Baffin Bay-Davis Strait and Hudson Bay-Foxe Basin Bowhead whales: A reassessment of the two-stock hypothesis

Mads Peter Heide-Jørgensen[1] Susan E. Cosens[2], Larry P. Dueck[2], Kristin Laidre[1,3], Lianne Postma[2]

1. Greenland Institute of Natural Resources
   Kivioq 2
   DK-3900 Nuuk
   Greenland

2. Fisheries and Oceans Canada
   501 University Crescent
   Winnipeg, Manitoba, Canada R3T 2N6

3. Polar Science Center
   Applied Physics Laboratory
   University of Washington

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ABSTRACT

Examination of historic and current data on distribution patterns and movements of bowhead whales in Baffin Bay and Hudson Bay has identified several discrepancies with the two stock model currently accepted by the IWC. Too few calves have been found in the putative Baffin Bay-Davis Strait stock (BB-DS) to maintain a viable population and too few adults have been found in the putative Foxe Basin-Hudson Bay stock (HB-FB) to produce the calves as mostly sub-adults are seen in this area. Satellite tracking data have shown that there is no geographical separation between the two putative stocks. Whales occupying Foxe Basin move through Fury and Hecla Strait into Prince Regent Inlet, waters traditionally assumed to summering areas for the whales from the BB-DS stock. Prince Regent Inlet and Gulf of Boothia has also been identified as a major summering area for whales tagged in West Greenland in spring. Whales tagged in southeast Baffin Island have been shown to circumnavigate Baffin Island both clock-wise and counter-clockwise and thereby moving through all areas used as summering grounds for whales from both the HB-FB and the BB-DS stocks. Tagging data also show that whales from the two putative stocks occupy the same wintering areas in Hudson Strait. Furthermore, genetic data collected to date do not support the two-stock model. We suggest the most reasonable explanation for the observed segregation patterns and migratory movements is that bowheads summering in the eastern Canadian Arctic and wintering off West Greenland consist of a single Eastern Canada-Western Greenland population, segregated by age and sex. We propose this new stock to be called the Baffin Bay bowhead whale stock.

INTRODUCTION

In 1977, the two-stock hypothesis for bowhead whales (*Balaena mysticetus*) occupying eastern Canadian and western Greenlandic waters was adopted as the working model of the IWC (Allen 1978). The designation of two stocks was based on a paper submitted by Mitchell to the International Whaling Commission (IWC) and was considered the most conservative approach for management (Allen 1978). The stocks (Figure 1) came to be identified as the Baffin Bay-Davis Strait (BB-DS) or Baffin Bay stock and the Hudson Bay-Foxe Basin (HB-FB) or Hudson Bay stock and have been treated as separate populations since (see Mitchell and Reeves 1981; Cosens *et al.* 1994; Bannister 1999; Cosens and Innes 2000; Finley 1990, 2001).

Reeves *et al.* (1983) examined whaling records and Reeves and Mitchell (1990) discussed arguments for and against the two-stock hypothesis. Both studies concluded that available data were insufficient for evaluating stock affinities. Reeves and Mitchell (1990) suggested that recognizing separate stocks, based on summer distributions, would be the most conservative approach for management purposes. The population identity of these bowheads, however, has remained unresolved. Given that these whales are subject to a limited hunt in Nunavut, Northern Canada, and that a quota was recently assigned by IWC to the West Greenland wintering aggregation of bowhead whales, it is timely to re-examine the population structure of these whales in light of new information that has been collected.

Heide-Jørgensen *et al.* (2006) suggested that the bowheads summering in eastern Canada and wintering in West Greenland might consist of a single population. Based on

satellite tracking studies of bowhead whales tagged in West Greenland, they argued that bowhead whales are capable of travelling long distances in relatively short periods of time and suggested that there was no reason why whales should be restricted to relative small portions of the total potential range in eastern Canada and Greenland waters. They also noted that there was little geographical separation between the two putative stocks. Results of recent field studies suggest that the two-stock model should be re-examined. These new lines of evidence will be outlined and discussed with respect to historic whaling data and recent research findings.

DISTRIBUTION AND MOVEMENTS

Historic Records

Holocene distribution. The postglacial distribution of bowhead whales can be described based on carbon dated bone remains from raised marine sediments (Dyke et al. 1996, Borge et al. 2007). In northern Canada postglacial bowhead whale remains have been found on raised seabeds in a continuum from Foxe Basin to the northern shores of Devon Island and from the eastern part of Lancaster Sound as far west as Prince of Wales Island, indicating a continuous distribution consistent with modern information on their range in Canada, with no obvious hiatus in occurrence in this area (Dyke et al. 1996). The large number of late holocene bone remains and remains from archaeological sites in the southern part of Gulf of Boothia, Fury and Hecla Strait and northern part of Foxe Basin confirm that even the southern part of Gulf Boothia was an important summering ground. Although Fury and Hecla Strait was a barrier to whalers, it does not currently constitute a natural border for the distribution of the bowhead whales.

Davis Strait and Baffin Bay. Accounts of the historical occurrence of bowhead whales in Baffin Bay and adjacent waters exist from the offshore fishery from 1719 to 1915 and from land-based stations especially in West Greenland.

Bowhead whales arrived as early as November at the West Greenland coast (see Figure 2 for place names) where they were found as far south as Sukkertoppen (65 ^{o} N, Eschricht and Reinhardt 1866). They were regularly caught from December through February by land-based stations along the West Greenland coast south of Disko Bay (Reeves et al 1983, Vaughan 1986). Eschricht and Reinhardt (1866) reported on the seasonality of the arrivals and departures of bowhead whales in West Greenland during the period from 1780 to 1839. Whales arrived at Holsteinsborg between 22 November and 10 February and, at Godhavn, the first whales arrived on 12 November and the last were seen as late as 25 June. Eschricht and Reinhardt (1866) were not clear about where these whales go once they leave the Greenland coast in the spring, but indicated that whales are found at the beginning of July in Whale Sound and Smith's Sound at 78^{o} N. Southwell (1898) also reported that bowheads wintered along the West Greenland coast between Upernavik and Sukkertoppen. Whales arrived at Upernavik during October, remaining again until December and reappearing again in April through July. At more southerly locations, whales arrived during December with departure dates being earlier in the south (February at Sukkertoppen, March at Holsteinborg and June at Disko Bay). Southwell (1898) also reports sighting records of bowhead whales in Wolstenholme Sound and the entrance of Smith Sound. Southwell (1898) did not indicate from where these whales were thought to arrive. Reeves *et al.* 1983, however, refer to one report

suggesting that whales crossed to the west side of Davis Strait before moving to Smith Sound.

A second wintering area was reported to be at the east end of Hudson Strait and south along the Labrador coast to about 57^{o} N (Figure 3). In the spring, *en route* to West Greenland waters, the offshore whalers exploited the "sou'west fishing grounds" in the eastern part of Hudson Strait and southeastern corner of Baffin Island around Resolution Island in April and May (de Jong 1983, Reeves *et al.* 1983). The whalers pursued the bowhead whales to the north towards Lancaster Sound and northeast toward Greenland.

Whalers found bowheads in large numbers at the so-called 'Pond's Bay', southeast of Bylot Island, from early June through beginning of July (Markham 1874). Once the ice moved out of Lancaster Sound in July, whales were thought to move into Prince Regent Inlet and other adjacent channels (Figure 3). Whalers found the bowheads in a continuum from Lancaster Sound through Prince Regent Inlet as far south as Creswell Bay where heavy ice conditions prevented the whalers from pursuing the whales into Gulf of Boothia (Markham 1874).

