

# **First Intersessional AWMP Workshop for the 2007 Bowhead *Implementation Review***



# First Intersessional AWMP Workshop for the 2007 Bowhead Implementation Review<sup>1</sup>

## 1. INTRODUCTORY ITEMS

The Workshop was held at the National Marine Mammal Laboratory, Seattle, USA from 24-27 April 2006.

### 1.1 Convenor's opening remarks

At IWC/57 in Ulsan, it was agreed that in order to meet the goal of finishing the bowhead *Implementation Review* at the 2007 Annual Meeting, a first intersessional Workshop is required to specify the basic structure and types of simulation trials needed for the *Implementation Review*.

The aims of the Workshop are to:

- (1) specify the basic structures and types of simulation trials needed for the *Implementation Review* – this will focus in particular on possible stock structure scenarios and any other new information that has become available since the *Bowhead Strike Limit Algorithm (SLA)* was agreed;
- (2) initiate discussions on the range of parameter values to be considered, but not the specific choices.

The Workshop held a minute's silence in honour of Kjartan Magnússon, who made such an important contribution to the work of the AWMP group over many years, and Geoff Kirkwood, who was one of the pioneers of the management procedure approach within the Scientific Committee. They will be sadly missed.

The Workshop also expressed its condolences to the family and friends of the Chukotkan hunter who died in an accident whilst trying to obtain biopsy samples from bowhead whales off Chukotka.

### 1.2 Election of Chair

Donovan was elected Chair.

### 1.3 Appointment of rapporteurs

Allison, Givens and Punt acted as rapporteurs, with assistance from the Chair.

### 1.4 Adoption of Agenda

The adopted Agenda is given as Annex B.

### 1.5 Available documents

The documents available for the Workshop were SC/A06/AWMP1-7 (Annex C).

### 1.6 Available data, especially since the 2005 Annual Meeting

Annex D summarises the data that are currently available for the *Implementation Review*, many of which can be used to make inferences on stock structure hypotheses.

## 2. STOCK STRUCTURE HYPOTHESES FOR MODELLING EXERCISE

Stock structure hypotheses serve two different but related purposes. Under Item 2.2 the emphasis is on general hypotheses useful for understanding the available data whereas under Item 2.3 and Item 4 the emphasis is on hypotheses useful for designing trials for the *Implementation Review*.

### 2.1 Brief review of status of discussions at the 2005 Annual Meeting

The discussions at the 2005 Scientific Committee Meeting had focused on the five stock structure hypotheses identified during a workshop held by the United States on 23-24 February 2005 (Anon., 2005):

- (1) the one-stock model presently accepted by the IWC;
- (2) a one stock hypothesis with generational gene shift;
- (3) a two stock hypothesis in which there is temporal segregation of the two stocks;
- (4) a two stock hypothesis in which there is spatial segregation; and
- (5) the two-stock Chukchi Circuit hypothesis.

The Workshop also had before it a review of previous discussions of stock structure hypotheses (SC/A06/AWMP4) and a document proposing a number of stock structure hypotheses based on discussions up to and including those held at a US Workshop in March 2006 (as yet, unpublished notes). These proved valuable in structuring the discussions of the available evidence on stock structure discussed under Item 2.2 below.

### 2.2 Available information (including review from March 2006 US Workshop)

#### 2.2.1 Genetic data

The genetics data for the B-C-B bowhead whales can be divided into four main groups:

- (1) mitochondrial DNA (mtDNA) sequences for 229 bowheads available in 2004;
- (2) mtDNA sequences for 140 additional bowheads caught subsequent to those analysed in the first portion, or generated recently by other means (e.g. bone and baleen samples from recent (*ca* 30 years) catches at St. Lawrence Island);
- (3) scores for 12 ('old') microsatellite loci for 177 bowheads available in 2004, of which 10 or 11 loci were considered suitable for analysis (Bickham *et al.*, 2004; Givens *et al.*, 2004);
- (4) scores for 24 different ('new') microsatellite loci for 173 bowheads available in 2006, including some of the whales from (3) and some new whales. Of these 24 loci, 22 were considered suitable for analysis (SC/A06/AWMP1).

<sup>1</sup> Presented to the meeting as SC/58/Rep2.

Table 1 summarises the available microsatellite and mtDNA data by village (see Fig. 1 for place names) and season. This table also indicates the extent of overlap in the sets of whales scored for each set of markers.

The Workshop spent some time discussing the differences between the new and old loci. All the new markers were specifically developed for bowhead whales and presented few biochemical or scoring difficulties (part of the selection was based on the reliability in being able to score the genotypes). This is in part because the sequence of primers designed for bowheads precisely match the sequence of bowheads being analysed, thus reducing important technical variables influencing data quality. By contrast, many of the old loci were developed for other whale species, or in one case, for *Tursiops*, and (especially when they were designed) were opportunistic. The new loci were also designed and selected based upon their ability to amplify consistently and with relative strength. Data for the new loci were generated on an ABI 3100 capillary machine, which is more sensitive for detecting the amplified products than the 377 machine used for the old loci. The ABI 3100 does not have problems with bleeding over into another lane, which provides for more consistent results than the 377. Finally, the larger number of loci leads to substantially increased statistical power in most analyses. For the above reasons, the researchers at Texas A and M University (TAMU) developing and analysing these data informed the Workshop that they had greater confidence in the new dataset than the old dataset.

In discussion it was noted that the new loci are all CA<sub>n</sub> dinucleotide repeats and the suggestion was made that efforts be made to develop additional tri- and tetranucleotide repeat loci, in particular because such loci amplify with fewer stutter bands. In response it was noted that TAMU have focused on CA<sub>n</sub> repeats because these are the most commonly used and best understood type of loci. In addition, in practice the 22 new loci showed no evidence of stutter bands. The Workshop **requested** that TAMU provide for the 2006 Annual Meeting, additional information on (1) the advantages/disadvantages of developing additional tri- and tetranucleotide repeat loci and (2) the feasibility of doing so before the Data Availability Agreement deadline (see Item 5).

SC/A06/AWMP3 presented results of analyses of the 22 new microsatellite loci. Samples consisted of 148 Barrow whales, 9 whales from Gambell, and 16 from Savoonga. This represents the largest sample from St. Lawrence Island analysed, and more than twice the previous number of loci. The samples exhibit significant heterozygote deficiency which is not easily isolated to any simple spatio-temporal group or age cohort. A thorough comparative investigation of allele frequencies revealed no significant differences among groups stratified by geography, season, or estimated age. Attempts to detect population substructure using STRUCTURE<sup>2</sup> (Falush *et al.*, 2003; Pritchard *et al.*, 2000) did not yield convincing results for distinguishing two groups. If forced to produce three groups, STRUCTURE preferred group assignments that could motivate speculative biological conjectures because estimated ancestries varied between whales, but the three-group analysis had an estimated posterior probability of 0, compared to 1.0 for the one-group analysis. Finally, a test to detect a historical population bottleneck found significant results. The authors stressed that all these results should be considered preliminary, since more data should become available later this year.

The Workshop noted that when STRUCTURE was forced to create three clusters, the clusters it created exhibited some interesting patterns, particularly with respect to autumn Barrow mixing and separation of St. Lawrence Island animals. However, after some discussion it was agreed that since the estimated marginal probability of the data and the estimated posterior probability for the number of clusters were overwhelmingly in favour of one cluster, further consideration of the two- or three-cluster STRUCTURE results was not warranted. However, as had also been noted at the recent TOSSM and fin whale Workshops (SC/58/Reps

<sup>2</sup> The program STRUCTURE is a free software package for using multi-locus genotype data to investigate population structure. Its uses include inferring the presence of distinct populations, assigning individuals to populations, studying hybrid zones, identifying migrants and admixed individuals, and estimating population allele frequencies in situations where many individuals are migrants or admixed. It can be applied to most of the commonly-used genetic markers, including microsatellites, RFLPs and Single Nucleotide Polymorphisms (SNPs). This method was described in an article by Pritchard *et al.* (2000). Extensions to the method were published by Falush *et al.* (2003).

Table 1

Summary of information on available genetic samples for the 'old' and 'new' datasets (see text for explanation). There are no samples in hand that have not yet been analysed. F=fall (autumn); S=spring and U=unknown. Note that: known duplicate samples have been removed from totals; mothers and foetuses were both included; for Savoonga and Gambell, fall=Nov-Jan, spring=Apr-May; strandings were considered to be of unknown season and, although many of the bone and baleen samples (St. Lawrence Island) were tentatively attributed to harvested whales, these were considered to be of unknown season.

Village	2004 data from LeDuc (old)			2006 data from LeDuc (new)		
	N	Seasonal breakdown	Not in current 2006 dataset	N	Seasonal breakdown	Not in 2004 dataset
Barrow	197	93F, 103S, 1U	0	257	131F, 125S, 1U	60
Savoonga	7	4F, 3S	0	23	14F, 6S, 3U	16
Gambell	4	1F, 3S	0	42	6F, 13S, 23*U	38
Chukotka	4	3F, 1S	0	4	3F, 1S	0
Kaktovik	6	6F	0	17	17F	11
Nuiqsut	1	1U	0	5	4F, 1U	4
Pt Hope	3	3S	0	9	9S	6
Wainwright	2	2S	0	6	6S	4
Commander Island	4	4U	0	4	4U	0
Diomed Island	0		0	1	1S	1
Unknown	1	1U	0	1	1U	0
Totals	229			369		140

\*Includes one taken on 12 Feb in Gambell – between the normal autumn and spring periods.

