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 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 380 samples were used in the comparisons. No significant differences were detected in spatial comparisons or in temporal comparisons along Alaska's North Slope. However, in the χ^2 analysis, there was 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 fall (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.

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 in press). 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%/year (George *et al*. 2004). Although the commercial harvest has long ended, subsistence hunting by aboriginal communities continues to this day in Alaska and along the Chukotka Peninsula in Russia, with an annual take of 30-40 whales per year over the past 2 decades (Suydam *et al*, 2006, Braham 1995). Since 1977, the International Whaling Commission has managed this population as a single stock (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. 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). 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. Here we present results from an examination of genetic diversity, 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 contains a complete 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). 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 strata applied are 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 (George *et al*. 1999, Rosa *et al*. 2004, Lubetkin *et al*., in prep). 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., 1918-1949, 1950-1979, 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 a permutation χ^2 (Roff and Bentzen 1994)were calculated using a program written by KKM. For all analyses 10,000 permutations were used to calculate the p-value.

RESULTS AND DISCUSSION

Results are summarized in Table 1. None of the spatial comparisons yielded significant differences. Significant differences were seen in χ^2analyses 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. Shifting haplotype frequencies have also been found for a recovering population of humpback whales (Rosenbaum *et al.* 2002).

Strata (sample size)	F_{st}	p	χ^2	p	Φ_{st}	p
Spatial						
Barrow (258) v SLI (58)	-0.001	0.540	0.979	0.533	0.002	0.266
Barrow (258) v Savoonga (20)	-0.004	0.581	0.857	0.682	-0.003	0.486
Barrow (258) v Gambell (38)	0.002	0.266	1.104	0.292	0.005	0.184
Barrow (258) v Chukotka (22)	-0.009	0.933	0.707	0.875	-0.009	0.758
AK (357) v Chukotka (22)	-0.007	0.852	0.788	0.751	-0.006	0.621
NS (299) v SLI (58)	-0.0003	0.436	0.997	0.490	0.002	0.289
NS (299) v Savoonga (20)	-0.002	0.505	0.884	0.631	-0.002	0.445
NS (299) v Gambell (38)	0.002	0.253	1.112	0.285	0.004	0.219
NS (299) v Chukotka (22)	-0.009	0.911	0.714	0.863	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 (143)	-0.001	0.640	1.026	0.421	0.0003	0.346
SLI F (13) v S (11)	**0.075**	**0.049**	1.254	0.051	0.009	0.340
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 (34)	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 (34)	0.010	0.230	**1.390**	**0.050**	0.007	0.294
Birth-year 1950-1979 (25) v >1979 (34)	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 (34)	0.009	0.204	**1.386**	**0.009**	0.010	0.236

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.

There has been several multi-stock hypotheses proposed for this population in recent years. 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. Our results are not consistent with these multi-stock hypotheses.

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 fall represent a mixed-stock assemblage. This hypothesis would predict some level of genetic differentiation between Barrow animals hunted in the spring and fall. No such differentiation was found.

There was a significant difference found between fall and spring whales from SLI. This may not necessarily be indicative of the presence of multiple stocks. There are not enough data to test if this result arises from differences between age cohorts (only one SLI sample came from an aged animal). Furthermore, it remains to be seen if this slightly significant difference (p=0.049) persists as samples are added. This case may be similar to that seen in seasonal comparisons (F v S) for Barrow and the North Slope, where slightly significant and near significant differences that were found with smaller sample sizes (Taylor *et al*. 2004) have disappeared with the addition of more samples (present results).

Available samples do not allow testing for a resident stock of bowheads off the Chukotka peninsula because samples for Chukotka were only available in the fall, which is a period when whales that migrate to the Canadian arctic are known to have moved to Chukotka for fall feeding (Moore and Reeves 1993, Krutzikowsky and Mate 2000, Mate *et al*. 2000). To test for the potential of a resident Chukotka group, samples need to be collected in spring or early summer.

Interpretation of genetic data for bowhead whales is complicated by both a population known to be out of 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 Barrow. The unusual longevity of bowhead whales contributes to a sample set that 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. Bowheads are known to migrate according to age and reproductive condition (More 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. Patterns found in other nuclear markers (e.g. Jorde *et al*. in press) could result from similar processes.

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SUPPLEMENTAL DATA

Haplotypes and variable sites

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Variable sites

                111111111112222222222222222223333333
        15788899000111124440224555666677778891257888
Tax./Bp 67745748129013741395169347134501473409024589

