Brief review of the hypotheses on stock structure in the B-C-B bowhead whale and implications for the specification of simulations trials needed for the *Implementation Review*

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ABSTRACT

This paper briefly outlines the hypotheses on stock structure developed in recent years for the B-C-B bowhead whales, and their supporting scientific evidences. Three stocks hypotheses are proposed for inclusion in the simulation trials needed for the *Implementation review*: a) single stock, b) two stocks with spatial separation and c) two-stocks Chukchi Circuit.

INTRODUCTION

Two major discussions on stock structure of the bowhead whale have occurred at the IWC Scientific Committee (SC) Meeting. The first, occurred in 1991, concluded that there are five stocks of bowhead whales, Spitsbergen, Davis Strait, Hudson Bay, Okhotsk Sea and Western Arctic (Bering-Chukchi-Beaufort) (Figure 1). Discussion on the identity of the B-C-B stock was based on distribution of sightings and historical catches, but no comparative analyses using genetic or non-genetic data were available (IWC, 1992). A comprehensive review of the studies on stock structure in bowhead whale was presented to the SC in 2000 (DeMaster et al., 2000). In this review, published later as Rugh et al. (2003), the authors recognized the importance of using multiple piece of evidence (genetics and non-genetics) to investigate stock structure. One of the relevant conclusions of this review paper was that only a limited amount of data was available for conducting comparative genetic or non-genetic analyses within the distributional range of the B-C-B stock (Figure 2) and that therefore no such studies had been conducted yet. It was clear that there was uncertainty on the stock identity of the B-C-B stock, notwithstanding the SC agreed in 2000 with the concept of single management stock for B-C-B whales. The SC noted that even if there is separation of sub-stocks after migration, for instance between Chukchi and Beaufort Seas, there is little risk of differential local depletion, because harvesting occurs almost entirely during migration, and is spread in time across the duration of the migration.

The next major review on stock structure was conducted at the 2004 SC meeting (IWC, 2005). Previous to that meeting the genetic and non-genetic data for B-C-B bowhead whales were made available by US scientists to interested SC members through the Procedure A of the SC data access protocol. Several of the analyses presented to the 2004 SC meeting showed a substantial degree of genetic heterogeneity in the samples from the B-C-B stock of bowhead whale samples suggesting the possibility of additional structure. At the same time, technical problems with some of the genetic data were recognized as well the necessity to increase the number and coverage of the sampling (spatial and temporal) through the range of distribution of the B-C-B stock.

The US held a workshop on B-C-B bowhead whale stock structure in Seattle on February 2005 and the workshop considered several stock structure hypotheses. Further statistical analyses of the available nuclear DNA data were presented at the 2005 SC meeting and the hypotheses developed during the US workshop were discussed in the context of the multiple stock structure hypotheses (IWC, 2006).

The SC will carry out the *Implementation Review* for B-C-B stock of bowhead whales in its 2007 meeting. In preparation for this review, the First Intersessional Workshop is held with the aim to specify the basic structure and types of simulation trials needed for the *Implementation Review* (IWC, 2006). The objective of this paper is to briefly outline the hypotheses on stock structure developed in recent years for the B-C-B whales, and the respective supporting scientific evidences. This information can be used as a background to specify the simulation trials.

OUTLINE OF THE HYPOTHESES ON STOCK STRUCTURE (based on the discussion of the 2004 and 2005 SC meetings)

Single stock hypothesis
This hypothesis proposes a single breeding ground in the western and central northern Bering Sea. In spring whales migrate northeast along the Alaskan coast and then east across the Beaufort Sea. The primary feeding ground is in the Canadian and eastern Alaskan Beaufort Sea. In autumn whales move west and after passing Point Barrow bifurcate with some whales moving southwest and other towards the Chukotka coast. Whales complete the migration by moving south along the Chukotka coast through the Bering Sea (Figure 2). This is the hypothesis currently adopted by the SC for management purposes.

