Synthesis of lines of evidence for population structure for bowhead whales in the Bering-Chukchi-Beaufort region

BARBARA L. TAYLOR[1], RICK LEDUC[1], CRAIG GEORGE[2], ROBERT SUYDAM[2], SUE E. MOORE[3] AND DAVID RUGH[4]

[1]Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037 USA
email contact: Barbara.Taylor@noaa.gov
[2]North Slope Borough, Department of Wildlife Management, Barrow, AK 99723 USA
[3]NOAA/AFSC @ APL-University of Washington, Seattle, EZ 98015 USA
[4]National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 99115 USA

ABSTRACT

We synthesize lines of evidence to examine the plausibility of multiple bowhead whale stocks in the Bering-Chukchi-Beaufort (BCB) region. The four lines of evidence that bear on understanding stock structure are: (1) movement and distribution, (2) basic biology, (3) history of commercial whaling, and (4) interpretation of genetic patterns. Bowhead whales have adapted to living in an arctic ecosystem where ice coverage and food resources vary through time. This varying environment makes both the evolutionary reason for multiple breeding stocks within the Bering Sea and the biological feasibility of maintaining separation within a relatively small pelagic area unlikely. We find no evidence that a small discrete stock, like the stock in the Sea of Okhotsk, is present and killed in any numbers during the spring or fall migration of BCB whales. We find no data supporting risk to a separate feeding group. Other insights using genetic data are weak, but nearly all results are consistent with a single stock that is out of equilibrium following commercial depletion. Bowhead whales being out of genetic equilibrium is supported by differences found between age cohorts both in empirical data and simulated data. The only significant genetic findings worth further consideration are differences involving St. Lawrence Island. However, the comparisons that were significant involved small sample sizes and could just as well result from genetic patterns found between different age cohorts.

INTRODUCTION

Management of bowhead whales through the IWC has entailed a combination of protection for the timely recovery of the whales while providing for the needs of the aboriginal people who hunt them. As with any wild population, there are uncertainties in the data that management schemes are designed to address. One such uncertainty concerns the possibility of multiple stocks in the bowhead whale population that occupies the Bering-Chukchi-Beaufort region (hereafter, BCB bowhead whales). Simply put, the management question is whether two stocks instead of only one are present, thereby exposing one or both stocks to unacceptable risk by the small aboriginal hunt, which now averages about 50 to 55 animals landed and struck-and-lost per year (Suydam et al., 2007). By unacceptable risk we mean the relative recovery of a small stock, that is where it is now compared to where it would be with no hunting, is deemed to be too dangerous. Here we synthesize the lines of evidence relating to stock structure to aide in assessing plausibility of management scenarios captured in models of the effects of the aboriginal hunt on bowhead whales in the BCB region.

A great deal of research (summarized in George et al., 2007) has been conducted since the 1970s and since the last review of BCB bowhead whale stock identity (Rugh et al., 2003). Here, we briefly review bowhead biology and history within the BCB region and synthesize the four lines of evidence that bear on understanding population structure: (1) movement and distribution, (2) basic biology, (3) history of commercial whaling, and (4) interpretation of genetic patterns. We strive to minimize jargon so that all the evidence can be understood without specific expertise.

Bowhead whales are the only large whale species evolved to live year-round in close proximity to sea ice and have one of the most unusual life histories of any whale. The evolutionary constraints of living in the highly variable sea ice environment have almost certainly led to the two most unique life history traits: (1) having a lifespan that regularly exceeds 100 and (2) not reaching sexual maturity until around

1

age twenty (George et al., 1999; Lubetkin et al., 2004; Rosa et al., 2004). The arctic ice pack is a dynamic environment that changes dramatically within a year, between years, over decades and over hundreds to thousands of years. At each of these time scales, bowheads have adapted their behavior to survive and breed in ice covered waters. Within recent times, on an evolutionary scale, available bowhead habitat has changed dramatically due to periods of exceptional cold and heat. For example, from 11,000 to 8,500 B.P. and again from 5,000 to 3,000 B.P. a large population of whales extended from the Beaufort Sea to Baffin Island during summer. In intervening years ice excluded bowheads from the central arctic of North America (Dyke and Morris, 1990). Commercial whaling in the North Pacific coincidentally began at the end of The Little Ice Age, which lasted from 1450-1850. The genetics of modern bowheads carries the patterns of these successive connections and fragmentations of bowhead populations as well as the effect of the severe and rapid depletion by commercial whaling. However, to fully understand the genetic patterns, we first need a foundation in bowhead biology. We start our synthesis by explaining the annual life cycle of a BCB bowhead.

The biology of BCB bowheads

We begin our biological year with spring, the time for birth and migration to summer feeding grounds. Young whales lead the migration in March out of the Bering Sea by following fractures through the thick spring ice pack. Juveniles and sub-adults predominate in the early part of the migration north through the Bering Strait and then northeast along the northern Alaskan coast towards Canada. Remarkably, bowhead young are born in the spring lead systems spanning from St. Lawrence Island to east of Barrow (Koski, 1993). Although adults are found in all stages of the spring migration, the largest adults, mothers with their newborn calves, migrate past Barrow last, usually in late May and June (Angliss et al., 1995). The timing of the migration depends somewhat on ice conditions. For example, in 1980 the migration was a full month later than normal due to an "ice plug" in the Bering Strait (Burns, 1993). Matching photographs of individual whales, Rugh et al. (2007) showed that the timing of when individual adult whales migrate changes markedly from year-to-year, perhaps driven by reproductive status or body condition.