BH1     ACTCTGTCCAGGCGCCGAGGACGGGTTCTCCATACTCGGTATTC
BH10    ......C.........AG.....A.C...T.....C...C.C.T
BH11    ......C................................C....
BH12    ..........A.................C.T....C...C....
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BH13    ..........A.................C.T........C....
BH14    ...........A...........................C....
BH15    .............A..A......................C....
BH16    .............A.................G...C...C....
BH17    ................A.....AAT...........T..C....
BH18    ................A......AT.......C...T..C....
BH19    ................A......AT..............C....
BH2     .A..............A....T.A.C...T.....C...C.C.T
BH20    ................A......AT...........T..C....
BH21    ................A......AT...........T..CC...
BH22    ................A...........C..........C....
BH23    ................A......................C....
BH24    ................A...................T..C....
BH25    ................A.............T........C....
BH26    ................A....T.AT...........T..C....
BH27    ................A....T.AT........G..T..C....
BH28    ................A....T.................C....
BH29    ................A...GT..............T..C....
BH3     ..C.........................C.....T....C....
BH30    ................AG.....A.CC..T.....C...C.C..
BH31    ................AG.....A.C...T.....C...C.C..
BH32    ................AG.....A.C...T.....C...C.C.T
BH33    ................AG.....A.C...T.....CT..C.C..
BH34    ................AG.....A.C...T.........C.C..
BH35    ................AG.......C...T.....C...C.C..
BH36    ................AG...T.A.C...T.....C...C.C..
BH37    ..................A.........................
BH38    ............................C.........AC....
BH39    ............................C..........C....
BH4     ....C...........A......................C..C.
BH40    .....................................A......
BH41    .......................................C.C..
BH42    .......................................C....
BH43    ............................................
BH44    ....................................T..C....
BH45    ....................................T.......
BH46    .................................G.....C....
BH47    ...............................G.......C....
BH48    .....................T..............T.......
BH49    .....................T...........G.....C....
BH5     ....C...........A......................C....
BH50    ...............TA......A.C...T......TA.C.C..
BH51    ...............TA......A.C...T......TA.C.C.T
BH52    ...............TA......A.C.T.T......TA.C.C.T
BH53    ..............T.A....T.................C....
BH54    ............TAT.AG.....A.C...T.........C.C.T
BH55    .........G......AG.....A.C...T.....C...C.C..
BH56    .........G.............................C....
BH57    ........G................................C..
BH58    ........T...TAT.AG.....A.C...T.........C.C.T
BH59    ........T...TAT.AG.....A.C...T....Y....C.C.T
BH6     ....C...........A...................TA.C..C.
BH60    ........T...TAT.AG...T.A.C...T.........C.C.T
BH61    .......T...............................C.C..
BH62    .......T...............................C....
BH63    ...TC...........A..............G.......C....
BH64    ...TC..........TA..T...A.C...T......TA.C....
BH65    ...T...................................C....
BH66    ...T...........................G.......C....
BH67    G......................................C....
BH68    ................A.....A.C...T.....CT..C.C.T