As mentioned above this hypothesis was adopted in absence of comparative genetic or non-genetic analyses in the area of distribution of the B-C-B whales. Since 2004 some spatial and temporal comparative genetic analyses have been conducted.

Two stocks with spatial segregation
This hypothesis proposes two different breeding grounds (polynias near St. Lawrence Islands and the northern Gulf of Anadyr) and two different feeding grounds (eastern Beaufort Sea and the western Chuckchi Sea). The time of the northern migration differ between the two stocks. The evidence come from information on pattern of sighting distribution that suggested that some whales initiate the northern migration in a later period and some remain along the east coast of the Chukotka Peninsula in summer (Bogoslovskaya et al., 1982; Melnikov et al., 1998).

Most of the genetic data have been collected for a particular locality (Barrow) and data are scarce for other localities. This makes the spatial comparison analysis difficult to interpret. Givens et al. (2004) examined samples from the spring hunt at Barrow and found a statistically significant difference in the comparison to St. Lawrence Island animals for a single locus (EV1). One of several possible explanations given by the authors for this result is that animals from St. Lawrence Island represent a distinct stock.

Two stocks with temporal segregation
This hypothesis proposes that two genetically distinct populations with sex-segregated migration past Barrow. Whales of one sex from sub-population A would migrate before whales of the same sex from population B, then followed by whales of the other sex, first from A and then from B. This is based on the results of the genetic analysis on Barrow samples presented in Jorde et al (2004). Genetic similarity was significantly less among individuals caught in the same village and season about 5 to 11 days apart, than among those caught less than 5 or more than 11 days apart. Results from this analysis showed a strong sign for microsatellite data but not for mtDNA. The microsatellite analysis was based on 11 microsatellites (locus TV18 had been excluded from the analysis due to technical problem).

Two-stock Chukchi Circuit hypothesis
This hypothesis proposes a primary population that migrates from the eastern Bering Sea to the Beaufort Sea in spring, return by a similar route in fall. A second population leaves the Bering Sea in late May and June and follows the Chukotka coast northward to the northern Chukchi and western Beaufort Seas. The evidence come from information on sighting distribution that suggested that some whales initiate the northern migration in a later period and some remain along the east coast of the Chukotka Peninsula in summer (Bogoslovskaya et al., 1982; Melnikov et al., 1998). There are also some genetic evidences supporting this scenario.

Schweder et al. (2005) conducted a microsatellite analysis to further examine the temporal pattern of variation found in the previous analysis by Jorde et al. (2004). This time the analysis was based on 117 samples from Barrow. Data were analyzed in generalized additive models. The authors examined support for the generational gene shift hypothesis (see below) by including the absolute age difference (years apart) between paired animals as a factor in the analysis. The effect of the sampling interval (days apart) was then evaluated after controlling for those absolute age differences. Pair-wise comparisons detected no significant effects in the spring migration. In the autumn migration, there was a significant elevated genetic difference in pairs of whales taken about a week apart in the fall hunt. No support for the generational gene shift hypothesis (see below) was found. Same results were found after excluding locus TV7 (the other locus with technical problems). The authors noted that a simulation of

the data suggested that the Chukchi Circuit hypothesis could produce the observed temporal genetic pattern.

Givens (2005) conducted an analysis similar to that of Schweder *et al.* (2005) but used the geometric mean of the two estimated birth years as a covariate, rather the absolute difference between those years. This analysis found a weaker pattern of elevated gene difference in pairs taken about a week apart, which was no longer quite statistically different.

Pastene *et al.* (2004) used the available mtDNA control region sequences and microsatellite (12 loci) to examine bowhead whales passing Barrow. For the analysis samples were separated into spring and fall. The analysis of mtDNA based on Fst showed significant differences between spring and autumn whales. A significant departure from Hardy-Weiberg equilibrium was observed for samples of both sexes in both spring and fall for all microsatellite loci combined. The analysis was repeated during the 2005 US workshop mentioned above in order to correct for the geographical position of some few samples. Analysis on mtDNA based on both Fst and chi-square resulted in a near-to-significant differences between spring and fall whales. Microsatellite analysis was repeated by excluding loci TV7 and TV18. No significant deviation from Hardy-Weinberg equilibrium was observed for the spring samples, however significant heterogeneity remained for the fall samples. The authors interpreted their results suggesting that samples from spring come from a single population while those from fall come from a mixed assemblage of at least two populations. These results are consistent with this hypothesis.