The pattern of segregation by age is also apparent on the summer feeding grounds in the Canadian Beaufort Sea. Adults are most commonly found in deeper waters and much less in the shallow (<20m) waters frequented by sub-adults (Moore and Reeves, 1993; Koski et al., 2004). Mothers and calves are found mostly with other adults where the mother can feed most efficiently. Juveniles are found in shallower waters probably because their short baleen, smaller size, or less-developed diving ability makes this a more suitable habitat. Areas with the best foraging opportunities, both for sub-adults and adults, vary somewhat from year-to-year.

By August, open waters predominate in coastal areas around the Arctic. Although many bowheads can be found in the Canadian Beaufort Sea in summer, there are also occasional sightings of bowheads along the Alaskan Beaufort Sea and along the coasts of the Chukotka Peninsula (Moore and Reeves, 1993) and more recently in the Chukchi Sea along the Alaskan coast. The earliest shift westward, generally in September, is made by large, and hence older, adults followed by a pulse of young sub-adults (Koski et al., 2004). The fall migration has been described as a 'feeding migration', with whales commonly seen feeding in the eastern, central and western Alaskan Beaufort Sea (Lowry, 1993; Lowry et al. 2004). Some whales swim west in early August, while others shift from slope/basin to shelf habitat during mid to late-August. The end of fall feeding may be ultimately driven by the increasing ice coverage that pushes whales south as winter begins usually in late October through November. Sea ice cover is forming later in autumn in the last decade, with open water remaining off Barrow even into late November in recent years.
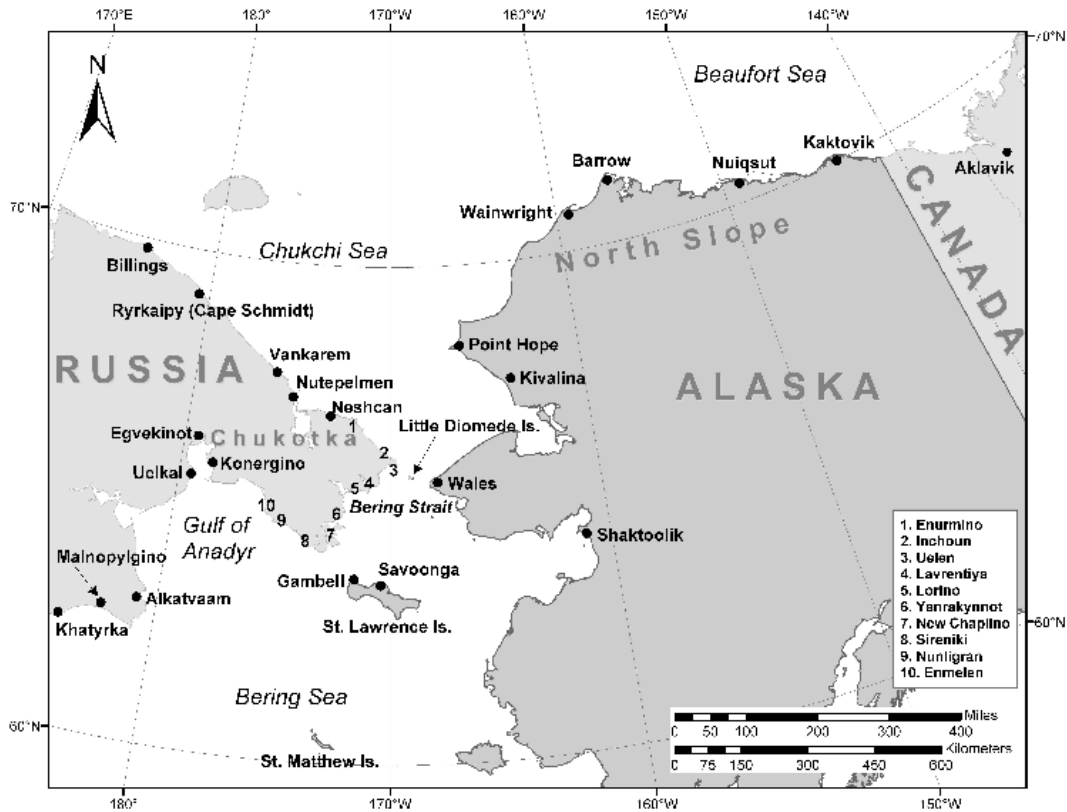
Figure 1. This map shows seas occupied by B-C-B bowhead whales and villages where hunts have historically occurred. In winter, bowheads are in the Bering Sea, perhaps concentrating in polynyas on the downwind side of St. Matthew and St. Lawrence Islands and the north side of Anadyr Gulf as well as along the ice front. April-June, most bowheads migrate north and east around Alaska, many spending the summer feeding in the Canadian Beaufort Sea. Sept-Oct, most bowheads return west and south across the Beaufort and Chukchi Seas, ending up in the Bering Sea by winter.

The extent of sea ice and availability of open-water polynyas determines to some degree bowhead wintering areas. In mild years, some whales may winter north of the Bering Strait (as reviewed in: Moore and Reeves, 1993; Nishiwaki 1967). In cold winters, some whales are seen as far south as the Pribilof Islands. In aerial surveys in 1979, 1983 and 1986, whales were widely distributed in the northern Bering Sea but were most frequently seen along the southern ice pack edge, in persistent polynyas in the Gulf of Anadyr or off St. Lawrence and St. Matthew Islands (Bogoslovskaya et al., 1982; Brueggeman et al., 1987). Distances between these polynyas are not great. Mate *et al.*, (2000) describe a satellite-tagged whale that traveled 3,886 km from the Canadian Beaufort to Siberia in 32.5 days, averaging 5.0 km/h. In contrast, the distance from Gambell on St. Lawrence Island to Sireniki on the coast of Russia at the mouth of the Gulf of Anadyr is only 80 km (45 miles), which would take a bowhead only about 16 hours to swim.