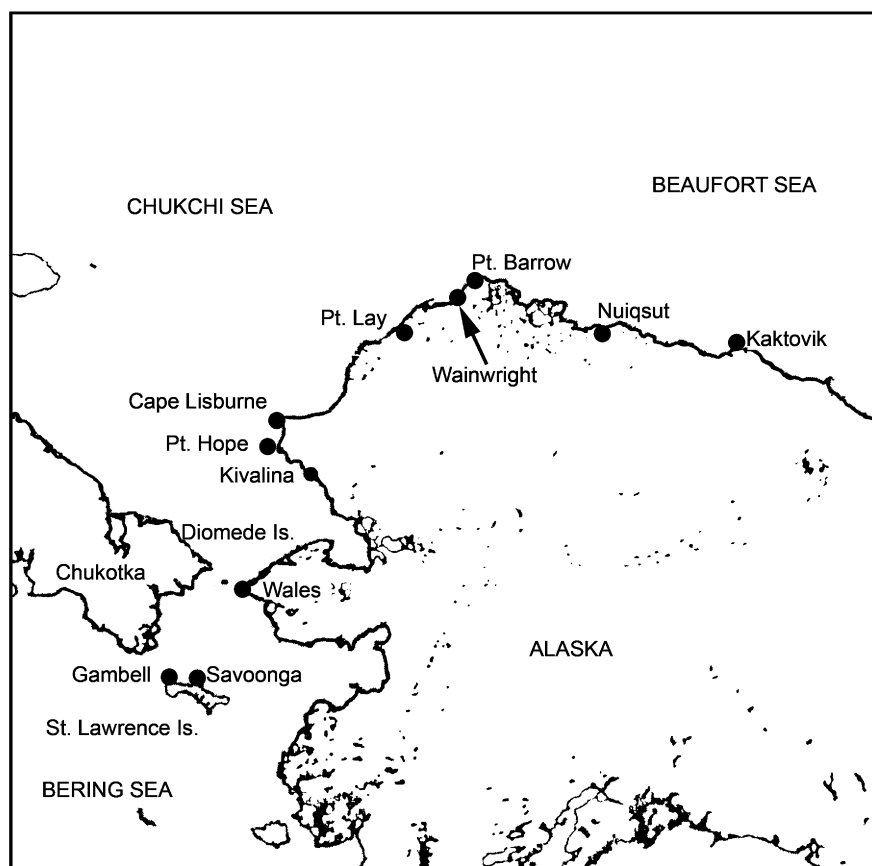


Fig. 1 Place names mentioned in the text.

2 and 3), the performance of STRUCTURE is not fully understood and the Workshop **supported** the recommendations from those workshops for a more thorough examination of the properties of STRUCTURE by the Scientific Committee.

The Workshop noted that the old loci had been found to exhibit no linkage (Givens *et al.*, 2004). It **recommended** that linkage disequilibrium analyses be run on the new loci.

The Workshop agreed that the finding of a genetic bottleneck was difficult to interpret, or to link firmly to any particular stock structure hypothesis. As the paper authors note, the bottleneck analysis can be less reliable if the sample originates from a mixture of two stocks, or from a single stock growing rapidly. Furthermore, the workshop **agreed** that even if there was a genetic bottleneck, it is not clear whether it occurred long (millennia) ago or at the end of commercial whaling in about 1914. Taylor indicated that she would analyse the mtDNA data for signs of a genetic bottleneck.

SC/A06/AWMP1 presented methodological development and simulation testing for a statistical method for detecting population structure based on pairwise microsatellite allele matching frequencies. This method is particularly designed to isolate patterns of genetic structure related to a covariate, such as in the Oslo bump<sup>3</sup> finding (where the covariate is 'days apart' of whale capture).

<sup>3</sup> The so-called Oslo bump was put forward by Jorde *et al.* (2004). They found a significant increase in genetic difference between pairs of whales sampled approximately one week apart at the Barrow fall migration versus those sampled at other time intervals. Considerable time was spent discussing this phenomenon at the 2005 Annual Meeting (IWC, 2006). The Committee had agreed that the Oslo bump appeared to be a real phenomenon, at least in the available data but had agreed that additional data are necessary to confirm whether this pattern reflects a real characteristic in the bowhead whales in the region; no single explanation has emerged to explain the effect.

SC/A06/AWMP2 reported the results of the analysis method of SC/A06/AWMP1 when it is applied to microsatellite data for bowheads. Using the 'old' 11 loci for 66 whales considered by Jorde *et al.* (2004), the Oslo bump was confirmed using this methodology ( $p=0.01$ ). However, there was no evidence for such a phenomenon when the analysis is based on the 'new' 22 loci for 112 whales (including the 66 for which the 11 loci are available) (essentially flat curve with  $p=0.21$ ).

In discussion, it was noted that the new dataset (new loci and 112 whales) contained many fewer missing data (8% now; 15% previously) than old dataset (11 loci and 66 whales). The new dataset also exhibited greater average heterozygosity (0.82 now; 0.64 previously).

The Workshop discussed how it might be possible to combine the old and new datasets to obtain a unified test for the Oslo bump. Initially it reviewed the available data for consideration. The full old dataset contained 83 fall Barrow animals and Jorde *et al.* (2004) selected 54 of these having at least 10 of 11 old loci scored for the analysis. None of the loci in the new dataset are the same as in the old dataset, but many of the whales are the same. Many of these 112 will have some missing data on the 'new' loci (the median percentage of missing loci among whales is 4.5%; about 1 of 22 of the 'new' loci). A total of 66 of the 112 animals are included in the '2004 dataset' of 83 whales, but it unknown how many of the 54 whales analysed by Jorde *et al.* (2004) are included in the 112 whales. The Workshop **recommended** that the 17 (83-66=17) whales that were included in the '2004 dataset' that have yet to be scored on the 'new' loci be prioritised for analysis in time for the 2006 Annual Meeting (see below). This will yield 83 whales which have been run on both the 'old' and 'new' loci. From these 83, analysis should be based on the subset of all whales having at least 30 of 33 loci scored.

The Workshop discussed whether analyses based on 'old' data should be superseded by analyses based on 'new' data. Specifically, the Oslo bump is present in the analyses of Jorde *et al.* (2004) and SC/A06/AWMP3 for the limited old dataset (54 and/or 66 animals and 11 loci) but not in the analyses in SC/A06/AWMP3 which are based on 112 animals and the 22 new loci.

The Workshop also discussed how best to interpret the findings of its planned unified analyses. It was noted that the Oslo bump phenomenon is robust in the sense that it does not depend on one or two of the 11 loci considered, or on a few out of the 54 animals considered. If the unified analysis shows no significant effect of the 'days apart' variable, the absence of a bump in this case indicates either (1) that the 'new' 22 loci carry information which, when combined with the information in the 'old' 11 loci, yields no evidence for a bump, and/or (2) that the finding of the bump in the 'old' dataset is a chance artifact of the particular samples and loci analysed. If the latter case is true, then the loss of the bump signal is a desirable and natural result of increasing sample size. If a significant bump is no longer detected, the Workshop **agreed** that very low priority should be assigned to increasing the number of whales scored on all 33 loci for such analysis, although these data might be important for other uses. If the 'unified' analysis shows a significant effect for the 'days apart' variable, the Workshop **agreed** that the implications for future data collection should be discussed in the 2006 Annual Meeting. Some initial hypotheses to explain such a finding for the planned 'unified' dataset would include the reduction in sample size and the usage of the 'old' loci.

There was some disagreement on the implications of a negative finding in the planned 'unified' analysis. Schweder believed that each locus constituted a separate signal carrier and if the bump was manifested in any carrier (as it was for at least some of the old loci), then any negative findings on further loci did not invalidate the original finding. Indeed, adding non-carrier loci to the analysis would dilute the signal and possibly lead to a Type II error. If the Oslo bump persists in the new data using the 11 old loci, he suggested additional research to identify those loci that carry the strongest signal of a bump or other stock structure, and then to focus analyses on those loci if identification is successful.

It was noted that the original finding was derived from a limited number of loci and individuals. Several members noted that if the signal was real, it should be found in some other loci as well. Most participants agreed that analysis of a more comprehensive dataset would not 'wash out' a real signal. They believed that it was not appropriate scientific practice to extract a signal from data-mining and then ignore all future data that did not support this signal; analyses and inferences should be based on the most comprehensive relevant data.

The Workshop was unable to decide on a general set of rules for deciding when results based on one microsatellite dataset are superseded by those based on a sample using larger number of animals/markers. It recognised the importance of these discussions not only for the bowhead whale case but for future use and interpretation of genetic data in the Scientific Committee. Given this, the Workshop **agreed** that it is important to obtain further expert advice from geneticists working in the field of microsatellites, particularly with regard to the implication of the differing quality of the two sets of data. It **agreed** that Donovan will refer this issue to a group comprising Palsbøll, Jørde, Kanda and Morin. He will request a written report from them that will be discussed further at the 2006 meeting.

However, the Workshop **agreed** that the results of analyses based on the most recent dataset superseded those based on the earlier data in the case of mtDNA.

Taylor reported results from mtDNA analyses on whales (see Table 1). No significant differences were found between samples obtained from whales at Barrow in autumn and spring, between samples from Barrow and those from St. Lawrence Island, or between age strata. She **agreed** to provide a paper to the 2006 Annual meeting documenting these analyses. The Workshop also requested that Taylor present information on the steps taken to eliminate possible duplicate samples.

In discussion, the Workshop noted that sample sizes were quite large for many of these comparisons, notably including 65 St. Lawrence Island samples, many of which were obtained from bone samples from skulls. Since these results were broadly unsupportive of multiple stock hypotheses, it was suggested that power analyses could be run to help interpret these negative findings. The Workshop **agreed** that, at this point, power calculations could only be recommended for comparisons between strata hypothesised to represent pure groups. However, it was unable to identify such hypotheses at this stage and, specific recommendations for power analyses were postponed to the 2006 Annual Meeting. Power analyses in other situations were not recommended because of the difficulty of setting up such tests and the slim likelihood that they would yield results that would lead to substantial changes to *Implementation Review* trial structure.

