3				
		1990					2					3				
		1992					2			1	8	1				
		1993				6	7									
		1995					3	1			2	2				
		1996				1	4				18					
		1997					8	1		1	14	5				
		1998					9				1	1		1[*1]		
		1999				1	8					6				
		2000				1	4				4	2				
		2001				1	16					4				
		2002					3				1	18				
		2003				1	8	1				5				
North Slope		2004				2	3	1			9	6				
		2005				2	12[*2]					13		5[*3]		
		2006					3								1	
	Wainwright	1981					2									
		1984					1									
		2003				1										
		2005				2	2									
		2006					1									
	Kaktovik	1986									2					
		1990									1					
		2000									3					
		2002									3					
		2003									2					
		2004									3					
		2005									3					
	Nuiqsut	1992									1					
		2004									3					
		2005									1					
	Pt. Hope	2003				3										
		2005				1	5									
	Sub-total		0	0	0	24	113	4	0	2	80	69	0	0	7	299

Table 1: continued

Strata	Village	Year	Month													
			1	2	3	4	5	6	7	8	9	10	11	12	UK	Total
	Savoonga	1984				1										
		1989					1									
		1996				2										
		2001											1			
		2002												3		
		2003												2		
		2005	1			3							3			
		UK													3	
St. Lawrence Is.	Gambel	1988				1[*4]										
		1992		1[*4]												
		1993				2[*4]										
		1995					1[*4]									
		1996				1	2[*5]									
		1997					1[*4]									
		2002											1			
		2003				1										
		2004				1[*4]							1			
		2005	1			1										
		UK													22	
	Sub-total		2	1	0	13	5	0	0	0	0	0	4	7	25	57
Russia	Chukotka	1998					2									
		2000									1					
		2001										1				
		2002											1			
		2003										1				
		2004											1			
		UK													16	
	Diomed	2005				1										
	Commander Is	2000						4								
	Sub-total		0	0	0	1	2	4	0	0	1	2	2	0	16	28
	Okhotsuk	1995								13						
		1996									11					
	Sub-total		0	0	0	0	0	0	0	13	11	0	0	0	0	24
Other	Unknown														1[*6]	

Notes:
*1: BMY17798.
*2: 05B12(Hap 59) was excluded because sequence of Hap59 included Y code.
*3: These 5 biopsy samples collected in fall.
*4: Assigned "TRUE" in the IDFairlyCertain field using skull data by US colleague.
*5: One individual were assigned "TRUE" in the IDFairlyCertain field using skull data by US colleague.
*6: 05AM1

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Table 2: Distribution of bowhead mtDNA haplotypes among different localities.

Hap	North Slope							St. Lawrence Is.		Chukotka	Diomed	Commander Island	Okhotsuk Sea
	Barrow			Kaktovik	Nuiqsut	Wainwright	Pt. Hope	Savoonga	Gambel				
	Spring	Fall	Unknown										
1	3	6	0	0	0	0	0	1	0	0	0	0	0
2	0	5	0	0	0	0	0	0	1	1	0	0	0
3	3	1	0	0	0	0	0	0	1.	2	0	0	0
4	3	2	0	0	0	0	0	0	0	1	0	0	0
5	9	5	0	0	0	0	0	2	1	2	1	1	0
6	0	0	0	0	0	1	0	0	0	0	0	0	0
7	3	2	0	1	0	0	0	1	1	0	0	0	0
8	1	1	0	0	0	0	0	0	0	0	0	0	0
9	2	1	0	0	1	0	1	0	0	1	0	0	0
10	1	2	0	0	0	0	0	0	0	0	0	0	0
11	0	1	0	0	0	0	0	0	0	0	0	0	0
12	0	1	0	0	0	0	0	0	0	0	0	0	0
13	1	1	0	0	0	0	0	0	0	1	0	0	0
14	1	0	0	0	0	0	0	0	0	0	0	0	0
15	2	3	0	1	0	0	0	0	1	0	0	0	0
16	1	0	0	0	0	0	0	0	0	0	0	0	0
17	1	2	0	0	0	0	0	0	0	0	0	0	0
18	3	1	0	0	0	0	0	0	0	0	0	0	0
19	1	2	0	0	0	0	0	0	0	0	0	0	0
20	2	4	0	0	2	1	2	0	0	0	0	0	0
21	0	1	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	2	0	0	0	0
23	7	11	1	1	0	1	2	1	3	3	0	0	0
24	1	2	0	0	0	0	0	0	0	1	0	0	0
25	1	1	0	0	0	0	0	0	0	0	0	0	0
26	2	0	0	0	0	0	0	0	0	0	0	0	0
27	1	1	0	1	0	0	0	0	0	0	0	0	0
28	3	4	0	0	0	1	0	0	3	0	0	0	0
29	0	2	0	0	0	0	0	0	1	0	0	0	0
30	0	0	0	0	0	0	0	0	1	0	0	0	0
31	3	3	0	0	0	0	1	0	3	0	0	0	0
32	3	1	0	0	0	1	0	1	1	0	0	0	0
33	0	0	0	1	0	0	0	0	0	0	0	0	0
34	0	1	0	0	0	0	0	2	0	0	0	0	0
35	0	2	0	0	0	0	0	0	0	0	0	0	0
36	1	1	0	1	0	0	0	0	0	1	0	0	0
37	1	0	0	0	0	0	0	0	0	0	0	0	0
38	0	1	0	0	0	0	0	0	0	0	0	0	0
39	1	2	0	1	0	0	0	0	0	0	0	0	0
40	0	0	0	1	0	0	0	0	0	0	0	0	0
41	2	1	0	0	0	1	0	0	0	0	0	0	0
42	34	29	0	7	0	1	0	6	10	5	0	2	13
43	3	0	0	0	0	0	0	2	0	1	0	0	7
44	0	1	0	0	0	0	0	0	0	0	0	0	0
45	2	1	0	0	0	0	0	0	3	0	0	0	0
46	3	5	0	2	0	0	0	0	0	1	0	0	0
47	0	2	0	0	0	0	2	1	0	0	0	0	0
48	0	1	0	0	0	0	0	0	0	0	0	0	0
49	0	1	1	0	0	0	0	0	0	0	0	0	0
50	0	2	0	0	0	0	0	0	1	1	0	0	1
51	0	3	0	0	1	0	0	0	2	0	0	0	0
52	0	0	0	0	0	0	0	0	1	0	0	0	0
53	1	2	0	0	0	0	0	0	0	0	0	0	0
54	2	0	0	0	0	0	0	0	0	0	0	0	0
55	0	3	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	1	0	0	0
57	0	1	0	0	0	0	0	1	0	0	0	0	0
58	1	2	0	0	0	1	0	0	1	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0	0	0
60	1	0	0	0	0	0	0	0	0	0	0	0	0
61	8	2	0	0	0	0	0	0	0	1	0	1	0
62	1	0	0	0	0	0	0	0	0	0	0	0	0
63	1	0	0	0	0	0	1	0	0	0	0	0	0
64	3	3	0	0	0	0	0	2	0	0	0	0	3
65	0	1	0	0	0	0	0	0	0	0	0	0	0
66	0	1	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	1	0	0	0	0	0	0	0	0
68	0	0	0	0	0	1	0	0	0	0	0	0	0
	123	134	2	17	5	9	9	20	37	23	1	4	24