BH7     ....C...........A...................T..C....
BH8     ....C....T......A......................C....
BH9     .....A..TG......A...................T..C....
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GeneticID	Haplotype	Year	Month	Day	Village	Barrow v SLI	Barrrow v village/Chukotka	Barrow F v S	AK v Chukotka	NS v SLI	NS v village/chukotka	NS F v S	Age I	Age II	season sli
81WW2	BH42	1981	5	19	Wainwright				1	1	1	1			
81WW3	BH68	1981	5	28	Wainwright				1	1	1	1	1	1	
83B1	BH41	1983	5	5	Barrow	1	1	1	1	1	1	1			
84B1	BH42	1984	5	19	Barrow	1	1	1	1	1	1	1			
84B3	BH3	1984	5	20	Barrow	1	1	1	1	1	1	1			
84B4	BH18	1984	5	21	Barrow	1	1	1	1	1	1	1			
84S1	BH32	1984	4	19	Savoonga	2	3		1	2	3				2
84WW1_2	BH6	1984	5	18	Wainwright				1	1	1	1			
86B1	BH46	1986	4	27	Barrow	1	1	1	1	1	1	1	4	3	
86B2	BH42	1986	4	27	Barrow	1	1	1	1	1	1	1	4	3	
86B5	BH23	1986	5	4	Barrow	1	1	1	1	1	1	1	4	3	
86B6	BH23	1986	5	5	Barrow	1	1	1	1	1	1	1	3	2	
86B7	BH5	1986	5	6	Barrow	1	1	1	1	1	1	1	3	2	
86KK2	BH7	1986	9	17	Kaktovik				1	1	1	2	2	1	
86KK3	BH40	1986	9	26	Kaktovik				1	1	1	2	3	2	
87B4	BH4	1987	5	19	Barrow	1	1	1	1	1	1	1			
88B9	BH55	1988	9	15	Barrow	1	1	2	1	1	1	2			
89B2	BH25	1989	5	15	Barrow	1	1	1	1	1	1	1	3	2	
89B3	BH13	1989	5	28	Barrow	1	1	1	1	1	1	1	1	1	
89B4	BH42	1989	10	2	Barrow	1	1	2	1	1	1	2			
89B5	BH8	1989	10	2	Barrow	1	1	2	1	1	1	2			
89B6	BH20	1989	10	2	Barrow	1	1	2	1	1	1	2			
89S1	BH43	1989	5	25	Savoonga	2	3		1	2	3				2
90B1	BH39	1990	5	9	Barrow	1	1	1	1	1	1	1			
90B2	BH26	1990	5	10	Barrow	1	1	1	1	1	1	1			
90B7	BH31	1990	10	1	Barrow	1	1	2	1	1	1	2	4	3	
90B8	BH53	1990	10	2	Barrow	1	1	2	1	1	1	2	3	2	
90B9	BH1	1990	10	11	Barrow	1	1	2	1	1	1	2			
90KK1	BH39	1990	9	11	Kaktovik				1	1	1	2			
92B1	BH7	1992	5	28	Barrow	1	1	1	1	1	1	1			
92B11	BH51	1992	9	17	Barrow	1	1	2	1	1	1	2			
92B12	BH15	1992	9	19	Barrow	1	1	2	1	1	1	2			
92B18	BH42	1992	10	9	Barrow	1	1	2	1	1	1	2			
92B2	BH64	1992	5	29	Barrow	1	1	1	1	1	1	1	1	1	
92B3	BH42	1992	8	31	Barrow	1	1	2	1	1	1	2	2	1	
92B4	BH5	1992	9	1	Barrow	1	1	2	1	1	1	2	2	1	
92B5	BH44	1992	9	2	Barrow	1	1	2	1	1	1	2			
92B6	BH53	1992	9	2	Barrow	1	1	2	1	1	1	2			
92B7	BH2	1992	9	2	Barrow	1	1	2	1	1	1	2	3	2	
92B8	BH27	1992	9	3	Barrow	1	1	2	1	1	1	2			
92B9	BH51	1992	9	4	Barrow	1	1	2	1	1	1	2	2	1	
92N-BC-1	BH67	1992	9	1	Nuiqsut				1	1	1				
93B10	BH46	1993	5	3	Barrow	1	1	1	1	1	1	1			
93B11	BH61	1993	5	3	Barrow	1	1	1	1	1	1	1			
93B12	BH42	1993	5	4	Barrow	1	1	1	1	1	1	1			
93B13	BH26	1993	5	7	Barrow	1	1	1	1	1	1	1			
93B15	BH54	1993	5	7	Barrow	1	1	1	1	1	1	1			
93B16	BH42	1993	5	11	Barrow	1	1	1	1	1	1	1			
93B2	BH1	1993	4	21	Barrow	1	1	1	1	1	1	1			
93B3	BH5	1993	4	21	Barrow	1	1	1	1	1	1	1			
93B4	BH3	1993	4	25	Barrow	1	1	1	1	1	1	1			
93B5	BH9	1993	4	25	Barrow	1	1	1	1	1	1	1			
93B6	BH42	1993	4	30	Barrow	1	1	1	1	1	1	1			
93B7	BH42	1993	4	30	Barrow	1	1	1	1	1	1	1			
93B9	BH42	1993	5	2	Barrow	1	1	1	1	1	1	1			
95B1	BH20	1995	5	6	Barrow	1	1	1	1	1	1	1			
95B13	BH47	1995	9	16	Barrow	1	1	2	1	1	1	2			
95B17	BH42	1995	10	16	Barrow	1	1	2	1	1	1	2			
95B18	BH17	1995	10	17	Barrow	1	1	2	1	1	1	2			
95B4	BH27	1995	5	9	Barrow	1	1	1	1	1	1	1	4	3	
95B7	BH37	1995	5	25	Barrow	1	1	1	1	1	1	1	1	1	
95B8	BH42	1995	6	1	Barrow	1	1	1	1	1	1	1	3	2	
95B9	BH42	1995	9	5	Barrow	1	1	2	1	1	1	2	1	1	
96B1	BH42	1996	4	25	Barrow	1	1	1	1	1	1	1	4	3	
96B10	BH1	1996	9	12	Barrow	1	1	2	1	1	1	2	3	2	
96B11	BH23	1996	9	14	Barrow	1	1	2	1	1	1	2			
96B12	BH45	1996	9	14	Barrow	1	1	2	1	1	1	2			
96B14	BH1	1996	9	16	Barrow	1	1	2	1	1	1	2			
96B15	BH35	1996	9	16	Barrow	1	1	2	1	1	1	2	4	3	