In the autumn, bowhead whales were thought to leave Lancaster Sound and head south along the east coast of Baffin Island (Figure 3). These whales were caught from late August to October along the coast in the 'rock-nosing' fishery, mainly between Clyde River and Cape Searle (Reeves *et al.* 1983). Crews that remained late in the season also caught whales in Cumberland Sound and along the Hall Peninsula. There are also records of bowhead whales moving east across Baffin Bay in the autumn and arriving in Upernavik, West Greenland, in September or October and gradually moving south along the Greenland coast over the winter (Reeves *et al.* 1983, de Jong 1983).

Both Southwell (1898) and Reeves *et al.* (1983) report that whales were thought to winter all along the pack ice of Davis Strait, from Hudson Strait to the coast of West Greenland. Whalers believed that whales occurring in Cumberland Sound in March crossed over to Greenland in May but whales were also found in Cumberland Sound in June and July (Mitchell and Reeves 1982; Reeves *et al.* 1983). These accounts suggest that two waves of bowhead migrants occupied the West Greenland coast, one arriving from the west in late fall and staying during winter and one arriving in early spring from Hudson Strait and Cumberland Sound.

Hudson Bay and Foxe Basin. Whalers did not venture into Foxe Basin so little historical information is available for this area. Nearly all whaling occurred in the region from Marble Island along the west side of Hudson Bay and north to Roes Welcome Sound, Repulse Bay and Lyon Inlet (Ross 1974). Whales were taken mainly from June through September (Reeves and Cosens 2003). Ross (1974) reported that early whalers believed that bowheads, found on the southwest fishing grounds (mouth of Hudson Strait and Cumberland Sound) early in the season, migrated westward through Hudson Strait in the spring (Ross 1974). Some whalers suggested that these whales migrated to Roes Welcome Sound, then to Repulse Bay and through Frozen Strait into Foxe Basin (Figure 3).

Present Day Evidence

Davis Strait and Baffin Bay. Aerial surveys conducted during the 1970s up to 2006 have reported sightings that are consistent with the bowhead whale distributions reported by whalers. In West Greenland waters, bowhead whales have been seen in March and April from Disko Island to as far south as about 66.6^{o} N (McLaren and Davis

1981, 1983; Reeves and Heide-Jørgensen 1996; Heide-Jørgensen and Acquarone 2002, Heide-Jørgensen *et al.* 2007). Ship-based sightings of bowhead whales in West Greenland waters in late February near 68^{o} N has also been reported (Turl 1987). In Disko Bay bowhead whales have been reported to arrive in early February and to leave in late May-early June during 2002-2007 (GINR unpublished information).

Bowhead whales are also known to winter off Cumberland Sound at southeast Baffin Island and satellite tracking has demonstrated the current usage of this area in February-March (DFO unpublished data).

Other known wintering areas in Baffin Bay include the North Water (Figure 3) where scattered bowhead whales have been observed as early as March (Richard *et al.* 1993, 1998). Observations in the North Water later in spring may include migrants from West Greenland (Holst and Stirling 1999). Bowhead whales have also been observed in leads and cracks in Lancaster Sound (Heide-Jørgensen *et al.* 2002) and at Cape Dyer (McLaren and Davis 1981) and there may be bowhead whales wintering at other scattered localities in small open-water *refugia* in the complex pack ice formation in Baffin Bay (cf. Heide-Jørgensen and Laidre 2004).

Davis and Koski (1980) conducted spring, summer and fall surveys in the vicinity of Lancaster Sound and northwest Baffin Island. They reported seeing bowhead whaless in eastern Lancaster Sound and north and east of Bylot Island in June and July. Bowhead whales were seen during late August and early September in Milne Inlet, Eclipse Sound and Admiralty Inlet. Previous surveys had also sighted bowhead whales in Prince Regent Inlet in small numbers in July and August (Finley 1976). Fall migrants were seen by Davis and Koski (1980) travelling south along the northeast Baffin Island coast. More

recent surveys (Cosens *et al.* 2006) found bowhead whales not only in Eclipse Sound, Admiralty Inlet, Prince Regent Inlet and Gulf of Boothia but also in the fiords along the east coast of Baffin Island during August (Figure 3). A sighting of 12-15 bowhead whales in the Robeson Channel (82^{o}N 62^{o}W), on 22 July 1978 must be considered an unusual northern occurrence (Davis and Koski 1980).

Recent tagging work has contributed considerable new knowledge about the movements of bowhead whales. Whales tagged with satellite transmitters in Disko Bay in 2001 through 2006 left West Greenland in late May and moved northwest to an area off Bylot Island (Heide-Jørgensen *et al.* 2003, 2006), corresponding to the area known by the whalers as Pond's Bay (e.g. Markham 1874, Reeves *et al.* 1983, Southwell 1898). Some tagged whales moved into the North Water en route to Bylot Island. Once at Bylot Island, the whales stayed through the end of June when some whales moved south along the east coast of Baffin Island. However, other whales returned to Lancaster Sound and visited Admiralty Inlet, Barrow Strait, Prince Regent Inlet and Gulf of Boothia in August-September before exiting through Lancaster Sound and travelling back along the east Baffin Island coast. An example of one spring migrant from Disko Bay that spent the summer in Gulf Boothia is shown in figure 4.

All the whales that spent the summer in Lancaster Sound and tributaries or along the east coast of Baffin Island headed south in November to Hudson Strait. One whale was located in the western part of Hudson Strait in an area where whales from Foxe Basin are also presumed to winter. The whales stayed in Hudson Strait at least through mid December as indicated by tag transmissions in 2003. An aerial survey in March 1981 covering the Hudson Strait demonstrated an abundance of 1,349 (95% CI 402-4,529)

whales in this area and at that time was the largest concentration of bowhead whales could be detected in the Eastern Canadian Arctic or in West Greenland (Koski et al. 2006).

Whales tagged with satellite transmitters in Cumberland Sound between May and July 2004-2006 moved out of the sound between early and late July. Animals moved either north or south from Cumberland Sound (Dueck et al. 2006). Those that moved south continued through Hudson Strait, Foxe Basin, and Fury and Hecla Strait and into Gulf of Boothia and Prince Regent Inlet. Those that moved north either remained along the east Baffin Island coast or continued through Lancaster Sound to Prince Regent Inlet. Fall movements of summering animals out of Prince Regent Inlet/Gulf of Boothia extended from late September to mid-November (L. Dueck, pers comm..). Routes in both directions were used. Whales took up winter residency in Hudson Strait and at the mouths of Cumberland Sound and Frobisher Bay. An example of one whale that circumnavigated Baffin Island is provided in Figure 4.

There is little information to assess the possibility of migrants arriving in West Greenland waters in the autumn. The capture of a young bowhead whale in a net in Upernavik in October 1980 (Kapel 1985) is the only recent evidence of autumn migrations of bowhead whales south along West Greenland towards the wintering ground. However, it agrees with the reports from whalers of an autumn migration across Baffin Bay (Figure 4).

Hudson Bay and Foxe Basin. There has been relatively little survey work done in the areas inhabited by these whales. Surveys of north-western Hudson Bay (Cosens and Innes 2000) and northern Foxe Basin (Cosens *et al.* 1997) in August located whales in

areas traditionally thought to be summering locations. More recent surveys (Cosens *et al.* 2006) found bowhead whales in northern Foxe Basin, along the coast of Melville Peninsula and relatively few in north-western Hudson Bay. These and previous photogrammetric surveys in northern Foxe Basin (Cosens and Blouw 2003) suggest that the location of summering areas may vary somewhat from year to year.

Little is known of migratory routes. Finley *et al.* (1982) reported eastward movements of bowheads into Hudson Strait in October and November. McLaren and Davis (1982) found bowheads at the western end of Hudson Strait and around Mansel Island during March surveys. Little information is available on spring migration routes, although recent observations suggest that whales migrate north into Foxe Basin through Foxe Channel (Figure 3) arriving at the northern Foxe Basin ice edge in late June (Cosens *et al.* 1997). No recent information is available on the routes used by whales to travel from wintering areas to summering locations in north-western Hudson Bay.