Single stock with generational gene shift hypothesis
Following the severe depletion of bowhead whales by commercial hunting, there may have been a period of a few decades with few reproductive adults. The small size of this reproductive cohort, possibly coupled with substantial skew in reproductive success among individuals, may have resulted in a substantial shift in the genetic frequencies of their offspring. This mechanism would result in genetic frequency differences between different age groups.

At the 2004 SC meeting a simulation study was suggested to establish whether generational gene shift really is capable of generating heterogeneities of the magnitude observed.

IMPLICATION FOR THE SPECIFICATION OF SIMULATION TRIALS

The Bowhead SLA was developed and tested under a single-stock hypothesis and the *Implementation Review* will examine the robustness of the Bowhead SLA with respect to plausible stock hypotheses via simulation trials. In 2004 the SC agreed that there is insufficient information at this stage to fully support or fully refute the hypothesis of a single stock. The SC also agreed that further work on genetics and migratory movements of individuals is particularly important (IWC, 2005). US scientists have started a large-scale research program on stock structure focused to collect the information necessary to test the different hypotheses outlined above. These new data will become available in the near future for interested SC members under Procedure A of the SC data access protocol. At this stage it can be concluded that there is a substantial degree of uncertainty with regard stock structure and the simulations trials need to capture the range of uncertainty.

Given the background outlined above, the specification of simulation trials in the First Intersessional workshop should consider a set of stock structure scenarios that are inclusive enough that it is deemed unlikely that the collection of new data will suggest a major novel hypothesis. What is important for the specification of trials from the point of view of stock structure is the determination of the number of scenarios to consider in the trials and the associated uncertainty.

Hypotheses for inclusion in trials
Given the current supporting evidences, the author supports the following stock structure scenarios candidates for inclusion in trials:

Single stock hypothesis
This is the baseline hypothesis currently adopted for management purpose (see description above and Figure 2).

Two stocks with spatial segregation

Stock A breed at a hypothetical breeding ground located at polynias near St. Lawrence Islands. Whales from this stock initiate the northern migration in spring from the eastern Bering Sea to the eastern Beaufort Sea (primary feeding ground) and it return by a similar route in fall.

Stock B breed at a hypothetical breeding ground located at the northern Gulf of Anadyr and leaves the Bering Sea later (in late May and June) and follows the Chukotka coast northward to the northern Chukchi and western Beaufort Seas (primary feeding ground). It returns by a similar route in fall.

A variant of this hypothesis is that some whales of Stock B migrate toward the northern Chukchi and western Beaufort Sea and other whales follow the migration path of Stock A but at a later stage.

As in the case of other large baleen whale species, little is known about distribution and segregation of bowhead whales in wintering breeding grounds. There are limited genetic data to make a comparison of the genetic composition of whales summering in the two different feeding grounds.

Two-stock Chukchi Circuit hypothesis
As in the previous hypothesis two different stocks, A and B, are proposed. Stock A migrates from the eastern Bering Sea to the Beaufort Sea in spring, return by a similar route in fall. Stock B leaves the Bering Sea later (in late May and June) and follows the Chukotka coast northward to the northern Chukchi and western Beaufort Seas. In fall this stock return the Bering Sea through Point Barrow where it would either mix with Stock A or separate from Stock A temporarily. Therefore Stock A would be vulnerable at Barrow in spring and fall while Stock B would be vulnerable at Barrow in autumn, but not during the spring migration.

The same uncertainty mentioned for the previous hypothesis is valid for this hypothesis.