SC/A06/AWMP6 investigated the power of testing for the Oslo bump on the old (11 loci, 54 whales) dataset, assuming three pulses in the fall migration with the middle pulse being made up of whales genetically distinct from the rest. The two population components have genes drawn from Dirichlet distributions based on the observed gene frequencies. For the observed configuration of days of catch by year, the power of the test based on the variability of the regression curve of pair wise gene difference by days between catch is low when the two population components are as genetically different as the Okhotsk Seas bowheads are from the Bering-Chukchi-Beaufort (B-C-B) Seas bowhead whales. If however, the days of catch are simulated from the assumed model (pulses with little overlap), the power can be better but still low (27% at 5% level), and a bump similar to that observed by Jorde *et al.* (2006) is seen in the effect curve.

In discussion, the Workshop noted that the simulations in SC/A06/AWMP6 were intended to be based on an  $F_{ST}$  value between clearly different bowhead whale populations i.e. between those from the Okhotsk Sea and the B-C-B Seas. However, the  $F_{ST}$  value 0.0062 used in SC/A06/AWMP6 appears to be a typographical error for the value of 0.062 given in LeDuc *et al.* (2005); the LeDuc *et al.* (2005) value was based on mtDNA rather than microsatellite data and estimates from the two types of data are not necessarily comparable. The Workshop **agreed** that choice of an appropriate  $F_{ST}$  value needs to be investigated further, and if necessary, additional simulations attempted. Taking the results presented in the paper at face value, the Workshop **agreed** that detection of the Oslo bump seemed unlikely unless there is population difference with high  $F_{ST}$ , a clear temporal separation between the populations and both stocks are reasonably large; generally, all three of these conditions are required.

SC/A06/AWMP7 reported the results of some simulations to assess how easily imbalances in whale pairings could be generated by two stocks passing by Barrow, thereby

providing the opportunity to generate a signal like the Oslo bump. SC/A06/AWMP7 concluded that if the two stocks mix in the fall at Barrow, then it would be difficult to generate a sufficient imbalance of pairings to generate a 'bump' unless the second stock is at least 1/3 the size of the main stock and its migration window covers at least 1/2 of the main migration window.

#### 2.2.1.1 AVAILABILITY OF SAMPLES FOR THE IMPLEMENTATION REVIEW

The Workshop identified additional genetic data that may become available in time to be considered at the 2007 *Implementation Review*, including:

- (1) mtDNA sequences and microsatellite scores (new and/or old loci) for all whales landed in spring 2006;
- (2) mtDNA sequences for approximately 20 biopsy samples taken from Chukotka (obtaining microsatellite data for these samples is still highly uncertain due to logistical problems with permitting and transport if the samples are analysed at TAMU, or due to calibration problems if the samples are analysed in any other laboratory);
- (3) some SNPs (single nucleotide polymorphisms) may be analysed by Morin at SWFSC (Southwest Fisheries Science Center, La Jolla) for a subset of existing samples, depending on available funds and researcher time;
- (4) some missing scores in the current microsatellite data may be filled in by repeating amplification and scoring for these samples;
- (5) the 'old' microsatellite loci may be scored for all whales not included in the 2004 dataset (see Table 2);
- (6) the new microsatellites may be scored for all remaining samples (currently, only a portion of available samples have been run; see Table 1).

The Workshop discussed the priorities for genetic data generation efforts. It was informed that TAMU will be able to run at most one plate of samples (about 80 samples) for the new loci before the 2006 Annual Meeting. If this plate can be completed in time for pre-meeting analysis, the Workshop **recommended** that it contain the following samples in the following priority order:

- (1) the 17 whales mentioned above for a unified analysis of the Oslo bump;
- (2) all St. Lawrence Island whales (if any) missing 3 or more new loci; and
- (3) some more spring Barrow whales.

The Workshop also discussed genetic data generation issues in the context of the DAA deadline in late 2006. A large number of options were considered but it was **agreed** that the following were of highest priority and it **recommends** analysis of the following samples:

- (1) the 11 old loci on all St. Lawrence Island animals not in the 2004 dataset;
- (2) all 33 loci for roughly 50 to 80 whales selected from a genetically homogeneous group of whales in the Canadian Arctic<sup>4</sup> (Foxye Basin whales, or if these number too few, Hudson Bay whales or a combination of whales from these two sites);

- (3) all loci (and any new mtDNA sequences) for any Chukotkan biopsies, to the extent that these can be obtained and calibrated (in a US lab for microsatellite loci); and
- (4) collection and analysis if possible of biopsy samples from Chukotka in the spring and summer.

The Workshop was informed that TAMU intends to run all available whales with the new loci before the next DAA (the Scientific Committee's Data Availability Agreement – see Item 5) deadline. It **supported** this effort, and further emphasises the value of obtaining data on all loci for all whales. It is unclear what limitations on the scope of the final dataset will be required to meet the DAA deadlines (see Item 5). Notwithstanding the official deadlines, the Workshop **recommended** that as much data as possible be provided for analysis by approximately 1 September 2006, in order to provide the best opportunity for progress at the planned October 2006 Workshop to finalise trial structure.

#### 2.2.2 Photo-identification and photogrammetric data

Rugh *et al.* (2004) examined the between-year variation in the date on which individuals pass Barrow during the spring migration, and found that, for the larger animals, this date is essentially random among years. The results in Rugh *et al.* (2004) suggest that the variability in the date of an animal passing Barrow is much greater than the inter-annual variation in migration timing (around 9 days). The sample size on which the Rugh *et al.* (2004) study was based was, however, relatively small (44 animals).

The spring migration is segregated by age and sex, with mothers and calves passing Barrow towards the end of the migration. If there was temporal segregation of two bowhead stocks that migrate past Barrow, and the pattern of how different ages and sexes migrate was the same during the spring migration for these two stocks, it might be expected that some young whales would be seen later in the migration. However, small whales have not often been observed late in the spring migration. The Workshop **recommended** that, if available, the data from aerial surveys in recent years be analysed to examine this further.

#### 2.2.3 Acoustic data

There are data on the calling behaviour of bowhead whales from the spring migration (Clark *et al.*, 1996) and from a one-year deployment of autonomous recorders northeast of Barrow (Moore *et al.*, 2006). Bowhead whale calls were recorded as late as mid-December 2003 and as early as the end of March 2004 (Moore, 2006); (SC/58/BRG8). The acoustic data provide information on presence of whales in areas and hence general movement patterns rather than direct evidence for or against specific stock structure hypotheses. A NOAA Ocean Exploration cruise that traversed the region north and east of Barrow during late-June to late-July 2005 did not detect any bowhead calls (Moore, 2006).

Considerable acoustic information is available from the spring census. George agreed to consult with Clark and report back to the 2006 Annual Meeting on whether this information can be used to infer any information on stock structure hypotheses.

#### 2.2.4 Telemetry

Twelve juvenile bowhead whales were tagged with Argos satellite-monitored radio tags in the Canadian Beaufort Sea off the Mackenzie River delta (Mate *et al.*, 2000). The whale with the longest record travelled 3,886km to Siberia in 32.5

<sup>4</sup> To provide a 'control' group where it is known the animals are genetically distinct. If the Canadian data cannot be obtained (e.g. due to data availability issues), then samples from the Sea of Okhotsk could be used.

Table 2

General summary of the information which might be useful when assessing the plausibility of the alternative stock-structure hypotheses later in the process. Note that the table has been simplified for reasons *inter alia* of space. It is NOT intended that the pluses and minuses should be summed to obtain a priority ranking. A '+' indicates evidence in favour of a hypothesis, '-' evidence against a hypothesis, '(+)' weak (or disputed) evidence in favour of a hypothesis, and '(-)' weak (or disputed) evidence against a hypothesis. Where no information is given the evidence provides no information on the particular hypothesis.

Hypothesis	Microsatellite	mtDNA	Photo-ID, acoustics	Visual	Isotopes
<b>Single stock</b>	+d, (+)j				
Baseline	-a, (-)f, (-)g	+h, +i		(-)s	
With social structuring					
With Generational Gene Shift	(+)e, (+)l, (-)p				
With feeding ground site fidelity	(-)g	(+)h	-r	(+)s	
<b>Two stocks</b>					
Chukchi Circuit-mixed	(-)b, (-)c, (+)m, (-)g, (-)o	-h, -i	(-)r		(-)t
Chukchi Circuit-segregated	(-)b, (-)c, (-)n, (+)m, (+)g	-h, -i	(-)r		(-)t
Temporal segregation	(-)c, (+)k	(-)i	(-)q		
Spatial segregation-SLI-mixed	(-)b, (+)f	-h		(+)s	(-)t
Spatial segregation-SLI-segregated				(+)s	

**Footnotes:**

<sup>a</sup>Tests for Hardy-Weinberg disequilibrium (Table 1 of SC/A06/AWMP3; Givens *et al.* 2004) are indicative of heterozygote deficiency and are therefore inconsistent with there being a single homogeneous stock. Slight Hardy-Weinberg disequilibrium could occur under the single stock hypotheses other than Baseline.

<sup>b</sup>Tests comparing microsatellite allele frequencies (Table 2 of SC/A06/AWMP3) did not find significant differences between whales from Barrow and St. Lawrence Island. In addition, St. Lawrence Island whales do not cluster in phylogenetic trees (Givens *et al.* 2004). Both of these results are inconsistent with the expectations under the two Chukchi Circuit hypotheses, because under these hypotheses, the second stock is hunted at Barrow but not St. Lawrence Island. They are also inconsistent with the 'Two stocks - spatial segregation-SLI-mixed' hypothesis, because under this hypothesis the second stock is hunted at SLI but not Barrow.