In 2002, the first evidence that HB-FB whales move into Prince Regent Inlet from northern Foxe Basin was collected when a whale tracked by satellite travelled from Foxe Basin to Prince Regent Inlet in September (Dueck *et al.* 2006). In 2003, however, six of nine whales tagged in Foxe Basin moved into Prince Regent Inlet in early August (Figure 3). These observations confirm that whales from Foxe Basin share the summering area in Prince Regent Inlet and Gulf of Boothia with whales from West Greenland and from Cumberland Sound.

When the two stock delineation was originally proposed it was argued that heavy and compact sea ice in Fury and Hecla Strait constitute a barrier for bowhead whales from Foxe Basin and that the whales would not be able to penetrate the ice pack and enter

Gulf of Boothia. Examination of the median ice coverage during 1972-2002 show that there is usually less than 3/10 sea in Fury and Hecla Strait in mid September when the least sea ice is present in the Arctic and that low coverage of sea ice can also be found earlier in the season (Figure 5, Canadian Ice Service). Bowhead whales are known to be able to migrate through 9/10 of sea ice and summer sea ice in Fury and Hecla Strait should normally not prevent the whales from moving freely through the strait. Bowhead whales can live up to 200 yrs (George et al. 1999) and even if they periodically encounter severe ice conditions at some part of their range there will be other periods in their life where the sea ice would be much less severe.

PATTERNS OF AGE AND SEX SEGREGATION

Historic Records

Early whaling records indicated that bowheads segregated on the basis of age and reproductive status (Southwell 1898). Females and young whales were thought to over-winter near the entrance of Hudson Strait as far south as the Labrador coast near the 57th parallel, then migrate north along the east coast of Baffin Island into Lancaster Sound and then into adjacent inlets such as Prince Regent Inlet for the summer (de Jong 1983, Southwell 1898). Small whales, as well as cows and calves, were taken in Prince Regent Inlet and northern Gulf of Boothia in July, August and early September. Southwell (1898) maintained that females and young whales migrated south from Prince Regent Inlet and Gulf of Boothia through Fury and Hecla Strait through Foxe Basin to Hudson Strait in the fall. He also reported that Ross observed both mature and immature whales moving south into the Gulf of Boothia from Prince Regent Inlet in mid-August.

Southwell (1898) proposed this migration route because females and young were absent from the west side of Davis Strait in the fall.

Old males were thought to over-winter off the entrance to Hudson Strait, move to Disko Island in April and May and then cross Baffin Bay to join the females and immature whales at Lancaster Sound (Southwell 1898). The sou'west fishery operated from April to June and generally took large whales, suggesting that this was an over-wintering area used by adults. However, Ross (1974) report that whalers also observed cows and calves during this fishing season. Eschricht and Reinhardt (1866) described 1 foetus and 2 newborn calves in the fishery along West Greenland in March-April but gave no other information on the proportion of newborns in that fishery. Considering the large number of whales taken along West Greenland the relatively few accounts of calves suggests a low abundance of calves in this area.

Ross (1974) indicates that early whalers believed that females with young headed west through Hudson Strait in the spring. This is consistent with whaling records showing that cows, calves and sub-adult whales were taken around Marble Island as well as in Repulse Bay from June through September (Reeves and Cosens 2003). Analysis of whaling records by Reeves and Cosens (2003) indicated that calves and sub-adults were taken by commercial whalers both south of Wager Bay along the Hudson Bay coast and in Repulse Bay and Frozen Strait. These results suggest that both north-western Hudson Bay and Repulse Bay were more likely to be calf-rearing areas than summering areas frequented primarily by adults.

Present Day Evidence

Observations made while collecting skin biopsies from bowhead whales near Disko Island in May 2001 through 2007 indicate that it is mainly adult whales (>14 m) that are found in this area in spring (Heide-Jørgensen *et al*. 2002, 2006). Calves or newborns are rarely seen and have not been detected in recent aerial surveys in West Greenland in winter (Heide-Jørgensen et al. 2007). Skin biopsies collected between 2001 and 2007 show that 80% of the bowhead whales sampled in April and May in West Greenland were females (n=207) (Heide-Jørgensen et al. SC/60/BRG19). The mid-winter (February-March) sex ratio in West Greenland still remain to be studied.

In 1976 and 1978 Davis and Koski (1980) found few calves (<3%, n=46) during fall aerial surveys of Lancaster Sound and the northeast coast of Baffin Island. In Isabella Bay, on the east coast of Baffin Island, 83 bowhead whales were measured on aerial photographs in September 1986 (Finley 1990). Mean length was 14.4 m and only one cow-calf (6 m) pair and one sub-adult whale (<10 m) were detected. Land-based observations in Isabella Bay during 1984-88 confirmed that mother-calf pairs and sub-adults were rarely seen. An aerial survey, conducted in 2003, located relatively large numbers of bowheads close to shore along the east coast of Baffin Island in August (Cosens et al. 2006, Dueck *et al.* 2008). Most of the sigtings were of adult whales (P. Richard pers. comm.) Results from these various studies strongly suggest that the bowhead whales occupying Baffin Bay and Davis Strait during summer and fall are mainly adults.

Prince Regent Inlet has been considered to be the calf-rearing area for Baffin Bay-Davis Strait bowheads (Moore and Reeves 1993). Surveys in 2002 (Cosens *et al.* 2006) confirmed that cow-calf pairs and sub-adults are present in relatively large numbers in

both Prince Regent Inlet and Gulf of Boothia. Recent tagging results in agreement with whaling records and Inuit traditional knowledge have demonstrated that the whales that summer in Prince Regent Inlet come from both Foxe Basin and Baffin Bay (Figure 4, Dueck *et al.* 2006, GINR unpublished data).

From a photogrammetric study, conducted in northern Foxe Basin between 1995 and 1999, Cosens and Blouw (2003) reported that over 80% of whales that were photographed and for which body lengths could be estimated were young-of-the-year calves and sub-adults. The adult component that had been photographed and measured was thought to be cows with young-of-the-year calves. Although Cosens and Blouw (2003) proposed that the adult males and resting females of the stock might be found in north-western Hudson Bay, the historic evidence suggests this area is also part of the calf rearing area (Reeves and Cosens 2003). The exception to this observation is the adult male that was landed by hunters in Repulse Bay in 1996. Thus, adult whales are present in this area but numbers seem relatively low (Cosens and Innes 2000; Cosens et al. 2006).

The observed age and sex distribution in Foxe Basin suggests that this component of the population is lacking adult males and resting females. There seems to be no location within Hudson Bay and Foxe Basin where significant numbers of adults can be reliably located. In Baffin Bay-Davis Strait, on the other hand, there seems to be ample evidence for the presence of old whales of both sexes. The exception is the net entanglement of a young bowhead whale (9-10 m) in Upernavik in November 1980 (Kapel 1985).

GENETIC EVIDENCE

To genetically test the patterns of genetic differentiation in bowhead whales from the Eastern Canadian Arctic and West Greenland skin biopsies have been collected from free-ranging bowhead whales in Nunavut, Canada (Pelly Bay, Igloolik, Repulse Bay and Pangnirtung) and West Greenland (Disko Bay) and analyzed for 34 nuclear DNA microsatellite loci (Postma et al. 2008). Twenty-one of these loci were amplified using primers specific for bowhead whales (Huebinger *et al.* 2007) and the remaining 13 loci were analyzed using primers developed for various other cetacean species (Valsecchi and Amos 1996; Buchanan *et al.* 1996; Palsbøll *et al.* 1997; Waldick *et al.* 2000; Rooney *et al.* 1999).