Although apparent mating behavior is seen much of the year, the time of conception is relatively short, occurring just prior to the onset of the spring migration in February and March. Mating activity is similar to that observed in right whales, with a female surrounded by males. Right whales (*Eubalaena*) have the largest testes of any whale (Brownell and Ralls, 1986); however, bowheads (*Balaena*) are a close second, which strongly suggests a mating strategy referred to as sperm competition (i.e., may the most sperm win). In this case, it is in the males' best interest to mate with as many females as possible. In the shifting ice-scape it makes little sense to attempt to hold a fixed territory or to restrict mating attempts to fixed geographic localities or breeding grounds.

3

In summary, there is variability in the timing that individual bowhead whales migrate, in the timing of the peak of the migration itself, and in the location of both summering and wintering grounds. The variation is a result of both changing environmental conditions as well as changes in the whales' age and reproductive state. Furthermore, the available area for any potential segregation of feeding or breeding groups is well within the ability of individual whales to travel in a few days time.

What was just described was the story of the typical BCB bowhead (for more detail on distribution and movements see Moore and Reeves 1993). However, there have been persistent reports of whales off the Chukotka Peninsula in late spring and summer when most bowheads are feeding in Canada (Bogoslovskaya, 2003; Melnikov et al,. 1998; 2002; 2004). In at least some years, about 1,000 whales migrate past the Chukotka Peninsula late enough that they could not have been included in the systematic counts conducted near Barrow (Melnikov and Zeh, submitted). The destination and identity of these whales remains unknown. It is plausible that they are not distinct from the larger BCB population, but merely consist of whales that occasionally visit a different feeding area (perhaps a certain age/sex class). However, whether or not these whales seen in Russian waters also visit Canadian feeding grounds where the majority spends the summer, the timing of their presence in Russian waters precludes nearly all of them from being a part of the spring migration along the North Slope. If they are distinct and later join the group counted at Barrow in spring and are exposed to the fall hunt, they would comprise a small fraction of the animals being hunted.

Humans and BCB bowheads

Bowhead whales have been hunted in artic and sub-arctic waters for at least 2,000 years (Stoker and Krupnik, 1993). One of the oldest traditions for bowhead hunting is from St. Lawrence Island with hunting settlements dating to 100 B.C. Despite its remote location in the middle of the northern Bering Sea, several thousand Inuit thrived there by hunting the reliable resources of bowhead whales and walrus prior to commercial harvest of those species. Estimates of historical abundance (i.e., pre-commercial whaling) of BCB bowheads range from 10-20,000 whales (Woodby and Botkin, 1993). By comparison, the Okhotsk stock was estimated at 3,000 and the North Atlantic at roughly 35,000 (Woodby and Botkin, 1993). BCB bowheads were discovered by Captain Roys in 1848 and by 1852 over 200 whaling boats harvested bowheads in the northern Bering and southern Chukchi Seas (Bockstoce and Botkin, 1983). As a result, the whales summering in this area were decimated in just a few years. No one knows whether this group of whales, which included many large adult females, was a separate stock, was an artifact of heavier ice during The Little Ice Age, or whether this was merely an age component of the larger population. Heavy exploitation of the BCB population continued until 1914, when there remained only around 1,000 whales in the entire western Arctic (Brandon and Wade, in press). The rapid decimation of both bowheads and walrus late in the 1800s accounted for starvation of at least two-thirds of the human population on St. Lawrence Island (Stoker and Krupnik, 1993).

Aboriginal hunting persisted at a low level through the mid-1960s, but increased in the late 1970s when increased numbers of whaling crews, and hence kills, (primarily along Alaska's North Slope) brought the potential impact of the hunt to the attention of the IWC. Since then, quotas have been instituted, a large body of research on bowhead status was conducted and a series of surveys have confirmed the strong recovery of these whales (George et al., 2004a). The abundance of whales migrating past Barrow in spring in 2001 was about 10,000 whales and the annual rate of increase was 3.4% (George et al., 2004a). This rate results in a doubling time for the population of only about 20 years. This means that roughly half of the current population is immature whales, while others are over 100 years old. The old whales were alive in days of Yankee whaling and carry the genetic pattern of that population. Their presence, alongside the large cohort of young whales, makes the current age composition of bowhead whales highly unusual relative to the composition of other species of large whales.

One other important piece of the puzzle regarding what we do and don't understand about bowhead population structure is that samples available for genetic analysis are not collected randomly with regard to spatial distribution of the whales or their age composition. They primarily come from the hunt along the western and northern coasts of Alaska. Villages with small quotas, like St. Lawrence Island and Wainwright, for various reasons have generally killed large, and hence older, whales. Most of the samples

come from Barrow, the village with the largest quota, and where hunters tend to prefer small whales. In the years following the quota, large whales were being taken during the fall hunt, so Barrow whalers now restrict the hunt later in the season so that small whales are more readily available for the hunters.

Genetics

Genetic data show the relatedness of individuals and hence have the potential to identify distinct populations. There are two types of population structure that are important to consider when evaluating risks from subsistence hunting: (1) separate breeding stocks and (2) separate feeding groups. Separate breeding stocks imply limited breeding between various groups and hence different frequencies of their nuclear DNA, which is inherited from both parents. Because whales generally learn their migratory route and feeding grounds by swimming with their mothers, it is also possible to have separate feeding groups without necessarily having separate breeding stocks. For example, most humpback whales (*Megaptera novaeangliae*) in the North Atlantic breed in the Caribbean, and therefore few differences are found in nuclear DNA between different feeding grounds (Palsböll et al., 1997). However, there is a genetic marker that is only passed from mothers to offspring called mitochondrial DNA (mtDNA). There are strong differences between the frequencies of mtDNA among North Atlantic humpback feeding grounds because there is strong site fidelity that is learned through mother/calf interactions. It would be very important to pay attention to mtDNA to conserve and manage subsistence whaling of humpbacks in, for example, Greenland.