Table 3: Nucleotide diversity in bowhead whale by locality and stock (in parenthesis is the standard error).

Locality	Nucleotide diversity
Barrow Spring, n=123	0.0105 (0.0009)
Barrow Fall, n=134	0.0121 (0.0008)
Kaktovik, n=17	0.0087 (0.0023)
Nuiqsut, n=5	0.0151 (0.0037)
Wainwright, n=9	0.0158 (0.0027)
Pt. Hope, n=9	0.0113 (0.0023)
Savoonga, n=20	0.0113 (0.0022)
Gambell, n=37	0.0127 (0.0015)
Chukotka+Diomed, n=24	0.0104 (0.0020)
Okhotsk Sea, n=24	0.0081 (0.0025)

Table 4: Results of the heterogeneity test for temporal variation at **St. Lawrence Island**. In parenthesis are the sample sizes.

	Chi-square p-value	Fst	P value for Fst
April+May(18)/Nov-Feb(14)	0.1547	0.057	0.0179

Table 5: Results of the heterogeneity test for temporal variation at **North Slope** for two periods: 'Early Years' (1983-2000) and 'Late Years' (2001-2006). In parenthesis are the sample sizes.

	Chi-square p-value	Fst	P value for Fst
'Early Years' April-June(73)/August-October(80)	0.2347	0.003	0.2226
'Late Years' April-June(68)/August-October(76)	0.6111	-0.003	0.7499
'Total Years' April-June(141)/August-October(156)	0.3485	-0.001	0.6464

Table 6: Results of the heterogeneity test for temporal variation at **Barrow** for two periods: 'Early Years' (1983-2000) and 'Late Years' (2001-2006). In parenthesis are the sample sizes.

	Chi-square p-value	Fst	P value for Fst
'Early Years' April-June(70)/August-October(73)	0.2048	0.003	0.2289
'Late Years' April-June(53)/August-October(61)	0.9348	-0.006	0.8907
'Total Years' April-June(123)/August-October(134)	0.4541	0.001	0.2930

Table 7: Results of the heterogeneity test for spatial genetic variation among four localities: Barrow, St. Lawrence Island, Chukotka and Okhotsk Sea. Above diagonal chi-square p value; below diagonal Fst and Fst p value. In parenthesis are the sample sizes.

	Barrow (259)	St. Lawrence Is. (57)	Chukotka (24)	Okhotsk Sea(24)
Barrow	-	0.5377	0.8818	0.0527
St. Lawrence Is.	-0.0022 p=0.7220	-	0.1725	0.0652
Chukotka	-0.0069 p=0.8527	-0.0018 p=0.4868	-	0.0006
Okhotsk Sea	0.0799 p=0.0000	0.0669 p=0.0000	0.1017 p=0.0000	-