96B16	BH28	1996	9	17	Barrow	1	1	2	1	1	1	2	3	2	
96B17	BH29	1996	9	19	Barrow	1	1	2	1	1	1	2	3	2	
96B18	BH46	1996	9	19	Barrow	1	1	2	1	1	1	2	3	2	
96B19	BH38	1996	9	19	Barrow	1	1	2	1	1	1	2	3	2	
96B2	BH4	1996	5	3	Barrow	1	1	1	1	1	1	1	4	3	
96B20	BH20	1996	9	19	Barrow	1	1	2	1	1	1	2			
96B21	BH42	1996	9	19	Barrow	1	1	2	1	1	1	2			
96B22	BH61	1996	9	24	Barrow	1	1	2	1	1	1	2	3	2	
96B23	BH42	1996	9	26	Barrow	1	1	2	1	1	1	2			
96B24	BH2	1996	9	26	Barrow	1	1	2	1	1	1	2	3	2	
96B3	BH16	1996	5	5	Barrow	1	1	1	1	1	1	1			
96B4	BH19	1996	5	24	Barrow	1	1	1	1	1	1	1	3	2	
96B5	BH61	1996	5	29	Barrow	1	1	1	1	1	1	1	1	1	
96B6	BH58	1996	9	10	Barrow	1	1	2	1	1	1	2	3	2	
96B7	BH42	1996	9	12	Barrow	1	1	2	1	1	1	2			
96B8	BH23	1996	9	12	Barrow	1	1	2	1	1	1	2			
96B9	BH51	1996	9	12	Barrow	1	1	2	1	1	1	2	3	2	
96G1_2	BH22	1996	4	1	Gambell	2	2		1	2	2				2
96G3	BH51	1996	5	3	Gambell	2	2		1	2	2				2
96S1	BH1	1996	4	7	Savoonga	2	3		1	2	3				2
96S2	BH34	1996	4	29	Savoonga	2	3		1	2	3				2
1BC97B	BH35	1997	8	16	Barrow				1	1	1				
97B1	BH5	1997	5	4	Barrow	1	1	1	1	1	1	1			
97B10	BH42	1997	6	4	Barrow	1	1	1	1	1	1	1	2	1	
97B11	BH3	1997	9	11	Barrow	1	1	2	1	1	1	2			
97B12	BH4	1997	9	12	Barrow	1	1	2	1	1	1	2			
97B13	BH55	1997	9	14	Barrow	1	1	2	1	1	1	2			
97B15_16	BH32	1997	9	20	Barrow	1	1	2	1	1	1	2			
97B17	BH46	1997	9	22	Barrow	1	1	2	1	1	1	2			
97B18	BH39	1997	9	22	Barrow	1	1	2	1	1	1	2			
97B19	BH2	1997	9	22	Barrow	1	1	2	1	1	1	2			
97B2	BH42	1997	5	7	Barrow	1	1	1	1	1	1	1			
97B20	BH23	1997	9	26	Barrow	1	1	2	1	1	1	2			
97B21	BH64	1997	9	27	Barrow	1	1	2	1	1	1	2			
97B22	BH10	1997	9	27	Barrow	1	1	2	1	1	1	2			
97B23	BH64	1997	9	27	Barrow	1	1	2	1	1	1	2			
97B24	BH21	1997	9	28	Barrow	1	1	2	1	1	1	2			
97B25	BH5	1997	9	28	Barrow	1	1	2	1	1	1	2			
97B26	BH23	1997	9	29	Barrow	1	1	2	1	1	1	2			
97B27	BH5	1997	10	2	Barrow	1	1	2	1	1	1	2			
97B28	BH42	1997	10	2	Barrow	1	1	2	1	1	1	2			
97B29	BH2	1997	10	17	Barrow	1	1	2	1	1	1	2			
97B3	BH18	1997	5	7	Barrow	1	1	1	1	1	1	1	2	1	
97B30	BH4	1997	10	18	Barrow	1	1	2	1	1	1	2			
97B31	BH42	1997	10	21	Barrow	1	1	2	1	1	1	2			
97B4	BH32	1997	5	8	Barrow	1	1	1	1	1	1	1			
97B5	BH1	1997	5	10	Barrow	1	1	1	1	1	1	1			
97B6	BH8	1997	5	12	Barrow	1	1	1	1	1	1	1			
97B7	BH32	1997	5	12	Barrow	1	1	1	1	1	1	1			
97B8	BH31	1997	5	15	Barrow	1	1	1	1	1	1	1	3	2	
98B1	BH18	1998	5	8	Barrow	1	1	1	1	1	1	1			
98B17	BH20	1998	9	24	Barrow	1	1	2	1	1	1	2			
98B2	BH61	1998	5	9	Barrow	1	1	1	1	1	1	1			
98B24	BH42	1998	10	7	Barrow	1	1	2	1	1	1	2	4	3	
98B3	BH28	1998	5	10	Barrow	1	1	1	1	1	1	1			
98B4	BH61	1998	5	17	Barrow	1	1	1	1	1	1	1			
98B5	BH17	1998	5	17	Barrow	1	1	1	1	1	1	1			
98B6	BH1	1998	5	23	Barrow	1	1	1	1	1	1	1			
98B7	BH42	1998	5	24	Barrow	1	1	1	1	1	1	1			
98B8	BH5	1998	5	25	Barrow	1	1	1	1	1	1	1			
98B9	BH31	1998	5	27	Barrow	1	1	1	1	1	1	1	3	2	
BWCH5	BH42	1998	5	27	Chukotka		4		2		4				
RUS021998	BH9	1998	5	27	Chukotka		4		2		4				
99B1	BH10	1999	4	28	Barrow	1	1	1	1	1	1	1			
99B14	BH61	1999	5	17	Barrow	1	1	1	1	1	1	1	2	1	
99B15	BH5	1999	5	17	Barrow	1	1	1	1	1	1	1	2	1	
99B17	BH42	1999	5	22	Barrow	1	1	1	1	1	1	1	1	1	
99B18	BH41	1999	5	23	Barrow	1	1	1	1	1	1	1	3	2	
99B19	BH15	1999	10	9	Barrow	1	1	2	1	1	1	2	4	3	
99B2	BH14	1999	5	2	Barrow	1	1	1	1	1	1	1			