<sup>c</sup>Tests comparing microsatellite allele frequencies (Table 2 of SC/A06/AWMP3; Pastene *et al.* 2004) did not find significant differences between whales sampled in spring and autumn at Barrow, as might be expected under the Chukchi Circuit and temporal segregation hypotheses.

<sup>d</sup>Results from the program *Structure* strongly support a single cluster in the microsatellite data (SC/A06/AWMP3). However, there is concern regarding how best to make inferences on the numbers of clusters in principle for *Structure*, even though in this case the evidence for a single stock is estimated to be very strong.

<sup>e</sup>The autumn microsatellite data for Barrow are indicative of a bottleneck (SC/A06/AWMP3).

<sup>f</sup>Givens *et al.* (2004) found statistically significant differences in microsatellite allele frequencies between St. Lawrence Island and Barrow based on the 2004 data. However, the updated dataset (see b) does not show this effect.

<sup>g</sup>Jorde *et al.* (2004, 2006) identified an 'Oslo bump'.

<sup>h</sup>Tests comparing mtDNA frequencies (B. Taylor pers. commn; Paper to be presented at the Annual Meeting) did not find significant differences between whales from Barrow and St. Lawrence Island, as might be expected under the Chukchi Circuit and the 'Two stocks - spatial segregation-mixed' hypotheses. The mtDNA data may not, however, be inconsistent with there being two stocks, one of which is much smaller than the other, mixing at Barrow and St. Lawrence Island. If there was site fidelity to feeding grounds and we had samples from multiple feeding grounds, then mtDNA should reveal different haplotypic frequencies with strong site fidelity. In fact we do not have samples from the feeding grounds, but rather primarily from the migration. Thus, we would only detect a signal if the feeding aggregations migrated and were sampled discretely (i.e. feeding aggregation A migrates first followed by feeding aggregation B). If they are mixed on migration then mtDNA could not find the signal (whereas nuclear DNA would be out of Hardy-Weinberg equilibrium).

<sup>i</sup>Tests comparing mtDNA frequencies (B. Taylor pers. commn; Paper to be presented at the Annual Meeting) did not find significant differences between whales sampled in spring and fall at Barrow, as might be expected under the Chukchi Circuit and temporal segregation hypotheses. The mtDNA data may not, however, be inconsistent with there being two stocks, one of which is much smaller than the other, mixing at Barrow.

<sup>j</sup>Le Duc *et al.* (2004) were unable to find any way to cluster the 2004 microsatellite data in a manner for which the clusters were in Hardy-Weinberg equilibrium.

<sup>k</sup>There is a temporal shift in spring in one locus (Givens *et al.* 2004).

<sup>l</sup>A phylogram suggests that older animals cluster together (Givens *et al.* 2004).

<sup>m</sup>Tests for Hardy-Weinberg disequilibrium for whales passing Barrow in fall are significant (Pastene *et al.*, 2004, 2005).

<sup>n</sup>The Oslo Bump that was detected using the 11 loci in the '2004 data set' is not longer evident when the 22 loci in the '2006 data set' are analysed (SC/A06/AWMP2).

<sup>o</sup>The power to detect an Oslo bump is very low unless both stocks are reasonably large and there is clear temporal separation between the stocks during the migration (SC/A06/AWMP6, SC/A06/AWMP7).

<sup>p</sup>There are only few situations in which simulated data can replicate a Generational Gene Shift (information from B. Taylor; a full paper documenting the simulations will be presented to the 2006 Annual meeting).

<sup>q</sup>The variation in the timing of individual whales passing Barrow in spring is high (Rugh *et al.* 2004) and occasional late spring surveys along the Alaskan coast south of Barrow have not seen many whales migrating northwards towards Barrow.

<sup>r</sup>The lack of acoustic calls of bowhead whales north and east of Barrow in June and July (Moore, 2006) is not suggestive of there being a feeding ground in this region and constrains how whales migrate to and feed at Barrow.

<sup>s</sup>Whales, including a few calves, are found around Chukotka during the months in which the bulk of the animals are north and east of Barrow.

<sup>t</sup>The evidence from animals sampled at St. Lawrence Island indicates feeding in the Beaufort Sea, with no animals appearing to have fed in the Chukchi Sea. However, sample sizes are very small ( $n=9$ ; Knoche *et al.* 2006). If this pattern persists with greater sample sizes it constrains the two stock hypothesis to have the second stock not harvested at St. Lawrence Island.

days, averaging  $5.0\text{km/h}^{-1}$  (between 30 August and 6 September 1992). Its westerly route through the Beaufort and Chukchi Seas was between  $70^\circ$  and  $72^\circ\text{N}$ .

The Workshop noted the value of appropriate telemetry data (with suitable sample sizes) for examining stock structure hypotheses, particularly with respect to the Chukotka animals.

### 2.2.5 Visual data

Bowhead whales are surveyed using visual techniques at Barrow, off Chukotka, in the northern Bering Strait, and at Cape Pe'ek (see Fig. 1). Bowhead whales are seen almost continuously (including June, July and August) off Chukotka (Melnikov *et al.*, 2004; 1998). These data confirm that at least some bowhead whales, including some calves,



are not counted during spring at Barrow. However, there are no data available to determine whether the whales off Chukotka exhibit site-fidelity (this would require individual identification studies). The Cape Pe'ek sightings are almost certainly whales that are not counted at Barrow during the Spring census.

#### 2.2.6 Historical catches

There is a large amount of data on historical catches of bowhead whales (65,000 days of observations, representing 19% of the known whaling cruises during the period of the commercial fishery). These data have recently been assembled by Bockstoce and Botkin, as a draft in graphical form by month and at a fine spatial scale (and see Bockstoce and Botkin, 1983). Historical catches were taken in locations where harvesting is not occurring at present. In particular, very large catches were taken in the west of the Bering Sea along the Kamchatka Peninsula and in the Gulf of Anadyr, while very few whales were caught in the eastern Bering Sea. There were also large catches from the north of Chukotka to west of Barrow and some catches to the east of Barrow.

While recognising the potential value of catch data for examining stock structure, interpreting such data is complex and there are a number of provisos one must bear in mind including:

- (1) catch locations and timings reflect the operational behaviour of whalers – this may or may not mask the behaviour of whales – understanding the strategy of the whalers is needed to fully understand the catch data;
- (2) 'it is also possible that the bowheads were a single, integrated population that responded rapidly to the activities of whaling ships and fled from areas of intensive hunting, receding farther and farther north and east to temporarily safer areas' (Bockstoce and Burns, 1993, p.572);
- (3) catches may reflect historical (rather than current) movement patterns – e.g. most of the catches in April-May (as well as June-August) were taken south of the Bering Strait; this could reflect the migration pattern of a group of whales that was extirpated by the commercial fishery or simply the implications of more southerly and persistent of summer sea ice during the last years of the 'Little Ice Age' (Bockstoce and Burns, 1993).

The Workshop **recommended** that the historical catch data be analysed in further detail from the perspective of stock structure (and see Item 5).

With respect to the aboriginal subsistence catches, it was noted that since 1913, at least 21 whales have been taken in June in Alaska villages. This may be relevant to catches of Stock 2 under the Temporal Segregation hypothesis (see Item 2.3 below).

#### 2.2.7 Stable isotopes

Knoche *et al.* (SC/58/BRG22) used stable isotope ( $\delta^{13}\text{C}$ ) analysis of baleen plates to show that the bowheads caught at St. Lawrence Island have migration patterns consistent with those sampled at and east of Barrow. It would be expected that had the whales sampled at St. Lawrence Island not fed in the Beaufort Sea, they would have exhibited different  $\delta^{13}\text{C}$  values than those animals sampled at and east of Barrow, all of which exhibit a Beaufort Sea  $\delta^{13}\text{C}$  signal. While the results of this study suggest that the whales that migrate close to St. Lawrence Island do not feed in the

Chukchi borderlands, the sample size was very low ( $n=9$ ) and the Workshop **recommended** that if possible, this analysis is expanded.

#### 2.2.8 Traditional knowledge

A survey of traditional knowledge was conducted at St. Lawrence Island (Noongwook *et al.*, 2007). It found that the hunters believed that in this area: the bowhead population is increasing; there is an increasing number of young whales; distribution is influenced by environmental factors; whales are now wintering north of St. Lawrence Island; and there are two migration paths near the island.

Schweder noted some information from whaling captains on 'pulses' of animals passing Barrow in the fall (SC/A06/AWMP6) but this will require clarification.

#### 2.2.9 Other information

The relationship between the lengths of fetuses and time (George *et al.*, 2004) shows that, for whales sampled during the Alaskan hunt, conception occurs in a narrow time period in late winter and spring and suggests synchrony in breeding among whales. The highly variable testes sizes (O'Hara *et al.*, 2002) are consistent with the possibility of 'supermales', which appears to be necessary for the Generational Gene Shift hypothesis (see Item 2.3).

### 2.3 Stock structure hypotheses

SC/A06/AWMP5 described and provided the basis of support for five potential stock structure hypotheses for the B-C-B Seas bowhead whales. One was a single stock hypothesis whilst the other four involved two stocks.

The Workshop reviewed the information in SC/A06/AWMP 4 and 5 in addition to that discussed under Items 2.1 and 2.2, in order to arrive at an inclusive group of stock structure hypotheses based on presently available information from the perspective of testing the *Bowhead SLA*. It is emphasised that these hypotheses do not attempt to fully specify biological reality, but are rather aimed at capturing only those elements of stock structure that might affect management advice for the subsistence hunts for bowhead whales off Alaska and Chukotka.