Samples of individual whales that were successfully scored for at least 30 loci were: Pelly Bay n=8 (6M;4F), Igloolik n=143 (62M:78F however, 2003 samples had 7M:20F), Repulse Bay n=16 (8M:8F however, 1997 and 2000 samples were almost all female,1M:4F in 1997 and 1M:3F in 2000), Pangnirtung n=82 (43M:38F), and Disko Bay n=80 (21M:59F however, 2003 and 2006 samples were entirely female, n=10 and n=22 respectively).

Data were tested for departures from Hardy-Weinberg equilibrium (HWE) using GENEPOP version 4.0.6 (Rousset 2007). There was HW disequilibrium in most of the sampling locations, however it was most notable in the Igloolik samples. This analysis is often used as a measure of population differentiation. If a population is divided into several breeding units, the frequency of homozygotes tends to be higher than the expected Hardy-Weinberg proportion (Nei and Kumar 2000). The results of the bowhead sample comparison may therefore indicate stock structure, however it could also be the result of a number of other factors such as inbreeding or other non-random mating,

assortative mating, natural selection, bottleneck effects from severe population depletion due to commercial whaling, non-random sampling, or data scoring errors.

An Analysis of Molecular Variance (AMOVA) revealed significant differences in allele frequencies among samples from different years at each location. These results are most likely influenced by sample sizes and the variation in the sample sexes and ages (and thus composition of the sample being from different population cohorts) in the collection from year to year. They may also reflect a lack of site fidelity from year to year by these bowheads and/or differences in habitat use by various sex and age class components of the population.

Analysis of allele frequencies among pooled samples from the sampling locations also revealed significant differences in most pairwise comparisons. As these locations were then pooled into groupings representing the putative Baffin Bay-Davis Strait (BB-DS) and Hudson Bay-Foxe Basin (HB-FB) populations, a significant difference in the allele frequencies persisted. However, the F_{st} value was very small (0.0038). Givens *et al*. (2007) found F_{st} values an order of magnitude larger when comparing bowhead samples from a known distinct population of bowhead (Sea of Okhotsk) to samples from Barrow, Alaska and samples from Igloolik (F_{st} values of 0.034 and 0.039 respectively). However, comparison of Barrow samples to Igloolik samples yielded an F_{st} value of 0.006. This raises questions over what magnitude of genetic divergence should be used to define populations or sub-populations of bowheads and the weight given to allele frequency differences for the delineation of separate populations.

A clustering analysis of the samples using STRUCTURE (Pritchard *et al*. 2000; Falush *et al*. 2003) was performed and the results were unclear. Overall, the only

samples that were clearly distinguished were the samples from 1997 and 2000 Repulse Bay. All other locations resulted in samples that were assigned in roughly equal proportions to the defined number of clusters, though perhaps with some temporal trend. This would suggest a single population of bowheads that show a lack of site fidelity during the seasons that sampling occurred. However, the STRUCTURE method has been criticized as being useful for detecting population structure only when genetic differences among groups are large (Taylor *et al*. 2007). However, the results of this analysis are supportive of the results of recent studies on the distribution and movements of bowhead whales in Western Greenland and the Eastern Canadian Arctic that directly challenge the two-population model (Heide-Jørgensen and Finley 2003; Cosens and Blouw 2003; Heide-Jørgensen *et al*. 2003; Heide-Jørgensen *et al*. 2006, Dueck *et al*. 2006).

There are several elements of biological information for this dataset that are not available that could improve the interpretation of the results of the microsatellite analyses. The ages of the individual whales are not known, though observation estimates on the length of the animals sampled in Disko Bay indicate that they are predominantly adult females (Heide- Jørgensen *et al*. 2007) and the bowheads sampled in Igloolik are mostly females with calves and juveniles (Cosens and Blouw 2003). Also, potential family relationships that may occur in some of the sample locations (i.e. Igloolik) are difficult to assess and family groups in the data will affect the statistical results of allele frequency comparisons. In fact, Givens *et al*. (2007) found that the main sources of genetic signal in a similar study of Bering-Chuckchi-Beaufort bowhead whales were scoring errors, familial relations, and birth year.

The molecular genetic evidence from microsatellite analyses of bowhead samples from Baffin Bay–Davis Strait and Hudson Bay-Foxe Basin does not provide support for two distinct populations. The small F_{st} values do not indicate a significant degree of genetic divergence and the Hardy-Weinberg disequilibria and significant differences in allele frequencies may be attributed to a number of biological factors other than population delineation. This conclusion is supported by the results of satellite tracking studies showing extensive movements of bowheads between these two areas. However, the genetic differences that were detected and the limited information on the sex and age class segregation among the sampling locations indicate that there is some structuring of bowheads throughout their range that may have management implications for this population.

Based on analyses of mtDNA from samples of holocene bowhead whale material from Svalbard Borge et al. (2007) found that there was considerable similarity between haplotypes of holocene bowhead whales from Svalbard and those presently inhabiting the Bering, Chuckchi and Beaufort seas. The lack of genetic differentiation between whales in the Pacific and the Atlantic, despite the fact the samples are taken several thousand years apart, suggests that large scale migrations occur between whales in the two areas and also questions the current definition of five different stocks of bowhead whales. Considering that there might historically or even presently have been an exchange of bowhead whales between the Atlantic and the Pacific it seems unrealistic that two separate stocks, sharing both summer and wintering grounds, should persist in the relatively small area between the Eastern Canadian Arctic and West Greenland.

LIFE HISTORY PATTERNS IN RELATION TO DISTRIBUTION

New information on movements and distribution suggests that the two-stock model currently adopted by IWC does not explain distribution patterns and movements of bowhead whales in eastern Canadian and West Greenland waters. Examination of whaling records in relation to new tagging and recent survey information suggests that segregation by age and reproductive status may account for what has appeared to be separate populations in Baffin Bay-Davis Strait and Hudson Bay-Foxe Basin.

Age and sex segregation of bowheads occurs in the Eastern Canadian Arctic and West Greenland waters on a large scale (Figure 4). For the most part, the waters of north-western Hudson Bay, Foxe Basin, Gulf of Boothia and Prince Regent Inlet appear to be occupied by cows, calves and sub-adults. The waters of the east coast of Baffin Island, Baffin Bay and Davis Strait seem mainly to be occupied by the adult males and, probably, resting females. A common wintering ground in Hudson Strait seems to host large numbers of bowhead whales in March. These distribution patterns are better explained by a single population model which includes segregation by age, sex and reproductive status.

Although the summer and winter distributions of bowheads are relatively well described, it is not clear what routes are used by different components of the proposed population in spring and fall. Possible migration routes, as indicated by whaling records, Inuit traditional knowledge and recent tagging data are illustrated in Figures 3 and 4. Southwell (1898) proposed a complex set of migration routes used by bowheads segregated by age and gender, based on the experiences of commercial whalers.

Although Reeves *et al.* (1983) dismiss some of these ideas, such as the circumnavigation of Baffin Island by females and young whales, evidence from recent studies are remarkably consistent with Southwell's proposed model of migrations and segregation of a single population in the Eastern Canadian Arctic and West Greenland.

It is likely that pregnant cows leave the wintering areas and either calve en route to summering locations or calve once they arrive. There are records of calves being taken by commercial whalers near Pond Inlet in early summer (Reeves *et al.* 1983). Mitchell and Reeves (1981) also noted that, in years when ice blocked Lancaster Sound and Pond Inlet, the catch was characterized by large numbers of whales and low oil yield, indicating that more young animals were taken in years when the ice formation prevented their escape into Prince Regent Inlet. Cows and calves occur in Lancaster Sound in the spring but it is not clear whether they arrive from Hudson Strait or from West Greenland. Southwell's proposed spring route used by females and young whales near the shore of the east Baffin coast is consistent with the Inuit Bowhead Knowledge Study (NWMB 2000) that reports spring movements of whales along the east Baffin Island coast and the presence of mother-calf pairs in the Pond Inlet area and Admiralty Inlet. Prince Regent Inlet was considered to be a calf-rearing area for the Baffin Bay stock, thus it seems likely that at least some cows, calves and sub-adults arrive from Baffin Bay-Davis Strait waters, using the east Baffin Island route. The small number of calves taken in West Greenland waters by the commercial whalers suggests that pregnant females may also migrate across Baffin Bay from Greenland, arriving at the Pond's Bay area either with near-term foetuses or newborn calves.