99B20	BH23	1999	10	10	Barrow	1	1	2	1	1	1	2	4	3	
99B21	BH23	1999	10	10	Barrow	1	1	2	1	1	1	2	4	3	
99B22	BH28	1999	10	12	Barrow	1	1	2	1	1	1	2	4	3	
99B23	BH50	1999	10	13	Barrow	1	1	2	1	1	1	2	4	3	
99B24	BH28	1999	10	13	Barrow	1	1	2	1	1	1	2	4	3	
99B3	BH23	1999	5	2	Barrow	1	1	1	1	1	1	1			
99B6F	BH15	1999	5	6	Barrow	1	1	1	1	1	1	1			
99B7	BH43	1999	5	8	Barrow	1	1	1	1	1	1	1	3	2	
JS-BM991105	BH56	1999	11	5	Chukotka		4		2		4				
00B1	BH42	2000	4	24	Barrow	1	1	1	1	1	1	1	4	3	
00B10	BH23	2000	9	30	Barrow	1	1	2	1	1	1	2	4	3	
00B11	BH1	2000	10	1	Barrow	1	1	2	1	1	1	2	2	1	
00B12	BH47	2000	10	3	Barrow	1	1	2	1	1	1	2	4	3	
00B2	BH42	2000	5	25	Barrow	1	1	1	1	1	1	1	3	2	
00B3	BH42	2000	5	25	Barrow	1	1	1	1	1	1	1	3	2	
00B4	BH5	2000	5	25	Barrow	1	1	1	1	1	1	1	2	1	
00B5	BH42	2000	5	30	Barrow	1	1	1	1	1	1	1	2	1	
00B6	BH42	2000	9	26	Barrow	1	1	2	1	1	1	2	4	3	
00B7	BH42	2000	9	29	Barrow	1	1	2	1	1	1	2			
00B8	BH23	2000	9	29	Barrow	1	1	2	1	1	1	2	4	3	
00KK1	BH46	2000	9	2	Kaktovik				1	1	1	2	4	3	
00KK2	BH42	2000	9	3	Kaktovik				1	1	1	2	3	2	
00KK3	BH36	2000	9	8	Kaktovik				1	1	1	2	4	3	
JS-BM000909	BH46	2000	9	9	Chukotka		4		2		4				
01B1	BH58	2001	4	28	Barrow	1	1	1	1	1	1	1			
01B10	BH4	2001	5	10	Barrow	1	1	1	1	1	1	1	4	3	
01B11	BH54	2001	5	11	Barrow	1	1	1	1	1	1	1			
01B12	BH42	2001	5	11	Barrow	1	1	1	1	1	1	1	4	3	
01B13	BH42	2001	5	12	Barrow	1	1	1	1	1	1	1	4	3	
01B14	BH64	2001	5	13	Barrow	1	1	1	1	1	1	1			
01B15	BH42	2001	5	13	Barrow	1	1	1	1	1	1	1			
01B16	BH42	2001	5	14	Barrow	1	1	1	1	1	1	1	4	3	
01B17	BH5	2001	5	15	Barrow	1	1	1	1	1	1	1	3	2	
01B19	BH42	2001	5	18	Barrow	1	1	1	1	1	1	1			
01B2	BH42	2001	5	1	Barrow	1	1	1	1	1	1	1			
01B24	BH28	2001	10	8	Barrow	1	1	2	1	1	1	2			
01B25	BH23	2001	10	8	Barrow	1	1	2	1	1	1	2			
01B26	BH65	2001	10	8	Barrow	1	1	2	1	1	1	2			
01B27	BH57	2001	10	9	Barrow	1	1	2	1	1	1	2			
01B3	BH46	2001	5	1	Barrow	1	1	1	1	1	1	1			
01B4	BH15	2001	5	1	Barrow	1	1	1	1	1	1	1			
01B6	BH31	2001	5	2	Barrow	1	1	1	1	1	1	1			
01B7	BH62	2001	5	3	Barrow	1	1	1	1	1	1	1			
01B8	BH5	2001	5	7	Barrow	1	1	1	1	1	1	1			
01B9	BH61	2001	5	8	Barrow	1	1	1	1	1	1	1			
01S3	BH57	2001	11	27	Savoonga	2	3		1	2	3				1
BWCH2	BH42	2001	10	19	Chukotka		4		2		4				
02B1	BH45	2002	5	3	Barrow	1	1	1	1	1	1	1			
02B10	BH39	2002	10	10	Barrow	1	1	2	1	1	1	2	4	3	
02B11	BH50	2002	10	15	Barrow	1	1	2	1	1	1	2			
02B12	BH42	2002	10	15	Barrow	1	1	2	1	1	1	2			
02B13	BH42	2002	10	15	Barrow	1	1	2	1	1	1	2			
02B14	BH42	2002	10	18	Barrow	1	1	2	1	1	1	2			
02B15	BH1	2002	10	18	Barrow	1	1	2	1	1	1	2			
02B16	BH15	2002	10	19	Barrow	1	1	2	1	1	1	2			
02B17	BH34	2002	10	19	Barrow	1	1	2	1	1	1	2	4	3	
02B18	BH1	2002	10	19	Barrow	1	1	2	1	1	1	2			
02B19	BH42	2002	10	19	Barrow	1	1	2	1	1	1	2	4	3	
02B2	BH42	2002	5	10	Barrow	1	1	1	1	1	1	1	2	1	
02B20	BH48	2002	10	19	Barrow	1	1	2	1	1	1	2	4	3	
02B21	BH31	2002	10	22	Barrow	1	1	2	1	1	1	2	4	3	
02B22	BH58	2002	10	25	Barrow	1	1	2	1	1	1	2			
02B3	BH24	2002	5	30	Barrow	1	1	1	1	1	1	1	1	1	
02B4	BH20	2002	9	30	Barrow	1	1	2	1	1	1	2			
02B5	BH42	2002	10	1	Barrow	1	1	2	1	1	1	2			
02B6	BH42	2002	10	3	Barrow	1	1	2	1	1	1	2			
02B7	BH18	2002	10	3	Barrow	1	1	2	1	1	1	2			
02B8	BH5	2002	10	3	Barrow	1	1	2	1	1	1	2			
02B9	BH23	2002	10	10	Barrow	1	1	2	1	1	1	2			
02G2	BH31	2002	12	5	Gambell	2	2		1	2	2				1