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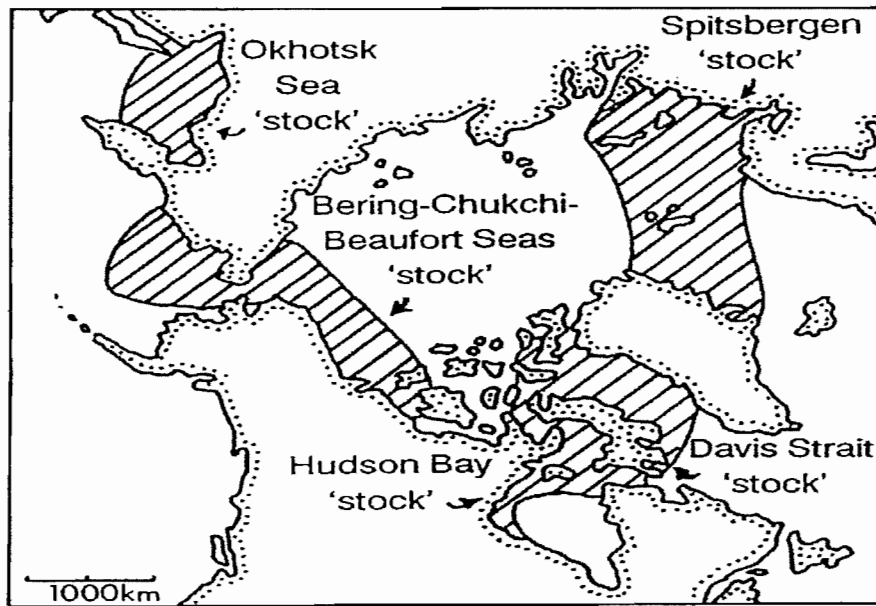the Scientific Committee.

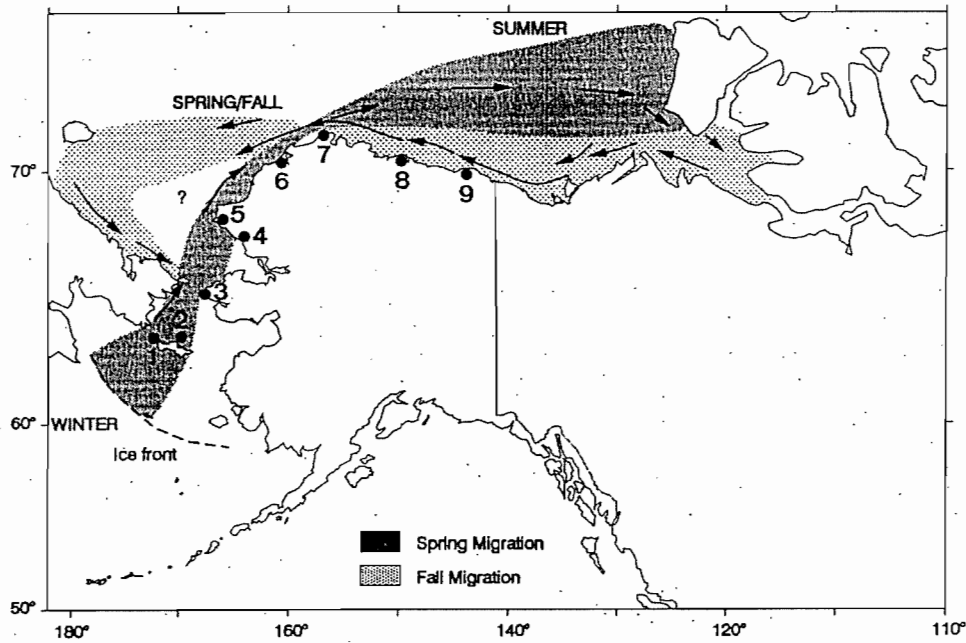Fig. 1: Putative stocks of the bowhead whale (modified from IWC, 1992).

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