The Workshop **agreed** that it was possible that a single stock could exhibit temporal and spatial segregation during migration. It therefore expanded the set of hypotheses in SC/A06/AWMP5 and those considered during the 2005 Annual Meeting to include hypotheses in which there is:

- (1) a single stock with multiple feeding grounds and site-fidelity to feeding ground; and
- (2) a single stock with non-random mating (e.g. family structure).

It also split some of the hypotheses identified during the 2005 Annual Meeting based on alternative assumptions regarding how movement may occur temporally and spatially.

The Workshop considered the possibility that some individuals from the eastern Canadian populations (Hudson Bay or Davis Strait stocks) occasionally emigrate into the western Arctic. There is evidence from two records from the 1800s of harpoons recovered from whales taken within the range of B-C-B Seas stock of bowhead whales that presumably came from the eastern Arctic whaling grounds to support this hypothesis (Bockstoce and Burns, 1993). However, it **agreed** that it was not necessary to include this hypothesis in trials because it would have no impact on the performance of an *SLA* to conserve the B-C-B stock of bowhead whales and allow for need satisfaction. Although

emigration of individuals from the eastern Canadian population may explain some of features of the genetics data, this hypothesis is not considered further.

The set of stock structure hypotheses considered by the workshop are summarised in Fig. 2. Table 2 summarises the level of support for or against these hypotheses from the various sources of evidence considered by the Workshop and also notes where the information is equivocal or uninformative.

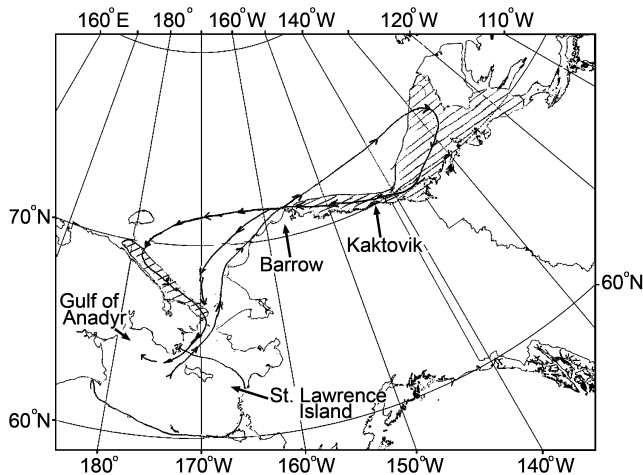


Fig. 2a. Baseline hypothesis (see text).

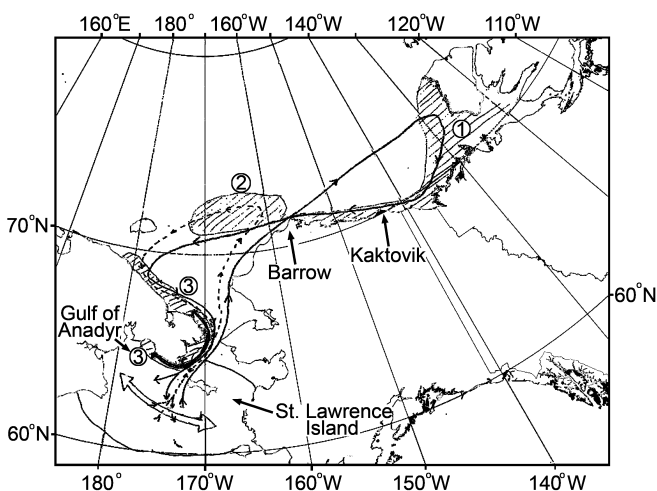


Fig. 2b. Feeding segregation (see text).

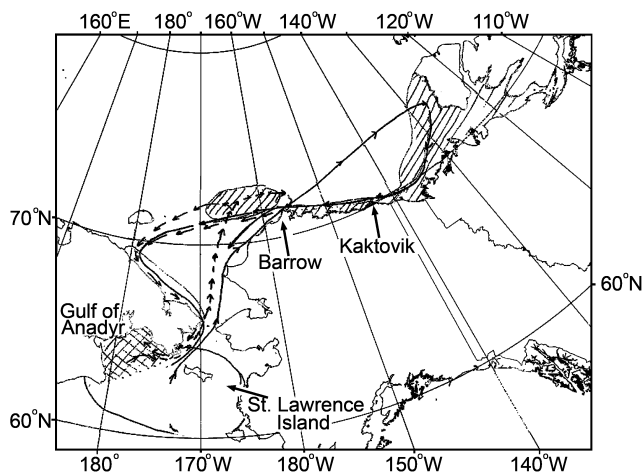


Fig. 2c. Chukchi circuit (see text).

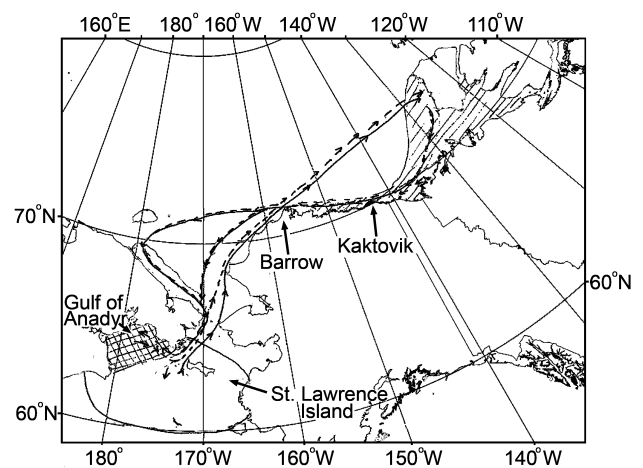


Fig. 2d. Temporal segregation (see text).

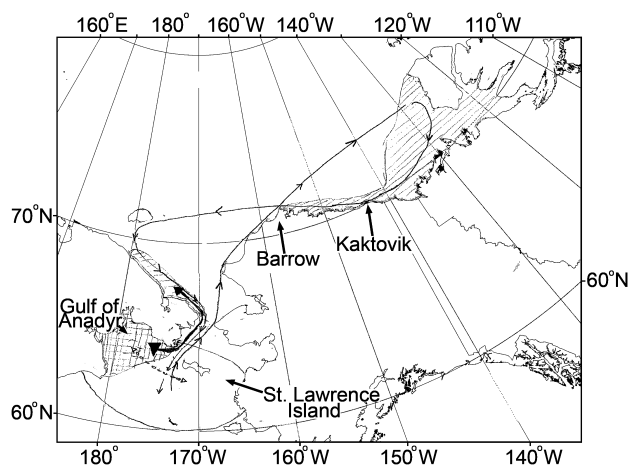


Fig. 2e. Spatial segregation (see text).

*Hypothesis 1. Baseline single stock.* There is one breeding area in the western and central northern Bering Sea, one primary summer feeding area in the Canadian and eastern Alaskan Beaufort Sea, and one primary spring migration route north along the Alaskan coast from April to early June and east across the Beaufort Sea. The western autumn migration in September through November bifurcates after passing Barrow, with some whales moving southwest and others west towards the Chukotka coast. The migration is completed when bowheads move south along the Chukotka coast through the Bering Strait and into the northern Bering Sea.

*Hypothesis 2. Single stock with social structuring.* This stock structure hypothesis is identical to the baseline single stock hypothesis in terms of migration routes and breeding and feeding grounds. However, non-random mating is postulated to occur which could lead to a genetic disequilibrium.

*Hypothesis 3. Single stock with 'Generational Gene Shift'.* This stock structure hypothesis is identical to the baseline single stock hypothesis in terms of migration routes and breeding and feeding grounds. It postulates that following the severe depletion of bowhead whales by commercial hunting, there may have been a period of a few decades with few reproductive adults. This, possibly coupled with substantial skew in reproductive success among individuals, may have resulted in a substantial shift in the genetic frequencies of their offspring.

*Hypothesis 4. Single stock with feeding ground site fidelity.*

There is one breeding stock and three summer feeding areas, and fidelity to feeding areas and migratory routes. Most whales (Group 1) migrate as for the baseline single stock hypothesis. Other whales (Group 2) migrate in April-May to the 'greater' Barrow Canyon area north of Barrow and then follow the Chukchi ice front during summer and feed near the 'Chukchi borderlands' between the Herald and Barrow Canyons, migrating in September-October along the northern Chukotkan coast and then south to the Bering Sea. The third set of whales (Group 3) migrates north through the Bering Strait in late May-June and summers along the Chukotka coast, with at least a few whales remaining in the northern Gulf of Anadyr throughout the summer. The whales from Group 3 return to the Gulf of Anadyr in the autumn and mix with the other groups during the breeding season. The Group 2 animals are assumed to be subject to harvest on the Chukotka coast. All three groups are available to hunters at St. Lawrence Island in fall while Groups 1 and 2 are available to these hunters in spring.

*Hypothesis 5. Two stocks – Chukchi Circuit-mixed.* There are two breeding stocks. The behaviour (migration routes, feeding and breeding grounds) for Stock 1 is the same as for the stock in Hypothesis 1. Whales from Stock 2 migrate from Gulf of Anadyr through the western Bering Strait past Cape Pe'ek in May and June. Most of these whales are assumed to feed in areas north and northwest of Barrow in summer, although a few may remain around the Chukotka Peninsula. During the return migration, some Stock 2 whales may be available to hunters at St. Lawrence Island in fall, but not in late winter. Some of the Stock 2 whales are available to Barrow hunters in fall. These two stocks are mixed during the fall migration past Barrow and through the Bering Strait.

*Hypothesis 6. Two stocks – Chukchi Circuit-segregated.* This hypothesis is identical to the Chukchi Circuit-mixed hypothesis except that the migration of Stock 1 is temporally segregated from that of Stock 2 when it passes Barrow in fall.