Commercial whalers did not venture into Foxe Basin so they would have had little direct knowledge of whale movements in that area. In fact, whales arrive at the Foxe Basin ice edge at the end of June and move north into the ice as it begins to melt out and break up (Cosens *et al.* 1994, Dueck *et al.* 2006). Satellite tracking shows that many whales tracked beyond mid-July continue north-west through Fury and Hecla Strait into Prince Regent Inlet. Some also remain in Foxe Basin and some in the Gulf of Boothia. Data on fall migration routes are not as detailed. Although Davis and Koski (1980) proposed that Prince Regent Inlet whales probably move into Lancaster Sound and south along Baffin Island, satellite tracking data from one whale showed movement south and east through Fury and Hecla Strait and south through Foxe Basin. This is exactly the pattern of fall movement suggested by Southwell (1898).

McLaren and Davis (1982) and Koski et al. (2006) documented the presence of bowheads at the west end of Hudson Strait in March and Richard *et al.* (unpublished data) sighted bowheads in both Cumberland Sound and the east end of Hudson Strait in March of 2003 (Figure 3). These observations as well as satellite tracking data suggest that whales from both Baffin Bay and Hudson Bay and Foxe Basin over-winter in Hudson Strait. It is likely that mating occurs there during the winter.

Age and sex segregation has been observed in the Bering-Chukchi-Beaufort population of bowheads (Cubbage and Calambokidis 1987, Angliss *et al.* 1995) as well as in northern right whales, *Eubalaena glacialis,* (Winn *et al.* 1996) and southern right whales, *E. australis,* (Payne 1986). Segregation may allow young animals to access more sheltered areas or isolate themselves from the vigorous activity of the adults (Winn *et al.* 1986). Gray (1939) has suggested that young whales and cows with calves try to escape

early into the dense sea ice. Similarly, de Jong (1983) argued that the development of ships that could move into heavy ice resulted in the demise of the Baffin Bay fishery because whalers could then take cows and calves which had previously been protected by their occupation of ice infested waters.

The Disko Bay has been demonstrated to be a springtime feeding ground (Laidre et al. 2007). Dive and telemetry studies together with simultaneous oceanographic and zooplankton sampling have demonstrated bowhead whales in West Greenland focus foraging effort on benthic zooplankton in the coastal zone at depths as deep as 400m. Seasonally dependable dense aggregations of zooplankton in specific localities around the Arctic likely play an important role in the recovery of the eastern Arctic bowhead whale population (Laidre et al. 2007).

Although there is evidence that Disko Bay is an important feeding ground for bowhead whales there is also evidence from acoustics that Disko Bay could be a mating ground. Intensive singing activity of bowhead whales with up to three unique songs have been recorded in April 2007 (Stafford et al. submitted). Singing is an activity that is usually attributed to male display in baleen whales and the fact that most singing activity was recorded during the spring mating period makes it plausible that mating between the relatively few males and the large fraction of females indeed occur in Disko Bay.

CONCLUSION

Examination of current data on distribution patterns and movements of bowhead whales in Baffin Bay and Hudson Bay has identified major difficulties with the two-stock

hypothesis. The first problem is that too few calves have been found in the putative Baffin Bay stock to maintain a viable population that is currently increasing (Heide-Jørgensen et al. 2007). The second problem is that too few adults have been found in the putative Hudson Bay stock to produce the calves and sub-adults that have been seen there (see Cosens and Blouw 2003). Under the two-stock hypothesis, Moore and Reeves (1993) suggested that cows, calves and juveniles of the Baffin Bay stock summer in the high Arctic archipelago including Admiralty Inlet and Prince Regent Inlet while adult males and, possibly, resting females occur mainly along the northeast coast of Baffin Island. Under the two-stock hypothesis, Prince Regent Inlet and other high Arctic inlets were considered to be the 'nursery' areas for the BB-DS stock (Finley 2001; Moore and Reeves 1993). The circumnavigation of Baffin Island by females and young whales was discounted by Moore and Reeves (1983) but recent satellite tracking of whales has proven that bowhead whales do indeed circumnavigate both clockwise and counter clockwise.

Little evidence of calves or young whales has been found outside of the high Arctic inlets and concerns have been raised about the reproductive rates of Baffin Bay bowheads being unusually low (Finley 2001). The opposite problem has been identified in Hudson Bay and Foxe Basin. One of the arguments proposed by Reeves and Mitchell (1990) in favour of the two-stock hypothesis was that bowheads of all ages could be found in whaling records from Hudson Bay. Cosens *et al.* (1994) similarly noted that whales of all ages were seen in northern Foxe Basin during aerial and boat-based surveys but Cosens and Blouw (2003) confirmed that the observed age distribution did not reflect that of a complete stock.

Tracking data have shown that there is no geographical separation between the two putative stocks. Recent tagging data has shown that whales occupying Foxe Basin move through Fury and Hecla Strait into Prince Regent Inlet, waters traditionally associated with the Baffin Bay stock. In Prince Regent Inlet whales from Foxe Basin mix with whales tagged in Disko Bay and Cumberland Sound. Tagging data also show that whales from the two putative stocks appear to occupy the same wintering areas in Hudson Strait.

The most reasonable explanation for these findings is that bowheads summering in the eastern Canadian Arctic and wintering off the west coast of Greenland consist of one population with those occupying Baffin Bay mainly being the adult males and resting females and the Prince Regent, Gulf of Boothia, Foxe Basin and north-western Hudson Bay animals being nursing females, calves and sub-adults. We propose that this new single stock of bowhead whales in the Eastern Canadian Arctic and West Greenland is recognised and hereafter called the Baffin Bay stock.

LITERATURE CITED

ALLEN, K.R. 1978. Report of the Scientific Committee. Rep. Int. Whal. Commn. 28: 38-92.

ANGLISS, R.P., RUGH, D.J., WITHROW, D.E., and HOBBS, R.C. 1995. Evaluations of aerial photogrammetric length measurements of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*). Report of the International Whaling Commission 45: 313-324.

BANNISTER, J.L. 1999. Report of the Scientific Committee. J. Cetacean Res. Manage.

1 (Suppl.): 1-284.

BORGE, T., L. BACHMANN, G. BJØRNSTAD and Ø. WIIG. 2007. Genetic variation in Holocene bowhead whales from Svalbard. Molecular Ecology doi: 10.1111/j.1365-294X.2007.03287.x

BORN, E.W. and HEIDE-JØRGENSEN, M.P. 1983. Observations of the bowhead whale (*Balaena mysticetus*) in central West Greenland in March-May 1982.

COSENS, S.E. 2003. Baffin Bay-Davis Strait and Hudson Bay-Foxe Basin bowheads: Update on research. Unpubl. Rep. to IWC. SC/55/BRG17.

COSENS, S.E. and BLOUW, A. 2003. Size- and age-class segregation of bowhead whales summering in northern Foxe Basin: A photogrammetric analysis. Marine Mammal Science 19: 284-296.

COSENS, S.E. and INNES, S. 2000. Distribution and numbers of bowhead whales (*Balaena mysticetus*) in northwestern Hudson Bay in August 1995. Arctic 53: 36-41.