02KK1	BH23	2002	9	8	Kaktovik				1	1	1	2			
02KK2	BH15	2002	9	11	Kaktovik				1	1	1	2			
02KK3	BH42	2002	9	13	Kaktovik				1	1	1	2			
02S2_4	BH42	2002	12	7	Savoonga	2	3		1	2	3				1
02S3	BH64	2002	12	11	Savoonga	2	3		1	2	3				1
02S5	BH42	2002	12	14	Savoonga	2	3		1	2	3				1
BWCH7	BH23	2002	11	15	Chukotka		4		2		4				
G-BAL-5	BH31	2002	12	5	Gambell	2	2		1	2	2				
03B1	BH28	2003	4	19	Barrow	1	1	1	1	1	1	1			
03B10	BH63	2003	6	1	Barrow	1	1	1	1	1	1	1			
03B11	BH46	2003	10	8	Barrow	1	1	2	1	1	1	2			
03B12	BH19	2003	10	9	Barrow	1	1	2	1	1	1	2			
03B13	BH46	2003	10	9	Barrow	1	1	2	1	1	1	2			
03B14	BH5	2003	10	9	Barrow	1	1	2	1	1	1	2			
03B16	BH42	2003	10	14	Barrow	1	1	2	1	1	1	2			
03B2	BH42	2003	5	3	Barrow	1	1	1	1	1	1	1			
03B3	BH42	2003	5	7	Barrow	1	1	1	1	1	1	1	4	3	
03B4	BH7	2003	5	8	Barrow	1	1	1	1	1	1	1			
03B5	BH60	2003	5	8	Barrow	1	1	1	1	1	1	1			
03B6	BH42	2003	5	9	Barrow	1	1	1	1	1	1	1			
03B7	BH9	2003	5	12	Barrow	1	1	1	1	1	1	1			
03B8	BH42	2003	5	24	Barrow	1	1	1	1	1	1	1			
03B9	BH23	2003	5	25	Barrow	1	1	1	1	1	1	1	2	1	
03G1	BH42	2003	4	6	Gambell	2	2		1	2	2				2
03H1	BH9	2003	4	20	Point Hope				1	1	1	1			
03H2	BH31	2003	4	22	Point Hope				1	1	1	1			
03H3_4	BH23	2003	4	22	Point Hope				1	1	1	1			
03KK1	BH42	2003	9	5	Kaktovik				1	1	1	2			
03KK2	BH42	2003	9	7	Kaktovik				1	1	1	2			
03S1	BH34	2003	12	6	Savoonga	2	3		1	2	3				1
03S2	BH42	2003	12	11	Savoonga	2	3		1	2	3				1
03WW1	BH58	2003	4	18	Wainwright				1	1	1	1			
BWCH6	BH42	2003	10	14	Chukotka		4		2		4				
04B1	BH23	2004	4	23	Barrow	1	1	1	1	1	1	1			
04B10	BH23	2004	9	22	Barrow	1	1	2	1	1	1	2			
04B11	BH55	2004	9	22	Barrow	1	1	2	1	1	1	2			
04B12	BH31	2004	9	22	Barrow	1	1	2	1	1	1	2			
04B13	BH25	2004	9	26	Barrow	1	1	2	1	1	1	2			
04B14	BH66	2004	9	26	Barrow	1	1	2	1	1	1	2			
04B15	BH42	2004	9	26	Barrow	1	1	2	1	1	1	2			
04B16	BH10	2004	10	21	Barrow	1	1	2	1	1	1	2			
04B17	BH42	2004	10	21	Barrow	1	1	2	1	1	1	2			
04B18	BH13	2004	10	22	Barrow	1	1	2	1	1	1	2			
04B19	BH42	2004	10	22	Barrow	1	1	2	1	1	1	2			
04B2	BH45	2004	4	26	Barrow	1	1	1	1	1	1	1			
04B20	BH17	2004	10	22	Barrow	1	1	2	1	1	1	2			
04B21	BH42	2004	10	23	Barrow	1	1	2	1	1	1	2			
04B3	BH5	2004	5	9	Barrow	1	1	1	1	1	1	1			
04B4	BH61	2004	5	12	Barrow	1	1	1	1	1	1	1			
04B5	BH32	2004	5	20	Barrow	1	1	1	1	1	1	1			
04B6	BH43	2004	6	4	Barrow	1	1	1	1	1	1	1			
04B7	BH7	2004	9	18	Barrow	1	1	2	1	1	1	2			
04B8	BH42	2004	9	18	Barrow	1	1	2	1	1	1	2			
04B9	BH2	2004	9	18	Barrow	1	1	2	1	1	1	2			
04G3	BH28	2004	12	31	Gambell	2	2		1	2	2				1
04KK1	BH46	2004	9	6	Kaktovik				1	1	1	2			
04KK2	BH42	2004	9	14	Kaktovik				1	1	1	2			
04KK3	BH33	2004	9	14	Kaktovik				1	1	1	2			
04N1	BH51	2004	9	5	Nuiqsut				1	1	1	2			
04N2	BH20	2004	9	6	Nuiqsut				1	1	1	2			
04N3	BH20	2004	9	14	Nuiqsut				1	1	1	2			
BWCH1	BH4	2004	11	11	Chukotka		4		2		4				
05B1	BH61	2005	4	28	Barrow	1	1	1	1	1	1	1			
05B10	BH42	2005	5	9	Barrow	1	1	1	1	1	1	1			
05B11	BH43	2005	5	9	Barrow	1	1	1	1	1	1	1			
05B12	BH59	2005	5	10	Barrow	1	1	1	1	1	1	1			
05B13	BH23	2005	5	10	Barrow	1	1	1	1	1	1	1			
05B15	BH28	2005	5	19	Barrow	1	1	1	1	1	1	1			
05B16	BH53	2005	5	23	Barrow	1	1	1	1	1	1	1			
05B17	BH61	2005	10	1	Barrow	1	1	2	1	1	1	2			