*Hypothesis 7. Two stocks – temporal segregation.* There are two breeding stocks. The two stocks have the same migration route and feeding grounds, although a few Stock 2 whales remain around Chukotka throughout the summer. The timing of the migration for Stock 1 is the same as for the single stock in Hypothesis 1, but the whales from Stock 2 are temporally separated (by approximately a month) from those from Stock 1 because these whales are migrating from the Gulf of Anadyr from the end of April. Animals from Stock 2 do not pass the Bering Sea villages Wales and Kivalina.

*Hypothesis 8. Two stocks – spatial segregation-St. Lawrence mixed.* There are two breeding stocks and two summer feeding areas (the eastern Beaufort Sea and the western Russian Chukchi Sea). There is sequential migration through the Bering Strait; the spring migration route for Stock 1 is northeast along the Alaskan coast from April to early June and east across the Beaufort Sea. The whales from Stock 2 migrate northwestwards along the Chukotkan coast from late May to mid-June. Stock 2 whales are available to hunters in the Russian villages from spring through the summer and into autumn, and to some degree to hunters in Savoonga and Gambell in autumn and winter. These whales are not available to any US mainland Alaskan villages.

*Hypothesis 9. Two stocks – spatial segregation-St. Lawrence segregated.* As for Hypothesis 8, except that the Stock 2 whales are not available to hunters at St. Lawrence Island.

### 3. OTHER NEW INFORMATION ON BOWHEAD WHALES RELEVANT TO THE IMPLEMENTATION REVIEW

#### 3.1 Abundance estimates and trends

The Workshop **agreed** that, as in the previous trials, the estimates of abundance resulting from the Barrow censuses would be used when conditioning and by the *Bowhead SLA*. The most recent estimates are given in Zeh and Punt (2005).

It has been known for some time (e.g. Bogoslovskaya *et al.*, 1982) that bowhead whales can be found around the Chukotka Peninsula throughout the year. Observations up to and including 1996 were summarised by Melnikov *et al.* (1998). It is not known whether the same whales migrate along the Chukotka coast each spring, nor is their relationship to whales found off Alaska known.

SC/58/BRG15 presented results from recent shore-based surveys from Chukotka carried out in May and June 1999-2001. The 1999 count was a feasibility study, and the counts from Cape Pe'ek in 2000 and 2001 were designed to permit estimation of the number of whales migrating past Cape Dezhnev. Survey methods were similar to those for bowhead whales off Barrow and gray whales off Monterey, CA except that no experiments designed for estimating detection probabilities  $P$  were conducted. The number of migrating bowheads (number recorded/ $P$ ) was estimated using three alternatives for  $P$ :

- (1)  $P = 1$  (all whales passing during watch with acceptable visibility conditions were seen);
- (2)  $P = P_b$ , bowhead detection probabilities estimated for the surveys near Barrow (except that >10km range from Cape Pe'ek was treated as equivalent to offshore distance >2km near Barrow because observation perch height was so much greater at Cape Pe'ek); and
- (3)  $P_g$  as analogous as possible to detection probabilities estimated for the gray whale surveys near Monterey.

Methods of estimating the number of migrating whales from the Cape Pe'ek data and the assumptions on which they were based were as similar as possible to those of the surveys near Barrow. Key assumptions were:

- (1) the migration period in a year was assumed to last from the first to the last days a bowhead was seen – 14 May to 13 June in 2000 and 23 May-15 June in 2001;
- (2) whales were assumed to migrate continuously throughout this period;
- (3) days were assumed to be 'watched' if observers counted for more than 2h with fair to excellent visibility. This was around 58% of the total number of days in each year;
- (4) a weighted mean was used to estimate whales passing on unwatched days.

Weighted geometric means of the 2000 and 2001 estimates of the number of migrating bowheads for the three alternatives for  $P$  with their 95% confidence intervals are: (1) 426 (301, 603); (2) 841 (601, 1,176); and (3) 774 (558, 1,073). Given observed migration speeds of bowheads in 2001, it is unlikely that any of the whales seen from Cape Pe'ek in June of 2001 were counted by the survey near Barrow that year.

At least four possible sources of bias were noted.

- (1) inability to estimate  $P$  from data collected during the surveys. Choice of  $P = 1$  would lead to a negative bias. The extent and nature of the bias from using the Barrow or Monterey values is unclear;

- (2) assumption that the migration period was known. This would lead to a negative bias if whales passed before or after the assumed period;
- (3) treatment of the 42% unwatched days. This might lead to either a negative or a positive bias depending on whether fewer or more whales passed than estimated;
- (4) limitation of the observed corridor compared to the actual width of the corridor. Whales passing beyond the observed corridor would lead to a negative bias.

The Workshop thanked both the Russians who conducted the survey and the authors of SC/58/BRG15, noting that it provided a valuable estimate of abundance in a previously unsurveyed area. The limitations of the data were discussed, in particular the lack of data on detection probability including whether whales reported as sighted up to 20km distance could be reliably identified. It was noted that the survey only included whales relatively close (within about 24km) to shore; other whales migrating through the strait would not be seen.

The Workshop believed that the analysis provided minimum estimates of abundance particularly when a detection probability of 1 was assumed, and so the estimates assuming detection probabilities from other counts should be used instead. The Workshop **agreed** that the abundance estimates were suitable for use in conditioning trials, but not necessarily for use by the *SLA*.

The Workshop **recommended** that a further survey be conducted in this area that will address some of these concerns, including undertaking direct estimation of detection probability.

### 3.2 Biological parameters (including age- and length-structure)

Punt (2006) extended the modelling framework used to assess the B-C-B Seas bowhead whales to make use of age- and length-frequency data. The results of fitting this model indicate that selectivity since 1914 is not uniform, as assumed in previous assessments, but rather domed-shaped, with young animals most vulnerable to harvest. The length-frequency, proportion, age-composition, and abundance data are inconsistent to some extent. Fitting the model to the age-composition data leads to the most pessimistic estimates of stock status and productivity. However, the results of projections based on these assessments in which strike limits are set using the *Bowhead SLA* suggest that all lie within the range of the single stock scenarios considered when testing the *Bowhead SLA*. So these refined assessments do not indicate any need for revision of the existing *Bowhead SLA*.

The Workshop **concurred** with this conclusion.

It was suggested that it would be valuable to extend the modelling framework to fit to both the length and age data together. If this analysis is to be conducted it should include the additional age data which are now available. The Workshop noted that this was of relevance to the Bowhead, Right and Gray whales sub-committee.

### 3.3 Other

No other new information was available.

## 4. MODELLING FRAMEWORK FOR THE 2007 IMPLEMENTATION REVIEW

### 4.1 Basic structure (including nature of mixing)

The Workshop briefly reviewed the evaluation trials used in the selection of the *Bowhead SLA* (IWC, 2003, table 6) which were modelled on a single stock and focussed on

different values for some pre-specified parameters such as *MSYR* as well as possible errors in the input data. Deterministic and stochastic versions of the operating model were used and the trials were conditioned using abundance and proportion data. The Workshop agreed that it would not be necessary to incorporate the stochastic model into any multistock trials.

The five models needed to implement the nine stock structure hypotheses described under Item 2.3 are:

Hypothesis	Underlying model	Comments
1. 1S	A	
2. 1S non-random mating	A	Model has same demographics as Hypothesis 1
3. 1S genetic gene shift	A	Model has same demographics as Hypothesis 1
4. 1S site fidelity	B	Model as 2 stock model
5. 2S Chukchi mixed	C	
6. 2S Chukchi segregated	D	
7. 2S temporal segregation	E	
8. 2S spatial segregation SLI mixed	B	
9. 2S spatial segregation SLI segregated	B	

Although Hypothesis 4 is a single stock hypothesis, it will be modelled using a two operating model. The postulated northern feeding ground will be ignored because there are no data from it (or indeed any data available for it). Using the two stock approach will lead to trials that are more difficult than if some arbitrary abundance estimate was assigned to this feeding group.

The Workshop noted that Hypotheses 4, 8 and 9 are all versions of the same model with Hypothesis 9 (2S spatial segregation SLI segregated) being the least difficult because the Stock 2 whales are harvested only around Chukotka, not by hunters from St. Lawrence Island. Hypotheses 5 and 6 (Chukchi circuit) are similar with Hypothesis 6 likely to be the more difficult as more harvest is likely to be taken from the smaller Russian stock. It was noted that if the most difficult trial in a group of similar trials is run and does not cause problems to the *SLA* then it would be unnecessary to run the other trials in the group. However, reference was also made to earlier discussions within the Standing Working Group on the Development of an Aboriginal Subsistence Whaling Management Procedure regarding the need for balance in trials and the need to concentrate evaluation of results on plausible scenarios. After discussion, the Workshop **agreed** that while it may not be necessary to run all trials for all of the hypotheses, it was not necessary to make that decision now given that the above information is sufficient to set up the trial structure.

Separate from the trials, a series of detailed individual based simulations are being conducted to aide in interpretation of the genetic data. Taylor reported on preliminary data from single stock simulations and plans for future two stock simulations. The intent is to better understand what genetic patterns might emerge from populations that are not only not in equilibrium, as most statistical analyses of genetic data assume, but are also not

randomly sampled. The extreme longevity of bowhead whales implies that the recovering population is likely to be out of genetic equilibrium. The oldest whales represent the genetic constitution of the population prior to commercial hunting, which depleted the population by roughly 90%. Younger cohorts inherited genes only from the much smaller set of whaling survivors. Further, the large and variable testes size in bowheads suggests sperm competition and consequently high variance in reproductive success in males. Simulations were used to investigate whether such dynamics result in genetic heterogeneity between cohorts (the Generational Gene Shift (GGS) hypothesis). Parameters were set at values to maximise GGS while still being plausible. Simulations began with historical large populations, reduced these to estimated low levels, and then grew them to current abundance estimates. Uncertainty in the magnitude of reduction was captured by running simulations bracketing the estimated lowest number (using the 95% confidence intervals). Two mating systems were simulated: one with super males and hence high reproductive variance and one with equal mating probability between all males and females. Both nuclear DNA (10 microsatellite loci) and mitochondrial DNA were simulated. Three cohorts were compared: the oldest whales (more than 90 years old and alive before 1909), the first post whaling offspring (60-90 years old) and the youngest (0-30 years old). For microsatellite data, out of 100 simulations more significant values of  $F_{ST}$  were found than would be expected due to chance for comparisons between whales born before and those born after commercial whaling, but only in super-male scenarios. Results were the same for both high and low minimum population sizes, but scenarios without super males did not show differentiation. The minimum abundance following commercial whaling had relatively little effect and thus this uncertainty is of lesser importance than the mating system. MtDNA results will be presented at the annual meeting.