COSENS, S.E., QAMUKAQ, T., PARKER, B., DUECK, L.P. and ANARDJUAK, B. 1997. The distribution and numbers of bowhead whales, *Balaena mysticetus*, in northern Foxe Basin in 1994. Canadian Field-Nat. 111: 381-388.

DAVIS, R.A. and KOSKI, W.R. 1980. Recent observations of the bowhead whale in the Eastern Canadian High Arctic. Rep. int. Whal. Commn 30: 439-444.

de JONG, C. 1983. The hunt of the Greenland whale: A short history and statistical sources. Rep. Int. Whal. Commn. Special Issue 5: 83-106.

ESCHRICHT, F. and REINHARDT, J. 1866. The Greenland right-whale with especial reference to its geographical distribution and migrations in times past and present, and to its external and internal characteristics. The Ray Society, Lond. 192: 1-49.

FINLEY, K.J. 1990. Isabella Bay, Baffin Island: An important historical and present-day concentration area for the endangered bowhead whale (*Balaena mysticetus*) of the Eastern Canadian Arctic. Arctic 43: 137-152.

FINLEY, K.J. 2001. Natural history and conservation of the Greenland Whale, or Bowhead, in the Northwest Atlantic. Arctic 54: 55-76.

GEORGE, J. C., BADA, J., ZEH, J., SCOTT, L., BROWN, S. E.,O'HARA, T. & SUYDAM, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. Can. J. Zool. 77, 571–580. (doi:10.1139/cjz-77-4-571)

GRAY, R.W. 1939. Statistics of Peterhead Whaling Fleet. The Naturalist 978: 101-104.

GREENDALE, R.G. and BROUSSEAU-GREENDALE, C. 1976. Observations of marine mammals at Cape Hay, Bylot Island during the summer of 1976. Environment Canada, Fisheries and Marine Service Technical Report No. 680, 25 pp.

HEIDE-JØRGENSEN, M.P. and ACQUARONE, M. 2002. Size and trends of the bowhead whale, beluga and narwhal stocks wintering off West Greenland. In Heide-Jørgensen, MP. and Wiig, Ø. eds. Belugas in the North Atlantic and the Russian Arctic. North Atlantic Marine Mammal Commission, Tromsø.

HEIDE-JØRGENSEN, M.P. and LAIDRE, K.L. 2004. Declining extent of open water refugia for top predators in Baffin Bay and adjacent waters. AMBIO 33(8): 488-495.

HEIDE-JØRGENSEN, M.P., RICHARD, P., RAMSAY, M. and AKEEAGOK, S. 2002. Three recent ice entrapments of Arctic cetaceans in West Greenland and the eastern Canadian High Arctic. In Heide-Jørgensen, MP. and Wiig, Ø. eds. Belugas in the North Atlantic and the Russian Arctic. North Atlantic Marine Mammal Commission, Tromsø.

HEIDE-JØRGENSEN, M.P., LAIDRE, K., WIIG, O., JENSEN, M.V., DUECK, L.,

SCHMIDT, H.C., and HOBBS, R. 2003. From Greenland to Canada in ten days: Tracks of bowhead whales, *Balaena mysticetus*, across Baffin Bay. Arctic 56: 21-31.

HEIDE-JØRGENSEN, M.P., LAIDRE, K.L., JENSEN, M.V., DUECK, L. and L. D. POSTMA, L.D. 2006. Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay. Marine Mammal Science, 22(1): 34-45.

HEIDE-JØRGENSEN, M.P., K. LAIDRE, D. BORCHERS, F. SAMARRA and H. STERN. 2007. Increasing abundance of bowhead whales in West Greenland. Biology Letters, doi:10.1098/rsbl.2007.0310

HOLST, M. and STIRLING, I. 1999. A note on sightings of bowhead whales in the North Water Polynya, Northern Baffin Bay, May-June, 1998. J. Cetacean Res. Manage. 1(2): 153-156.

KAPEL, F.O. 1985. A note on the net-entanglement of a bowhead whale (*Balaena mysticetus*) in northwest Greenland, November 1980. Rep. int. Whal. Commn 35; 377-378.

KOSKI, W., HEIDE-JØRGENSEN, M.P. and LAIDRE, K. 2006b. Winter abundance of bowhead whales, *Balaena mysticetus*, in the Hudson Strait, March 1981. *J. Cetacean Res. Manage.* 8(2):139-44.

LAIDRE, K. L., HEIDE-JØRGENSEN, M.P.,, and T. NIELSEN. 2007. The role of the bowhead whale as a predator in West Greenland. Marine Ecology Progress Series 346: 285-297.

MAIERS, L., de MARCH, B.G.E., CLAYTON, J.W., DUECK, L.P. and COSENS, S.E. 1999. Genetic variation among populations of bowhead whales summering in Canadian waters. Canadian Stock Assessment Secretariat Research Document 99/134, 22 pages.

MARKHAM, A.H. 1874. A whaling cruise to Baffin's Bay and the Gulf of Boothia in the whaler *Arctic* commanded by Captain Adams. London, Low and Searle. 319 p.

McLAREN, P.L. and DAVIS, R.A. 1981. Distribution of wintering marine mammals in southern Baffin Bay and northern Davis Strait, March 1981. Unpubl. Rep. by LGL for the Arctic Pilot Project, Calgary.

McLAREN, P.L. and DAVIS, R.A. 1982. Winter distribution of arctic marine mammals in ice-covered waters of eastern North America. Unpubl. Rep. by LGL for Petro-Canada Exploration Inc., Calgary.

MITCHELL, E. and REEVES, R.R. 1981. Catch history and cumulative catch estimates of initial population size of cetaceans in the eastern Canadian Arctic. Rept. Int. Whal. Commn. 31: 645-682.

MITCHELL, E. and REEVES, R.R. 1982. Factors affecting abundance of bowhead whales *Balaena mysticetus* in the Eastern Arctic of North America, 1915-1980. Biological Conservation 22: 59-78.

MOORE, S.E. and REEVES, R.R. 1993. Distribution and movement. In Burns, J.J., Montague, J.J. and Cowles, C.J. eds. The bowhead whale. Society for Marine Mammalogy, Lawrence, Kansas.

NUNAVUT WILDLIFE MANAGEMENT BOARD. 2000. Final Report of the Inuit Bowhead Knowledge Study, Iqaluit, Nunavut, Canada.

PAYNE, R. 1986. Long term behavioural studies of the southern right whale (*Eubalaena australis*). Rep. Int. Whal. Commn. Special Issue 10: 161-167.

REEVES, R.R. and COSENS, S.E. 2003. Historical population characteristics of bowhead whales (*Balaena mysticetus*) in Hudson Bay. Arctic 56:283-292.

REEVES, R.R. and HEIDE-JØRGENSEN, M.P. 1996. Recent status of bowhead whales, *Balaena mysticetus,* in the wintering grounds off West Greenland. Polar Research 15 (2): 115-125.

REEVES, R.R. and MITCHELL, E. 1990. Bowhead whales in Hudson Bay, Hudson Strait, and Foxe Basin: A review. Naturaliste can. (Rev. Ecol. Syst.) 117: 25-43.

REEVES, R.R., MITCHELL, E., MANSFIELD, A. and McLAUGHLIN. 1983. Distribution and migration of the bowhead whale, *Balaena mysticetus,* in the eastern North American Arctic. Arctic 36: 5-64.

RICHARD, P.R., ORR, J., DIETZ, R. and DUECK, L. 1998. Sighthings of belugas and other marine mammals in the North Water. Arctic 51: 1-4.

ROSS, W.G. 1974. Distribution, migration and depletion of bowhead whales in Hudson Bay, 1860 to 1915. Arctic and Alpine Research 6: 85-98.

SOUTHWELL, T. 1898. The migration of the Right Whale (*Balaena mysticetus*). Natural Science 12: 397-414.