05B18	BH24	2005	10	1	Barrow	1	1	2	1	1	1	2			
05B19	BH42	2005	10	2	Barrow	1	1	2	1	1	1	2			
05B2	BH20	2005	4	28	Barrow	1	1	1	1	1	1	1			
05B20	BH42	2005	10	2	Barrow	1	1	2	1	1	1	2			
05B21	BH46	2005	10	3	Barrow	1	1	2	1	1	1	2			
05B22	BH36	2005	10	3	Barrow	1	1	2	1	1	1	2			
05B23	BH11	2005	10	3	Barrow	1	1	2	1	1	1	2			
05B24	BH29	2005	10	4	Barrow	1	1	2	1	1	1	2			
05B25	BH7	2005	10	4	Barrow	1	1	2	1	1	1	2			
05B26	BH64	2005	10	4	Barrow	1	1	2	1	1	1	2			
05B27	BH41	2005	10	5	Barrow	1	1	2	1	1	1	2			
05B28	BH49	2005	10	5	Barrow	1	1	2	1	1	1	2			
05B29	BH42	2005	10	5	Barrow	1	1	2	1	1	1	2			
05B3	BH7	2005	5	4	Barrow	1	1	1	1	1	1	1			
05B4	BH42	2005	5	5	Barrow	1	1	1	1	1	1	1			
05B5	BH36	2005	5	6	Barrow	1	1	1	1	1	1	1			
05B6	BH42	2005	5	6	Barrow	1	1	1	1	1	1	1			
05B7	BH64	2005	5	7	Barrow	1	1	1	1	1	1	1			
05B8	BH42	2005	5	8	Barrow	1	1	1	1	1	1	1			
05B9	BH23	2005	5	8	Barrow	1	1	1	1	1	1	1			
05BpB1	BH9	2005	9	14	Barrow	1	1	2	1	1	1	2			
05BpB12	BH19	2005	10	6	Barrow	1	1	2	1	1	1	2			
05BpB13	BH12	2005	10	6	Barrow	1	1	2	1	1	1	2			
05BpB2	BH24	2005	9	14	Barrow	1	1	2	1	1	1	2			
05BpB8	BH42	2005	10	6	Barrow	1	1	2	1	1	1	2			
05D1	BH5	2005	4	20	Little Diomede				1						
05G1	BH42	2005	1	4	Gambell	2	2		1	2	2				1
05G2	BH5	2005	4	27	Gambell	2	2		1	2	2				2
05H1	BH23	2005	4	30	Point Hope				1	1	1	1			
05H3	BH20	2005	5	7	Point Hope				1	1	1	1			
05H4	BH47	2005	5	8	Point Hope				1	1	1	1			
05H5	BH20	2005	5	19	Point Hope				1	1	1	1			
05H6	BH63	2005	5	21	Point Hope				1	1	1	1			
05H7	BH47	2005	5	23	Point Hope				1	1	1	1			
05KK1	BH42	2005	9	3	Kaktovik				1	1	1	2			
05KK2	BH42	2005	9	5	Kaktovik				1	1	1	2			
05KK3	BH27	2005	9	14	Kaktovik				1	1	1	2			
05N1	BH9	2005	9	14	Nuiqsut				1	1	1	2			
05S1	BH47	2005	1	4	Savoonga	2	3		1	2	3		4	3	1
05S2	BH23	2005	4	11	Savoonga	2	3		1	2	3				2
05S3	BH5	2005	4	22	Savoonga	2	3		1	2	3				2
05S4	BH7	2005	4	22	Savoonga	2	3		1	2	3				2
05S5	BH42	2005	11	29	Savoonga	2	3		1	2	3				1
05S6	BH43	2005	11	29	Savoonga	2	3		1	2	3				1
05S7	BH42	2005	11	29	Savoonga	2	3		1	2	3				1
05WW1	BH41	2005	4	28	Wainwright				1	1	1	1			
05WW2	BH20	2005	4	28	Wainwright				1	1	1	1			
05WW3	BH32	2005	5	10	Wainwright				1	1	1	1			
05WW4	BH23	2005	5	19	Wainwright				1	1	1	1			
BWCH11	BH23	2005	10	24	Chukotka		4		2		4				
BWCH12	BH42	2005	10	24	Chukotka		4		2		4				
BWCH13	BH5	2005	10	25	Chukotka		4		2		4				
BWCH14	BH24	2005	10	28	Chukotka		4		2		4				
BWCH16	BH61	2005	10	30	Chukotka		4		2		4				
BWCH18	BH36	2005	11	5	Chukotka		4		2		4				
BWCH19	BH3	2005	10	5	Chukotka		4		2		4				
BWCH20	BH5	2005	10	28	Chukotka		4		2		4				
BWCH21	BH13	2005	10	29	Chukotka		4		2		4				
BWCH8	BH2	2005	10	21	Chukotka		4		2		4				
06B1	BH42	2006	5	11	Barrow	1	1	1	1	1	1	1			
06B2	BH3	2006	5	12	Barrow	1	1	1	1	1	1	1			
06B3	BH42	2006	5	18	Barrow	1	1	1	1	1	1	1			
06BpB60010	BH49	2006	5	12	Barrow	1	1	1	1	1	1	1			
06WW1_2	BH28	2006	5	10	Wainwright				1	1	1	1			
CH1	BH50	2006	4	28	Chukotka		4		2		4				
CH2	BH3	2006	4	28	Chukotka		4		2		4				
CH3	BH23	2006	4	30	Chukotka		4		2		4				
03G1	BH42				Gambell	2	2		1	2	2				
BWCH4	BH42				Chukotka		4		2		4				
G-BAL-5	BH31				Gambell	2	2		1	2	2				