Taylor noted that she plans to carry out the following tasks before the 2007 Annual Meeting:

- (1) run control assuming only one population and compare two stocks versus one stock by genetic identity measure;
- (2) see if each population is in Hardy-Weinberg equilibrium;
- (3)  $F_{ST}$  between populations;
- (4) apply STRUCTURE and rule out scenario if it can pick out two populations.

The Workshop thanked Taylor for this work. After discussion, the Workshop **agreed** that, at present it is not in a position to give detailed instructions regarding the best simulations to conduct or questions to address. It **agreed** that the simulations are unlikely to be able to give sufficient information on plausibility to enable elimination of any hypothesis at the 2006 Annual Meeting, but the results of these simulations could be used in future to aid interpretation of results from conditioning the trials and to give information about their plausibility. It was also suggested that consideration be given to using other approaches than STRUCTURE, such as those being discussed as part of the TOSSM project (SC/58/Rep6).

#### 4.2 Parameter values

The most recent estimates of the biological parameters are:

Parameter	Prior distribution
$MSYL_{1+}$	$U[0.4, 0.8]$
$MSYR_{1+}$	$U[0.01, 0.7]$
$a_T$	$DU[1, 9]$
$a_m$	$N(20, 3^2)$ , truncated at 13.5 and 26.5
$S_{adult}$	$N(1.059, 0.0378^2)$ truncated at 0.995 with no constraint on the maximum age
$S_{juv}$	Constrained by the population dynamics equation to be less than $S_{adult}$
$f_{max}$	$1/f_{max} \sim U[2.5, 4]$
$N_{1993}^{1+}$	$N(7,800, 1,300^2)$

The Workshop **agreed** that there was no evidence to suggest that, in two stock hypotheses, the two stocks have different biological parameters. Information is needed on how to allocate both the historic and future catches to stocks, which is provided to the operating model in the form of mixing matrices.

Three periods of harvest need to be considered: (1) the period of commercial harvest (1848-1914); (2) the years between 1915 and the present; and (3) the future. The historical catches need to be allocated to time-steps within the year and spatial strata that are chosen to represent the stock structure hypotheses. The trials on which the *Bowhead SLA* will be evaluated will include specifications regarding the timing and location of future catches (i.e. the fraction of the catch taken in each month at each village).

It will be necessary to specify two sets of mixing matrices for each stock structure hypothesis: (1) one for the period of commercial harvest; and (2) one for the period after 1915 (including the future). The Workshop **agreed** that the mixing matrix for each stock should, for each time-step, specify the proportion of animals that are exposed to harvest and/or available to capture by location in the middle of each time-step. It is necessary to define an 'other' location to represent animals north and south of the area in which catches and surveys occur. The sum of the proportions over location will therefore equal 1.

#### 4.3 Conditioning

The Workshop had an initial discussion regarding how to condition any trials. The workshop **agreed** that the single-stock trials would be conditioned in the same way as the trials used to develop the *Bowhead SLA*. This implies that the abundance data used to determine the values for the model parameters will be negatively biased because they ignore any whales that do not arrive at Barrow (e.g. whales that may be resident off the Chukotka coast). Ignoring these whales will tend to make it slightly (though not substantially) more difficult to achieve conservation objectives for given need scenarios.

The Workshop suggested that the following method should be considered as the approach to condition the trials in which there are two stocks:

- (1) specify the values for the parameters of the population dynamics model that are the same for all of the simulations in the trial (e.g. survey bias,  $MSYL$ ,  $MSYR$ );
- (2) generate values for the biological parameters of the population dynamics model (survival, fecundity, etc.) from their priors;
- (3) generate values for the abundance of the whales that pass Pe'ek and Barrow from their priors. The prior for the number of whales passing Barrow will be that used for the trials used to develop the *Bowhead SLA* while the

prior for number of whales passing Pe'ek will be based on the results of the surveys conducted there in 2000 and 2001 (SC/58/BRG15);

- (4) calculate the values for the carrying capacities of the two stocks so that if these values are projected forward, the abundances of the two stocks equal those generated at step (3);
- (5) calculate the likelihood of the trajectory. The data included in the likelihood function will be the estimates of abundance from the visual and acoustic surveys at Barrow as well as the data on the proportion of calves and mature animals during 1988/89, although consideration should also be given to including the age- and/or length data in the likelihood function;
- (6) repeat steps (2)-(5) many times;
- (7) select 100 parameter vectors from those generated at steps (2)-(5) with replacement and with probabilities proportional to the likelihoods associated with each projection; and
- (8) apply diagnostic methods to evaluate the conditioning.

The Workshop noted that it was not certain that it will always be possible to calculate the values for the carrying capacities as anticipated in step (4) and, of course, it is possible that the results of conditioning the trials may be inconsistent with information for the B-C-B bowhead whales. The Workshop **agreed** that diagnostic statistics need to be developed to check whether the conditioning is consistent with auxiliary information. It **agreed** that an initial set of diagnostic statistics for first stage evaluation should include:

- (1) the rate of increase of the bowheads predicted to pass Barrow in spring (perhaps summarised using the Akaike Information Criterion (AIC));
- (2) the lowest size of the smaller stock; and
- (3) whether the total population dropped to levels consistent with the collapse of the commercial fishery.

The Workshop examined the results from a simple two-stock population dynamics model and noted that some choices for the mixing matrices may lead to population trajectories for which these diagnostics are inconsistent with *a priori* expectations. Punt and Givens volunteered to develop software to assist Zeh and George to determine the implications of possible mixing matrices in terms of these diagnostic statistics. The workshop encouraged the development of other statistics to evaluate whether the results of the conditioning appear plausible and that could be used for final trials. An example of such a statistic is the Bayes Factor.

It was noted that the estimates of abundance at Cape Pe'ek are probably negatively biased (see Item 3.1). The Workshop **agreed** that the baseline two stock trials should not be based on the assumption that all whales at Cape Pe'ek are sighted. It was further noted that process of conditioning the trials might be simplified if the values for the biological parameters are pre-specified rather than being generated from priors. Finally, the Workshop noted that the simulations that Taylor intends to conduct (see Item 4.1) may be useful when assigning plausibility ranks to trials.

## 5. WORKPLAN

An approximate timeline for the bowhead whale *Implementation Review* was agreed at the 2005 Annual meeting (IWC, 2006, p.16).

### 5.1 Data availability issues

In accordance with the Data Availability Agreement (DAA) Procedure A, all data relevant to management advice for the 2007 meeting should be submitted six months in advance of that meeting (i.e. probably in November 2006). However, it had been noted last year that given the collaborative nature of the analyses being undertaken, if all collaborators concurred, consideration could be given to allowing an extension to this deadline should it be required. However, at this Workshop, it was **agreed** that as much data as possible be provided for analysis by approximately 1 September 2006, in order to provide the best opportunity for progress at the planned October 2006 Workshop to finalise trial structure (see Item 2.2.1.1).

The Workshop highlighted the great importance to the *Implementation Review* process of the historic (pre-1914) catch data. While the total catch information already published is adequate for single stock hypotheses, much more detailed information is required to adequately examine two stock hypotheses. It **draws the Committee's attention** to the fact that without this detailed information (at least catch position and date for each of the whales) included in the subset of the catches documented in Bockstoe and Botkin (1983), it will be extremely difficult to satisfactorily complete the *Implementation Review*. It therefore **strongly urges that every effort be made** to obtain these data and that they are made available under Procedure A of the DAA. It emphasises the protection for data owners inherent in the DAA – the data can only be used in the context of the *Implementation Review* and the data owners retain publication rights.

### 5.2 Work for the 2006 Annual Meeting

The Workshop identified the items below for completion for the 2006 Annual Meeting.

*(1) Develop an initial set of mixing matrices for the stock hypotheses discussed under Item 2.3 following the guidance given under Item 4.2*

This work (to be undertaken by Zeh and George with assistance from a group comprising Punt, Butterworth, Donovan and Givens) will be greatly assisted by the development of a program (by Punt and Givens – see Item 4.3) to determine the extent to which these matrices lead to population trajectories consistent with auxiliary information about the stock(s).

*(2) Assemble the historical (commercial and aboriginal) catch data by position (latitude and longitude or village) and date*

This work for the aboriginal subsistence catches will be undertaken by George. It was noted that past documents submitted by the USA to the Commission's Aboriginal Subsistence sub-committee with respect to the documentation of need will be of relevance here. Issues related to the commercial catch are dealt with under Item 5.1 above.

*(3) Advice on interpretation of microsatellite data.*

This refers to the issues surrounding the 'old' and 'new' datasets and questions related to the existence of the Oslo bump (see Item 2.2.1). An advisory group comprising Palsbøll, Jørde, Kanda and Morin will be approached to provide this advice;

*(4) Advice on development of new loci*

The Workshop **requests** that TAMU provide for the meeting in St. Kitts and Nevis, additional information on (1) the advantages/disadvantages of developing additional tri- and tetranucleotide repeat loci and (2) the feasibility of doing so before the Data Availability Agreement deadline (see Item 5).