To have the best chances to interpret population structure from genetic data, samples should be available from the breeding grounds. If allele frequencies from breeding grounds are known, there is the potential of interpreting samples taken on migration to assess the magnitude of kill from different breeding groups. While "breeding grounds" have not been identified for bowhead whales, groups of breeding whales have been identified in the Bering Strait (Koski et al., 2005; 2006). Whales can be found over a wide geographic area during February and March, and in any case changing ice conditions means that breeding is likely not tied to the same geographic area each year. Despite the desire for obtaining samples during the breeding period, it has proven logistically impossible in the past four years. The examination of feeding ground differences is also currently impossible in that the only available samples are through the subsistence harvest – which occurs during the whales' migration. There is no a priori means of designating feeding groups among the samples obtained from migrating whales.

In addition, geneticists would ideally like a random sample from each putative stock. Dangers from comparing different age cohorts are known: one cohort can have quite different allele frequencies than another cohort from the same population (Waples, 1989). So, in the case of bowhead whales, the size selectivity by hunters in different villages has the potential of making age differences appear as though it is a geographic variation. Similarly, the age segregation of the migration can result in *apparent* population structure on a temporal scale.

Another uncertainty is interpreting data from a stock or stocks known to not be in genetic equilibrium. In 1840 the population had some 15,000 bowheads (Brandon and Wade, in press) with many old whales. The chances of sampling 400 individuals and obtaining numerous close relatives would be small. The exponential growth, with half the current population born in the past 25 years, means that there are many more closely related individuals than would normally be found. This unusual structure resulted in biased statistics when comparing entire cohorts using simulated data (Ripley et al., 2006). Statistical methods for detecting stock structure using genetic data assume genetic equilibrium and random sampling, both of which are decidedly lacking in current bowhead research. Interpreting the bowhead data required creating detailed individual-based genetic simulations that re-created the state of genetic dis-equilibrium (Archer et al., 2007).

A large number of analyses (117 tests in 2004 and 91 tests in 2007) have been conducted to test for genetic differences among spatial, temporal and age-related groups of bowhead whales, using mitochondrial sequences (Jorde et al., in press; Jorde and Schweder, 2007; LeDuc et al., 2004; LeDuc et al., 2007; Pastene et al., 2004; Pastene et al., 2007) and microsatellites (Givens et al., 2004; Givens et al., 2007; Jorde et al., 2004; Jorde and Schweder, 2007; Pastene et al., 2004; Kitikado et al., 2007). Most have not

resulted in any significant differences being found that suggest multiple stocks, and some of those that were found proved to be transitory (e.g., near significant differences between fall and spring in Barrow using mtDNA disappeared with the addition of more samples and the differences within microsatellite DNA of Barrow animals during the fall migration (Jorde et al., in press) disappeared with more samples or more markers (Givens et al., 2007; Jorde and Schweder, 2007). There have been significant differences found between age cohorts, such as between whales born before and after about 60 years ago (LeDuc et al., 2007; Givens et al., 2007). These differences were consistent with simulations of a single stock that matched the genetic, life history and population trajectory of bowheads as closely as possible (Archer et al., 2007). In other words, statistically significant findings in the empirical data were also found in the detailed simulations emulating bowhead dynamics and assuming a single stock. Other patterns of genetic heterogeneity that have been reported may be attributable to these age differences: seasonal differences at St. Lawrence Island (LeDuc et al., 2007; Pastene et al., 2007), differences between St. Lawrence Island and Barrow (Givens et al., 2007; Jorde and Schweder, 2007) or temporal patterns within the migration off Barrow (Jorde et al., 2007). For example, it is easy to imagine how fall and spring whales around St. Lawrence Island could be of different age cohorts, since it is soon after one of these periods that the mating period begins. Aggregation of mating adults could skew the "fall" sample towards older whales.

The other pattern found in genetic data involves use of the program STRUCTURE (Pritchard et al., 2000; Falush et al., 2003). The program was designed to group together individuals such that resulting groups are in genetic equilibrium. The method works best when genetic differences between groups are large. One strength of the method is that the scientist does not have to group individuals beforehand (*a priori* stratification), which is ideal for cases where groups are mixed. This is important for bowhead whales because we are looking for two possible different breeding groups that are mixed together during migration. Two important results came from the STRUCTURE analysis: 1) the program easily picked out a small discrete population (the Okhotsk stock) and 2) the program could NOT pick out differences between two historically large populations (BCB and Atlantic bowheads) that currently have very separate breeding areas. Small populations have few different genetic types (low diversity) and the frequencies of these types drift relatively rapidly. Thus, small discrete populations tend to be quite different from large ones, which gives large enough genetic differences that STRUCTURE can perform well. Being able to easily pick out the Okhotsk whales using STRUCTURE gives confidence that if a similar small discrete stock existed in the North Pacific that was being harvested in significant numbers, the genetic methods used would have detected it.

The second result, not being able to pick out Atlantic from BCB samples, simply means that the method has insufficient power to detect the magnitude of differences expected in two relatively large populations. However, the program did appear to indicate the presence of two groups within these samples (Givens et al., 2007; Jorde and Schweder, 2007; Kitakado et al., 2007). These two genetic groups identified by STRUCTURE are relatively evenly distributed within the BCB and within the Atlantic samples. Whatever these groups are, they are clearly not consistent with known stock structure that would split Pacific and Atlantic whales into separate groups. BCB and Atlantic whales are clearly significantly different using traditional hypothesis testing methods (Givens et al., 2007; Jorde and Schweder, 2007). In other words, STRUCTURE was unable to differentiate two well defined and significantly different populations (BCB and Atlantic), but instead created two groups, each of which was a chimera consisting of whales from each ocean basin. It is difficult to imagine that these results reflect anything about real stock structure in BCB bowheads. Also, using simulations of a single stock yield results that do not statistically differ from what was observed for STRUCTURE results (Archer et al., 2007). Further, Martien et al. (2007) show that the results that Kitikado et al. (2007) interpret as indicating more than one stock within the BCB are also consistent with only a single stock using simulated data. When using the approach employed by Kitakado et al. to infer the number of stocks, Martien et al. found that STRUCTURE incorrectly indicated the presence of 2 stocks 30% of the time when it was used to analyze simulated datasets generated by the Archer et al. (2007) model of a single stock that mimics bowhead dynamics.