G-BAL-6	BH52	Gambell	2	2	1	2	2
G-BAL-7	BH45	Gambell	2	2	1	2	2
G-BAL-8	BH42	Gambell	2	2	1	2	2
GSK1	BH15	Gambell	2	2	1	2	2
GSK10	BH32	Gambell	2	2	1	2	2
GSK11	BH45	Gambell	2	2	1	2	2
GSK12	BH3	Gambell	2	2	1	2	2
GSK13	BH31	Gambell	2	2	1	2	2
GSK15	BH30	Gambell	2	2	1	2	2
GSK16	BH42	Gambell	2	2	1	2	2
SK17_G-BAL-	BH42	Gambell	2	2	1	2	2
GSK18	BH42	Gambell	2	2	1	2	2
GSK19	BH45	Gambell	2	2	1	2	2
GSK20	BH2	Gambell	2	2	1	2	2
GSK21	BH42	Gambell	2	2	1	2	2
SK22_G-BAL-	BH42	Gambell	2	2	1	2	2
GSK23	BH22	Gambell	2	2	1	2	2
GSK24	BH23	Gambell	2	2	1	2	2
GSK25	BH23	Gambell	2	2	1	2	2
GSK26	BH42	Gambell	2	2	1	2	2
GSK27	BH28	Gambell	2	2	1	2	2
GSK28	BH58	Gambell	2	2	1	2	2
GSK29	BH28	Gambell	2	2	1	2	2
GSK5	BH51	Gambell	2	2	1	2	2
GSK6	BH7	Gambell	2	2	1	2	2
GSK7	BH42	Gambell	2	2	1	2	2
GSK8	BH29	Gambell	2	2	1	2	2
GSK9	BH23	Gambell	2	2	1	2	2
SAV-BAL-1_4	BH5	Savoonga	2	3	1	2	3
SAV-BAL-2	BH64	Savoonga	2	3	1	2	3
SAV-BAL-3	BH42	Savoonga	2	3	1	2	3