STAFFORD, K. M., S.E. MOORE, K.L. LAIDRE and M.P. HEIDE-JØRGENSEN. Submitted. Bowhead whale springtime song off West Greenland.

WINN, H.E.,PRICE, C.A. and SORENSON, P.W. 1986. The distributional biology of the right whale (*Eubalaena glacialis*) in the western North Atlantic. Rep. Int. Whal. Commn. Special Issue 10: 129-138.

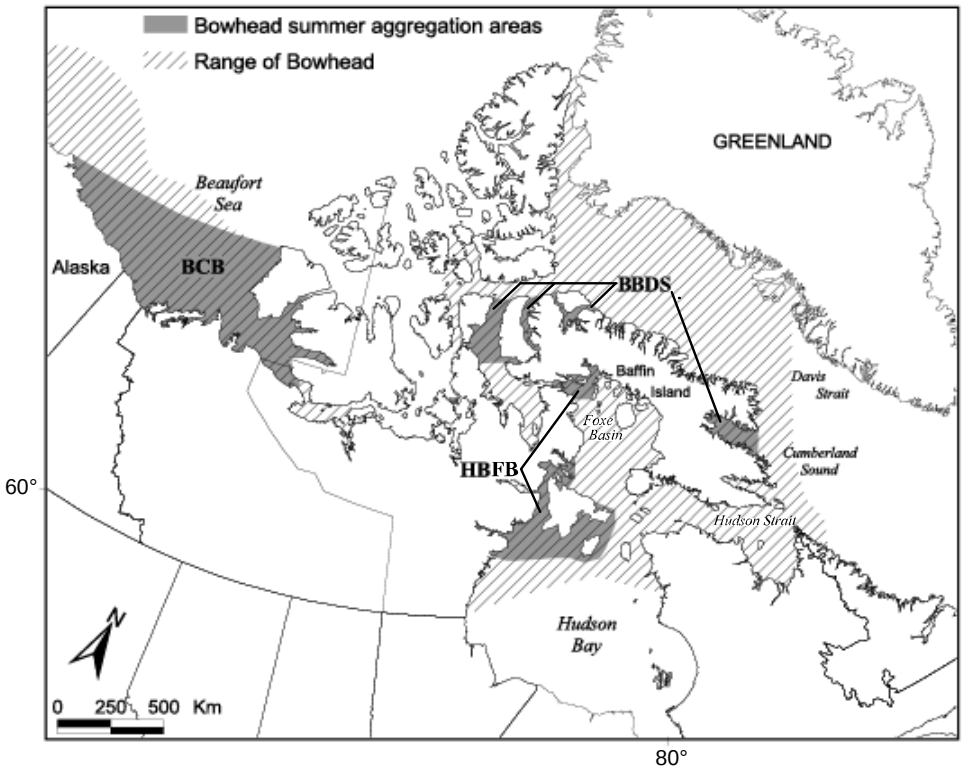
FIGURE CAPTIONS

Figure 1. Presumed ranges and summer aggregation areas of the three putative stocks of bowhead whales.

Figure 2. Place names of locations mentioned in text.

Figure 3. Wintering grounds, spring and fall movements of bowhead whales between Greenland and Canada. Proposed migration routes are based on whaling records, Inuit traditional knowledge and satellite telemetry data.

Figure 4. Examples of tracks of bowhead whales from Disko Bay (left) and Cumberland Sound (right). From Disko Bay, West Greenland, two examples of female bowhead whales tagged in April and tracked by satellite into Gulf of Boothia (straight line 2002) and into the wintering ground in Hudson Strait (dotted line 2006) are shown. From Cumberland Sound one female tagged in July 2006 and tracked through April 2007 shows a complete circumnavigation of Baffin Island.



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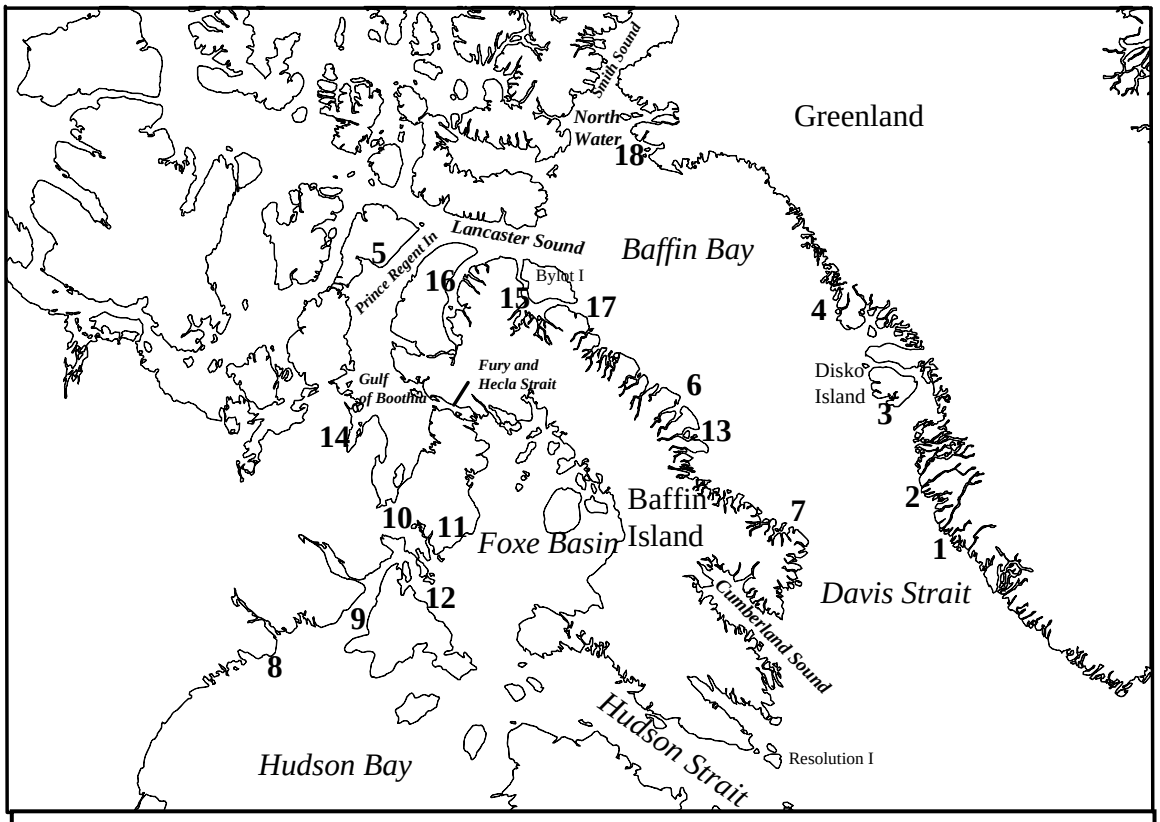
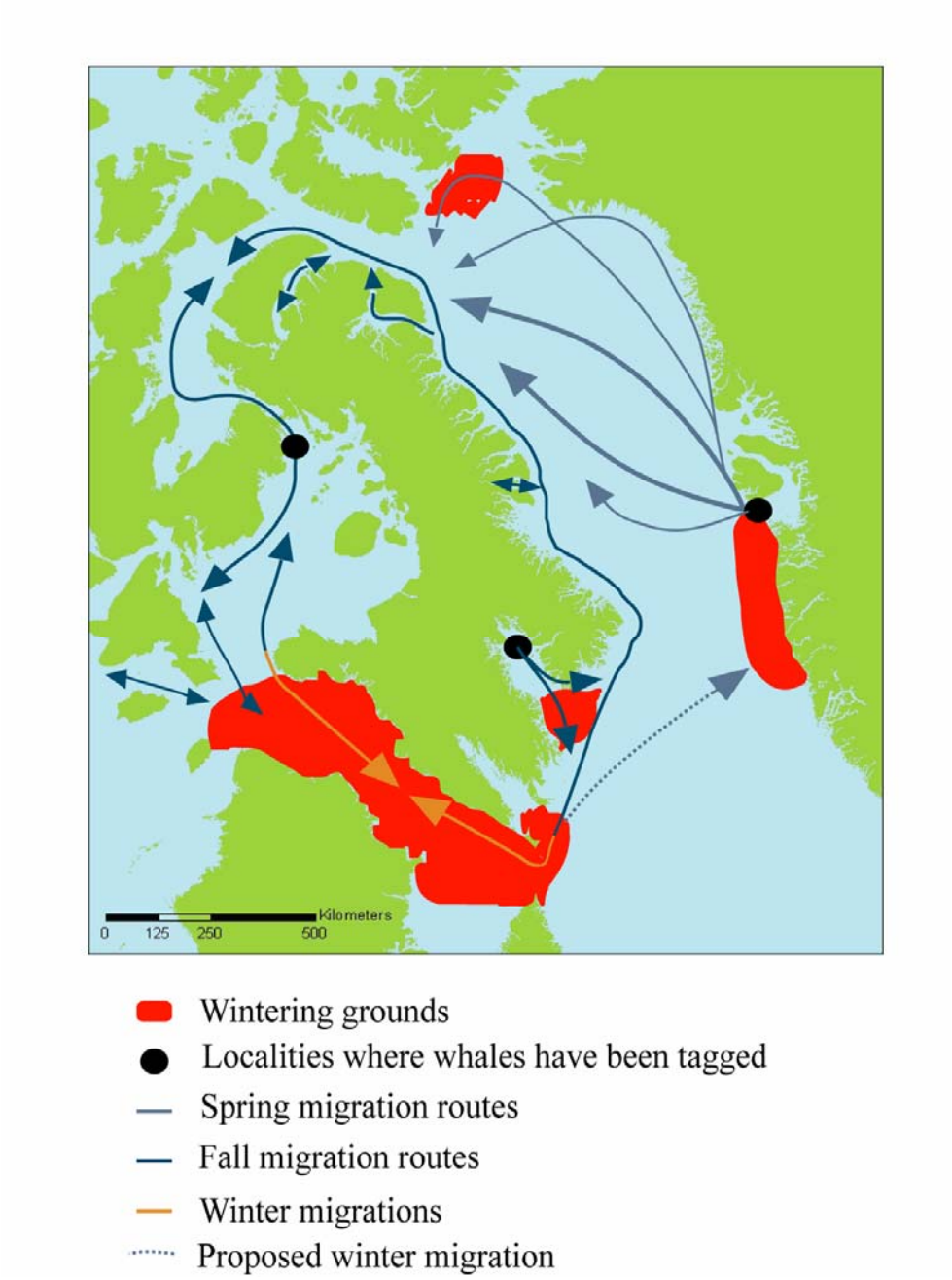