CONCLUSION: Assembling the lines of evidence
      Synthesizing the lines of evidence provides little support for multiple BCB stocks (Table 1).

Table 1. Summary of the information for assessing the plausibility of the alternative stock-structure hypotheses. It is NOT intended that the plusses and minuses should be summed to obtain a priority ranking. A '+' indicates evidence in favor of a hypothesis, '-' evidence against a hypothesis, '(+)' weak (or disputed) evidence in favor 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.

Project	Hypothesis A. Single stock – no feeding ground site fidelity.	Hypothesis B. Single stock with feeding ground site fidelity.	Two stocks - spatial segregation-St Lawrence mixed.	Hypothesis D. Two stocks – mixed migration
Satellite tracking[1]	(+)			
Spring photoID (Barrow arrival)[2]	+			(-)
PhotoID (Bering Sea v. Barrow)[3]	(+)			
Large-scale aerial surveys[4]	+	(-)		
Russian coastal surveys[5]	(-)	(+)	(+)	
Historical analysis[6]	(+)	(+)	(+)	
Chukchi July acoustic (surveys)[7]	(+)			
Traditional Ecological Knowledge[8]	(+)	(+)	(+)	
Visual surveys Russia	(-)	(+)	(+)	
Tag recoveries[9]	+			
Long variable migration[10]	+			
Visual census[11]	(+)			
Reproductive timing[12]	+			
Distribution during mating period[13]	+	+	-	-
Mating strategy[14]	(+)			
Isotopes[15]	(+)			
mtDNA genetic data[16]	(+)		(+)	
Microsatellite data[16]	(+)		(+)	
Simulated genetic pattern[16]	(+)			

[1] Satellite telemetry tracks are quite consistent with known migratory behavior of BCB bowhead whales. SC/59/BRG12

[2] Arrival time of marked whales at Barrow in the spring migration is variable between years. Rugh et al., 2007.

[3] Three photo-recaptures found between Bering Sea (2005) and Barrow Alaska (2003) indicate migration between these areas; and large breeding aggregation seen in Bering Strait in April. SC/59/BRG6

[4] 30 years of aerial surveys by NOAA, LGL and Minerals Management Service (BWASP) suggest that the bulk of the BCB population summers in the Canadian Beaufort Sea. Moore and Reeves, 1993

[5] Coastal surveys conducted by Russian native observers and researchers suggest some aggregations of summering whales around Chukotka. Bogoslovskaya et al. 1982, Melnikov and Zeh, submitted

[6] Analysis of commercial whaling data is equivocal as to whether a second "Bering Sea" stock existed in the mid-1800s

[7] No bowhead calls detected during a July acoustic survey along cruise track northwest of Barrow. SC/58: Annex F

[8] TEK suggests two migratory routes past St. Lawrence Island with animals of unknown stock origin. Noongwook et al. 2007

[9] Recoveries of a radio tag in a Gambell whale (attached in Canada) and a Russian discovery tag at Wainwright (attached near Chukotka) suggest interchange between regions. Rugh et al., 2003

[10] Long migrations (>1500 km) of bowhead whales suggest mixing between large spatial areas. Moore and Reeves, 1993

[11] Pulses of whales migrating past Barrow in spring show temporal size/age structure in the manner of one stock, not as in pulses of "stocks" each with all age groups present. Angliss et al., 1995; George et al., 2004a

[12] Strong synchrony between in fetal growth curves suggest narrow conception timing in Bering Sea. George et al., 2004b

[13] There is a lack of site fidelity in mating areas due to interyear shifts in sea ice and a pelagic environment. Brueggeman et al. 1987

[14] Sperm competition breeding strategy makes reproductive isolation unlikely.

[15] Analysis of bowhead whale baleen from St. Lawrence Island suggests annual migration between the Bering and Eastern Beaufort Seas. Knoche et al., 2007.

[16] Differences found between age cohorts, suggests genetic differences result from a single population out of genetic equilibrium. Differences within St. Lawrence Island suggest weak potential for 2 stocks. LeDuc et al. 2007.

What evidence supports both different feeding groups and risk to any feeding group?

In the years of intensive bowhead research of the late 1970s, the focus was on estimating population size and trends in abundance. To do so, aerial and ship-based surveys were conducted to determine summering areas and migratory routes in an almost 'desperate' attempt to find bowheads in areas other than expected since the early population size index-estimates numbered only ~ 600 animals (Braham et al. 1980). Few bowheads were found other than in the stereotypical wintering, migratory and summering areas, and it appeared that nearly all BCB bowheads migrated annually past Point Barrow. Three decades of aerial surveys with thousands of photographs have revealed no evidence of multiple consistent discrete feeding grounds in the BCB region. In the Canadian Beaufort Sea, there are areas where whales feed with some consistency (e.g., Yukon coast, Franklin Bay), but "areas of concentration vary greatly from year to year" (Moore and Reeves, 1993), and there is little evidence of individual site fidelity. Feeding areas differ by depth for sub-adult and adult whales and change somewhat from year-to-year (Moore and Reeves, 1993; Koski and Miller, 2004).