*(5) Further processing of genetic samples and data analysis*

If TAMU can process one further plate for the new loci it should contain (in priority order): (1) the 17 whales mentioned under Item 2.2.1.1 for a unified analysis of the Oslo bump; (2) all St. Lawrence Island whales (if any) missing 3 or more new loci; and (3) some more spring Barrow whales. It also **recommends** that linkage disequilibrium analyses be run on the new loci for the available dataset.

The Workshop also **requests** the paper by Taylor on mtDNA analyses (see Item 2.2.1)

**5.3 Work beyond the 2006 Annual Meeting**

The Workshop did not have time to discuss details of the workplan for the period after the 2006 Annual Meeting, but noted the general objectives and timeline outlined in IWC (2006, p.16).

The Workshop discussed genetic data generation issues in the context of the late 2006 DAA (Item 2.2.1.1). It was **agreed** that the following were of highest priority and it **recommends** analysis of the following samples:

- (1) the 11 old loci on all St. Lawrence Island animals not in the 2004 dataset;
- (2) all 33 loci for roughly 50 to 80 whales selected from a genetically homogeneous group of whales in the Canadian Arctic<sup>5</sup> (Foxye Basin whales, or if these number too few, Hudson Bay whales or a combination of whales from these two sites);
- (3) all loci (and any new mtDNA sequences) for any Chukotkan biopsies, to the extent that these can be obtained and calibrated (in a US lab for microsatellite loci); and
- (4) collection and analysis if possible of biopsy samples from Chukotka.

The following items were highlighted as work which would be valuable to the current and any future *Implementation Reviews*:

- (1) a further survey should be conducted in the Chukotka area using two platforms to generate an estimate of detection probability (see Item 3.1);
- (2) telemetry experiments, particularly off Chukotka in the spring/early summer (see Item 2.2.4);
- (3) increased sample size for the stable isotope analyses for St. Lawrence Island (see Item 2.2.7).

Items (2) and (3) could provide data that effectively preclude or strongly support certain stock structure hypotheses. Therefore the Workshop **strongly urges** that such research commence if at all possible.

<sup>5</sup> To provide a 'control' group where it is known the animals are genetically distinct. If the Canadian data cannot be obtained (e.g. due to data availability issues), then samples from the Sea of Okhotsk could be used.

**6. ADOPTION OF REPORT**

The report was adopted by consensus on 27 April 2006. The Chair thanked the participants for their hard work and particularly the rapporteurs for quickly producing such a well written report.

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## Annex B

### Agenda

1. Introductory items
    - 1.1 Convenor's opening remarks
    - 1.2 Election of Chair
    - 1.3 Appointment of rapporteurs
    - 1.4 Adoption of Agenda
    - 1.5 Available documents
    - 1.6 Available data, especially since the 2005 Annual Meeting
  2. Stock structure hypotheses for modelling exercise
    - 2.1 Brief review of status of discussions at the 2005 Annual Meeting
    - 2.2 Available information (including review from March 2006 US Workshop)
      - 2.2.1 Genetic data
      - 2.2.2 Photo-identification and photogrammetric data
      - 2.2.3 Acoustic data
      - 2.2.4 Telemetry
      - 2.2.5 Visual data
      - 2.2.6 Historical catches
      - 2.2.7 Stable isotopes
      - 2.2.8 Traditional knowledge
      - 2.2.9 Other information
    - 2.3 Stock structure hypotheses
  3. Other new information on bowhead whales relevant to the *Implementation Review*
    - 3.1 Abundance estimates and trends
    - 3.2 Biological parameters (including age- and length-structure)
    - 3.3 Other
  4. Modelling framework for the 2007 *Implementation Review*
    - 4.1 Basic structure (including nature of mixing)
    - 4.2 Parameter values
    - 4.3 Conditioning
  5. Workplan
    - 5.1 Data availability issues
    - 5.2 Work for the 2006 Annual Meeting
    - 5.3 Work beyond the 2006 Annual Meeting
  6. Adoption of report
-

## **Annex C**

### **List of Documents**

#### **SC/A06/AWMP**

1. GIVENS, G.H. and I. OZAKSOY. Population structure and covariate analysis based on pairwise microsatellite allele matching frequencies.
2. GIVENS, G.H. and OZAKSOY, I. Transience of a temporal lag correlation feature in bowhead microsatellites.
3. GIVENS, G.H., HUEBINGER, R.M., BICKHAM, J.W., GEORGE, J.C. and R. SUYDAM. Re-examination of stock structure in bowhead whales from the Western Arctic; preliminary analyses based on new microsatellites.
4. PASTENE, L.A. Brief review of the hypotheses on stock structure in the B-C-B bowhead whale and implications for the specification of simulation trials needed for the *Implementation Review*.
5. ANON. Hypothetical stock structure archetypes and temporal spatial vulnerability to hunting for the Bering-Chukchi-Beaufort Seas bowhead whale population.
6. SCHWEDER, T. The Chukchi circuit hypothesis, and its simulation.
7. GIVENS, G.H. Report of the intersessional email group on pulsed migration structure.

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## **Annex D**

### **Summary of Available Bowhead Whale Data**

*Table on facing page.*

Data type	Years covered	Approx. <i>n</i>	File name	Key fields	Contact person	Original explanation file <sup>1</sup>
Indiv. master for sampled whales	1969-2005	962 (some 2005 need checking)	Bh.individual master:1974-2005.xls	Whale ID, date, sex, length, village, how sample obtained	George: <i>Craig.George@north-slope.org</i>	Bh_individual.README.2005.doc
Age determination	Need to link with whale ID	178	Bh.agemaster05.xls	Whale ID, length, baleen length, age aging technique	George: <i>Craig.George@north-slope.org</i>	-
Age determination	1978-2000	105	Bh.aspartic_age rev04.xls	Whale ID, info (e.g. foetus, left/right), length, dextro-rotary/levo-rotary ratio, batch, year, village, comments	George: <i>Craig.George@north-slope.org</i>	Bh.aspartic_age.readme-06.doc
Reproductive data <sup>2</sup>	-	-	-	-	-	-
Foetal data	1960-2000	28	bh.fetus.txt	Whale ID, foetus ID, date, length of foetus, length of mother	George: <i>Craig.George@north-slope.org</i>	Bh.reproduction.README.doc
Pregnant females	1976-2002	34	bh.pregfem.txt	Whale ID, date, length (m), pregnant, village	George: <i>Craig.George@north-slope.org</i>	Bh.reproduction.README.doc
Mature females <=15m	1976-2000	25	bh.matfemLT15m.xls	Whale ID, date, length, pregnant, comment	George: <i>Craig.George@north-slope.org</i>	Bh.reproduction.README.doc
Aerial surveys <sup>3</sup>	1979, 1981, 1985, 1986	120 records	Bh.transectkm.txt	date, time, flight/transect numbers, no. whales, distance from ice edge	Zeh: <i>zeh@stat.washington.edu</i>	Readme.bh_aerial surveys.txt
Aerial surveys	1979, 1981, 1985, 1986	68 records	Bh.transecthr.txt	Dates, effort, no. whales seen, comments	Zeh: <i>zeh@stat.washington.edu</i>	Readme.bh_aerial surveys.txt
Visual census	1978-88, 1993, 2001	Very large!	Bh.visual_census.zip	All aspects of the visual census. Well described in details.new.pdf so not summarised here. Unzips to 32 files -7 for north perch (1978-83, 1985) and 9 for south perch (1978-83, 1985-88, 1993 and 2001), 2 Fortran programs and input files	Zeh: <i>zeh@stat.washington.edu</i>	details.new.pdf and readme.bh.visual_census.pdf
Aerial survey data (photo-ID)	1976-1998	> 30 surveys	Bh.photo.zip	> 30 fields, includes Image Number, whale Number, photo quality, whale length, etc.	Rugh: <i>David.rugh@noaa.gov</i>	Readme.bh.photo.pdf
Chukotka bowhead survey	1999-2001	3 surveys; several hundred primary sightings	Dezhnev 1999.xls; Dezhnev 2000.xls; Dezhnev 2001.xls	Observer, date, visibility, species, angle, bearing, distance, calf, etc.	V. Melnikov	Melnikov and Zeh, 2006
Acoustic locations	1982, 1985, 1986, 1988, 1993, 2001	6 surveys, 1,000s of locations	Bh.acoustics_locations.zip	Multiple files; key fields include: location_Id, track ID, date, time, xy position, etc.	Clark: <i>cwc2@cornell.edu</i> ; Zeh: <i>zeh@stat.washington.edu</i> ; Data owner: NSB DWM	readme.bh.acoustic_locations.txt
Genetics data <sup>4</sup> (sequence)	1992-2003	137	Bh.bcb_genetics_sequence.xls	Whale ID, SWFSC ID, date, sex, length, village, sequence	George: <i>Craig.George@north-slope.org</i>	Readme.bh.bcb_genetics.tds_JCG.doc
Genetics data (microsatellite)	Need to link with whale ID	215	Bh.bcb_genetics_microsats_Jan26.xls	Whale ID, sample ID, loci	George: <i>Craig.George@north-slope.org</i>	Readme.bh.bcb_genetics.tds_JCG.doc
St. Lawrence Is. baleen	~1985-2005	11	NYA	Whale ID, position on plate, C12/13 ratio	Suydam: <i>Robert.Suydam@north-slope.org</i>	NYA

**Footnotes:**

<sup>1</sup>These have been compiled into the remainder of this document by GPD which some of you may find useful. <sup>2</sup>The three files have been put into one Excel file by GPD which some of you may find useful. <sup>3</sup>The two text files have been put into one Excel file by GPD which some of you may find useful. <sup>4</sup>Craig George notes that new genetics data will rapidly develop over the next 6 months.