1. Sukkertoppen, 2. Holsteinsborg, 3. Godhavn, 4. Upernavik, 5. Creswell Bay, 6. Clyde River, 7. Cape Searle, 8. Marble Island, 9. Roes Welcome Sound, 10. Repulse Bay, 11. Lyon Inlet, 12. Frozen Strait, 13. Isabella Bay, 14. Pelly Bay, 15. Eclipse Sound, 16. Admiralty Inlet, 17. Pond Inlet, 18. Wolstenholme Fiord

Figure 2. Place names of locations mentioned in text.



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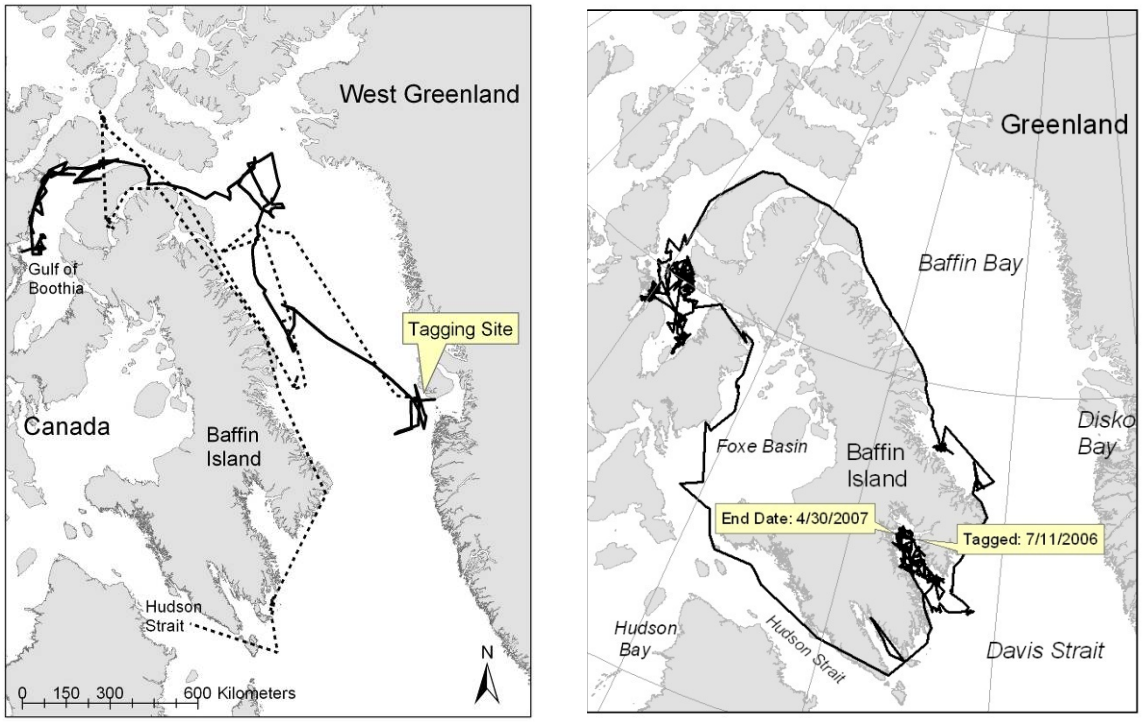

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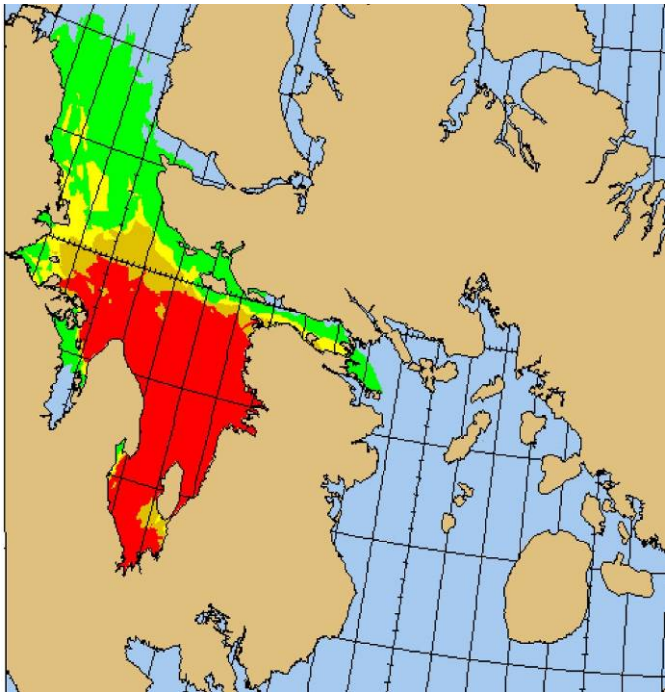

Figure 5. Ice coverage in the Eastern Canadian Arctic at the minimum of ice extent in mid September. The ice coverage is shown as the median of 30yrs of ice coverage. (Canadian Ice Service).