Although sample sizes are small, no evidence was found for a resident group off St. Lawrence Island using stable isotopes in baleen and comparing whales killed off Barrow and off St. Lawrence Island (Knoche et al., 2007). A radio transmitter applied to a whale near Herschel Island (Canadian Beaufort) was recovered in a whale landed at St. Lawrence Island. Genetic data also found closely related pairs of individuals where one was killed at Barrow and the other at St. Lawrence Island (Skaug and Givens, 2007). There are no kills at St. Lawrence Island during the summer feeding months, so even if there was a feeding stock using those waters, there would be no risk of harvesting them when they were separate from the main large BCB group of whales. No samples are available from the Chukotka coast in early summer to examine whether there might be a separate feeding group, but again there is also no hunt there at that time. Even if the entire Russian catch of 5 whales per year was from the group enumerated at about 1,000 (Melnikov and Zeh, submitted), which is a highly unlikely scenario, it would amount to one half of one percent -- a removal rate that is sufficiently small that a population exposed to such a hunt would be expected to recover to healthy levels or remain at healthy levels. The reason this scenario is unlikely is because the much more abundant group of animals that passes Barrow in the spring also uses the Chukotka coast as a feeding ground in late summer and fall (Moore et al., 1995) and would be far more likely to be killed by whalers there at those times than whales from the putative Chukotka feeding group.

In conclusion, there are no data supporting risk to a separate feeding group off the Chukotkan coast or elsewhere.

What evidence supports different breeding groups?

This appears to be the key question before the Scientific Committee in providing scientific advice to service the management needs of the IWC. There is no evidence of consistent discrete breeding grounds. The three geographical areas likely to be consistently available during the breeding time are polynyas in the Gulf of Anadyr, and around St. Lawrence Island and near St. Matthew Island. In terms of travel time for a bowhead whale, these are all quite close with no real barriers between them. In theory, bowheads could show temporal breeding separation; however, examination of fetus length data indicated highly synchronized conception (George et al., 2004b). If the whales seen in Russian waters in early summer do constitute a separate feeding group, they almost certainly mix with BCB whales in the fall because they would probably not depart from an area with sufficient food to attract the larger group that migrates to Canada. It is hard to posit how or why the putative Chukotka summer feeding group of whales would segregate for breeding purposes. Such segregation would require fairly distinct behavioral patterns that would keep one group of whales apart from others in a small area with dynamic ice patterns, and this kind of separation would have to persist over many generations.

In the years 2004 and 2007, the primary genetics papers have conducted over 200 statistical tests concerning population structure. The only findings consistent with multiple stocks within the BCB are also consistent with a single stock out of genetic equilibrium or may result from small sample size. In summary, these findings are:

Nuclear (microsatellite)

- Temporal differences during the autumn at Barrow, which disappeared with increased samples sizes and markers (Jorde et al. in press, Jorde and Schweder, 2007, Givens et al. 2007).
- Differences between Barrow and St. Lawrence Island (perhaps a function of small sample size or possibly age related)
- STRUCTURE results (also consistent with a single stock)
- Not in genetic (Hardy-Weinberg) equilibrium (consistent with additive effects of a population out of demographic equilibrium (Archer et al. 2007) and errors in genotyping (Morin et al. 2007))

mtDNA

- Differences between spring and fall samples from St. Lawrence Island (perhaps a function of small sample size or possibly age related)

With respect to the last point, TEK interviews with hunters at St. Lawrence Island suggest that whales have increased significantly in that area over the last 50 years and, in fact, some now winter near the Island in significant numbers since 1990 (Noongwook et al, 2007).

In conclusion, genetic data suggesting multiple stocks are weak and biological mechanisms to maintain separate breeding areas, such as discrete breeding grounds or behavioral mechanisms, are not supported with any present data.

What evidence supports a small discrete breeding group in the BCB region?

None. There is no evidence that a small discrete stock, like the one present in the Sea of Okhotsk, is present and killed in any numbers during the spring or fall migration of BCB whales. Okhotsk whales were easily detected using STRUCTURE and no other such group was detected.

ACKNOWLEDGEMENTS

REFERENCES

Angliss, R.P., D.J. Tugh, D.E. Withrow, and R.C. Hobbs. 1995. Evaluations of aerial photogrammetric length measurements of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (Balaena mysticetus). Rep. Int. Whal. Commn. 45: 313-324.

Archer, E., Martien, K.K. And Taylor, B.L. 2007. Use of an individual-based simulation of BCB bowhead whale population dynamics to examine empirical genetic data. SC/59/BRG17.

Bockstoce, J.R. and Botkin, D.B. 1983. The historical status and reduction of the western Arctic bowhead whale (*Balaena mysticetus*) population by the pelagic whaling industry, 1848-1914. *Rep. int. Whal. Commn.* (special issue) 5:107-41.

Bogoslovskaya, L.S., L.M. Votrogov and I.I. Krupnik. 1982. The bowhead whale off Chukotka: migrations and aboriginal whaling. Report of the International Whaling Commission 32:391-399.

Bogoslovskaya, L. 2003. The bowhead whale off Chukotka: integration and scientific and traditional knowledge. In: Allen P. McCartney (ed.) Indigenous ways to the present: Native whaling in the western Arctic. Edmonton, Canadian Circumpolar Institute Press, Studies in Whaling No. 6, pp.209-253.

Braham, H.W., W.M Marquette, T.W. Bray and J.S. Leatherwood (eds.). 1980a. The Bowhead Whale: Whaling and Biological Research. Marine Fisheries Review 42: 1-96.

Brandon, J. and Wade, P.R. In press. Assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales using Bayesian model averaging. Journal of Cetacean Research and Management.

Brownell, R.L. and Ralls, K. 1986. Potential for sperm competition in baleen whales. Rep. Intl. Whal. Commn. Si8:97-112.

Brueggeman, J.J., B. Webster, R. Grotefendt and D. Chapman. 1987. Monitoring the winter presence of bowhead whales in the Navarin Basin through association with sea ice. Report for the U.S. Minerals Management Service by Envirosphere Company. NTIS No. PB88 101258/AZ. 179pp.

Burns, J.J. Epilog. In: Burns, J.J., Montague, J. and C.J. Cowles (eds.). 1993. The Bowhead Whale. Society for Marine Mammalogy. 787 pp.

Dyke, A.S. and T.F. Morris. 1990. Postglacial history of the bowhead whale and of driftwood penetration: implications for paleoclimate, central Canadian Arctic. Geological Survey of Canada Paper 89-24. 17pp. (Available from Canadian Government Publishing Centre, Supply and Services Canada, Ottawa, Canada K1a 0S9.)

Falush, D., M. Stephens, and J.K. Pritchard. 2003. Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. Genetics 164:1567-1587.

George, J.C., Zeh, J., Suydam, R. and Clark, C. 2004a. Abundance and population trend (1978-2001) of western arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20 (4): 755-773.

George, J.C., Suydam, R., Zeh, J. And Koski, W.R. 2004b. Estimated pregnancy rates of bowhead whales from examinations of landed whales. Paper SC/56/BRG10 presented to the IWC SC in Sorrento, Italy.

George, J.C., Moore, S. And Suydam, R.S. 2007. Summary of stock structure research on the Bering-Chukchi-Beaufort Seas stock of bowhead whales: 2003-2007. SC/59/BRG3.

Givens, G., Bickham, J.W., Matson, C.W., Ozaksoy, I., Suydam, R.S., and George, J.C. 2004. Examination of Bering-Chukchi-Beaufort Seas bowhead whale stock structure hypotheses using microsatellite data. SC/56/BRG17.

Givens, G., Huebinger, R.M., Bickham, J.W., George, J.C. and Suydam, R.S. 2007. Patterns of genetic differentiation in bowhead whales (*Balaena mysticetus*) from the western Arctic. SC/59/BRG14.

Jorde, P.E., Schweder, T., Bickham, J.W., Givens, G.H., Suydam, R., and Stenseth, N.C. In press. Detecting genetic structure in migrating bowhead whales off the coast of Barrow, Alaska. Submitted.Molecular Ecology.

Jorde, P.E. And Schweder, T. 2007. Further analysis of stock structure for BCB bowhead whales using microsatellite DNA data. SC/59/BRG27.

Kitakado, T., Pastene, L.A., Goto, M., and Kanda, N. 2007. Updates of stock structure analyses of B-C-B stock of bowhead whales using microsatellites. SC/59/BRG30.

Knoche, M., Suydam, R.S., George, J.C. And Morita, J. 2007. Using stable isotopes in baleen to examine migratory behaviour of Bering-Chukchi-Beaufort Sea bowhead whales (*Balaena mysticetus*): a pilot study. 12pp. SC/59/BRG 13.

Koski, W.R, Davis, R.A., Miller, G.W., and Withrow, D.E. 1993. Reproduction. In: Burns, J.J., Montague, J. and C.J. Cowles (eds.). The Bowhead Whale. Society for Marine Mammalogy. 787 pp.

Koski, W.R. and Miller, G.W. 2004. Habitat use by different size classes of bowhead whales in the central Beaufort Sea during late summer and autumn. Paper SC/56/BRG28 presented to the IWC Scientific Committee.

Koski, W.R., J.C. George, B.D. Mactavish, R. Acker, A.R. Davis, R. Suydam and D.J. Rugh. 2005. Observations of Bowhead Whale Mating in the Bering Sea. Presentation at the 16th Biennial Conference on the Biology of Marine Mammals, 12-16 December 2005, San Diego, CA.

Koski, W.R, Rugh, D.J., Zeh J., George, J.C., Suydam, R., Davis, A.R. and Mocklin, J. 2006. An update on analyses of bowhead whale aerial photographs obtained in 2003-2005. 5pp. SC/58/BRG20.

Koski, W., Rugh, D., Zeh, J.E., George, J.C., Suydam, R.S., Davis, A.R., Mocklin, J. and Trask, K. 2007. A review of bowhead aerial photographic studies in 2003-06. 6pp. SC/59/BRG6.

Leduc, R. and Taylor, B. 2004. A comparison of age/length classes of bowheads in the North Pacific using mtDNA. SC/56/BRG 14.

Leduc, R.G., Martien, K.K., Morin, P.A., Hedrick, N., Robertson, K.M., Taylor, B.L., Mugue, N.S., Borodin, R.G., Zelenina, D.A. and George, J.C. 2007. Mitochondrial genetic variation in bowhead whales in the western Arctic. 11pp. SC/59/BRG9.

Lowry, LF. 1993. Foods and feeding ecology. pp. 201-38. *In*: J.J. Burns, J.J. Montague and C.J. Cowles (eds.) *The Bowhead Whale*. Spec. Pub. 2, Society for Marine Mammalogy. 787 pp.

Lowry, L.F., Sheffield, G. and George, J.C. 2004. Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. *J. Cetacean Res. Manage*. 6(3):215-23.

Lubetkin, S.C., Zeh, J.E., Rosa, C., and George, J.C. 2004. Deriving von Bertalanffy age-length relationships for bowhead whales (Balaena mysticetus) using a synthesis of age estimation techniques. Paper SC/56/BRG3 presented to the IWC SC, June 2004. 19 pp.

Martien, K.K., Givens, G.H., and Archer, E. 2007. A note on the ability of STRUCTURE to correctly infer the number of populations for Bering-Chukchi-Beaufort Seas bowhead whales. SC/59/BRG34.

Mate, B.R., Krutzikowsky, G.K., Winsor, M.H. 2000. Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi seas during the late-summer feeding season and fall migration Can J. Zool. 78 1168-1181.

Melnikov, V.V., Zelensky, M.A. and Ainana, L.I. 1998. Observations on distribution and migration of bowhead whales (*Balaena mysticetus*) in the Bering and Chukchi Seas. Paper SC/50/AS3 presented to the IWC SC, April 1998. 23 pp.

Melnikov, V.V., Litovka, D.I., Zagrebin, I.A., Zelensky, G.M. and Ainana, L.I. 2002. Results of shore-based counts of bowhead whales in Chukotka: at the western Bering Strait, and the eastern Gulf of Anadyr; in May and June 1999 to 2001. Paper SC/54/BRG15 presented to the IWC SC, April 2002. 19pp.

Melnikov. V.V., Litovka, D.I., Zagrebin, I.A., Zelensky, G.M., and Ainana, L.I. 2004. Shore-based counts of bowhead whales along the Chukotka Peninsula in May and June 1999 to 2001. Arctic 57 (3): 290-298.

Melnikov. V.V. and Zeh J. E. Submitted. Chukotka Peninsula counts and estimates of the number of migrating bowhead whales. Journal of Cetacean Research and Management.

Moore, S.E. and Reeves, R.R. 1993. Distribution and movement. pp. 313-386, in The Bowhead Whale, J.J. Burns, J.J. Montague and C.J. Cowles (eds.), Special Publication No. 2, The Society for Marine Mammalogy.

Moore, S.E., George, J.C., Coyle, K.O. and Weingartner, T.J. 1995. Bowhead whales along the Chukotka coast in autumn. Arctic 48(2): 155-160.

Morin, P.A., Leduc, R.G., Archer, E., Taylor, B.L., Huebinger, R.M. And Bickham, J.W. 2007. Estimated genotype error rates from bowhead whale microsatellite data. SC/59/BRG15.

Nishiwaki, M. 1967. Distribution and migration of marine mammals in the North Pacific area. Bulletin Ocean Research Institute, University of Tokyo 1:1-64.

Noongwook, G., The Native Village of Savoonga, The Native Village of Gambell, Huntington, H.P., and George, J.C. 2007. Traditional knowledge of the bowhead whale (*Balaena mysticetus)* around St. Lawrence Island, Alaska. Arctic 60 (1): 47-54.

Palsböll P.J., Allen J., Berube M., Clapham P.J., Feddersen T.P., Hammond P.S., Hudson R.R., Jorgensen H., Katona S., Larsen A.H., Larsen F., Lien J., Mattila D.K., Sigurjonsson J., Sears R., Smith T., Sponer R., Stevick P., Oien N. 1997. Genetic tagging of humpback whales. Nature, London 388:767-769.

Pastene, L.A., Goto, M. and Kanda, N. 2004. Genetic heterogeneity in the B-C-B stock of bowhead whale as revealed by mitochondrial DNA and microsatellite analyses. SC/56/BRG 32.

Pastene, L.A. Update of mitochondrial DNA analyses on stock structure in the B-C-B stock of bowhead whales. SC/59/BRG 29.

Pritchard, J.K, M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945-959.

Quakenbush, L. 2007. Preliminary telemetry results for Bering-Chukchi-Beaufort bowhead whales. 2pp. The Alaska Department of Fish and Game (ADF&G) has begun a cooperative project (with the AEWC and the NSB and funded by the US Minerals Management Service (MMS) to study bowhead whale movements and behavior using satellite telemetry. SC/59/BRG12.

Ripley, B. J. Martien, K.K. and Taylor B.L. 2006. A simulation approach to understanding non-equilibrial dynamics in a recovering long-lived species: the bowhead whale. 12pp. SC/58/BRG13.

Rosa, C., George, J.C., Zeh, J., O'Hara, T. Botta, O. and Bada, J. 2004. Update on age estimation of bowhead whales using aspartic acid racemization.NOAA. 1978. Bowhead Whales: A Special Report to the International Whaling Commission, National Oceanic and Atmospheric Association (NOAA), US Department of Commerce, 63 pp + appendices.

Rugh, D.J., Koski, W.R. and George, J.C. 2004. Interyear re-identifications of bowhead whales during their spring migration past Barrow, Alaska, 1984-1994. Paper SC/56/BRG6.BRG24 presented to the IWC SC, June 2004.

Rugh, D., DeMaster, D., Rooney, A., Breiwick, J., Shelden, K. and Moore, S. 2003. A review of bowhead whale (Balaena mysticetus) stock identity. J. Cetacean Res. Manage 5 (3): 267-279.

Rugh, D., Koski, W. And George, J.C. 2007. Interyear re-identification of bowhead whales during their spring migration past Barrow, Alaska, 1984-1994. 9pp. SC/59/BRG2.

Skaug, H. And Givens, G. Relatedness among individuals in genetic BCB bowhead samples. SC/59/BRG20.

Stoker, S.W. and I.I. Krupnik. 1993. Subsistence whaling. pp. 579-629, in The Bowhead Whale, J.J. Burns, J.J. Montague and C.J. Cowles (eds.), Special Publication No. 2, The Society for Marine Mammalogy.

Suydam, R., George, J.C., Rosa, C., Person, B., Hanns, C., Sheffield, G. and Bacon, J. 2007. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos during 2006. SC/59/BRG4.

Waples, R. 1989. Temporal variation in allele frequencies: testing the right hypothesis. Evolution 43:1236-1251.

Woodby, D.A. and D.B. Botkin. 1993. Stock sizes prior to commercial whaling. pp. 387-407, in The Bowhead Whale, J.J. Burns, J.J. Montague and C.J. Cowles (eds.), Special Publication No. 2, The Society for Marine Mammalogy.