

Large scale sexual segregation of bowhead whales

M.P. Heide-Jørgensen¹, K. L. Laidre^{1,2},

Ø. Wiig³, L. Postma⁴, L. Dueck⁴,

L. Bachmann³

¹Greenland Institute of Natural Resources, Box 570, DK-3900 Nuuk, Greenland

²Polar Science Center, Applied Physics Laboratory, University of Washington, Seattle, USA

³Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

⁴Fisheries and Oceans Canada, Central and Arctic Region, 501 University Crescent, Winnipeg, Manitoba, R3T 2N6, Canada

ABSTRACT: Skin biopsy samples from 596 bowhead whales (*Balaena mysticetus*) collected between 1995 and 2009 at four localities in Nunavut, Canada, (Foxe Basin, Pelly Bay, Repulse Bay and Cumberland Sound) and at one locality in West Greenland (Disko Bay) were used for determination of sex and sexual segregation of bowhead whales in the Baffin Bay stock. There was a significant dominance of females (76%) in the Disko Bay samples whereas the sex ratio in whales from other localities in the Nunavut was not significantly different from an even sex ratio (~50% females). Observations on the length of whales suggest that primarily large mature whales without calves use Disko Bay whereas mother-calf pairs are primarily found in Foxe Basin. The reason for this large scale spatial segregation of sexes in bowhead whales is not fully understood. However, the most parsimonious explanation is that mature females that are without calves utilize the productive Disko Bay as a foraging ground during certain parts of their reproductive cycle. Acoustic recordings of singing males indicate that Disko Bay may also be a mating ground, where some males may be following females in estrous to the bay. Accordingly, bowhead whales summering in the eastern Canadian Arctic and wintering off the west coast of Greenland must belong to one population. The Baffin Bay is mainly used by adult males and resting females whereas the Prince Regent, Gulf of Boothia, Foxe Basin and north-western Hudson Bay animals are nursing females, calves and sub-adults.

KEY WORDS: Bowhead whale *Balaena mysticetus*, sexual segregation, skin biopsies, genetic sex determination

INTRODUCTION AND METHODS

Bowhead whales (*Balaena mysticetus*) congregate predictably at several coastal locations in the Canadian eastern Arctic and in West Greenland at different seasons. At Disko Bay, West Greenland (Fig. 1), bowhead whales are present between February and June, and this temporal pattern has been observed since the 1700s (Eschricht and Reinhardt, 1861). Satellite tracking studies have demonstrated that bowhead whales wintering off the west coast of Greenland can spend the summer in the eastern Canadian Arctic and move to the Hudson Strait for the subsequent winter (Heide-Jørgensen et al. 2003, 2006). The abundance of bowhead whales in West Greenland was estimated at 1229 individuals (95% CI: 495–2939) in 2006 (Heide-Jørgensen et al. 2007). Similarly, bowhead whales are found in large concentrations at specific locations in Foxe Basin, Northern Hudson Bay, in fjords along the east coast of Baffin Island and in the Canadian high Arctic during summer. In winter they tend to congregate in the Hudson Strait, at the mouth of Cumberland Sound, along West Greenland and in the North Water.

Based on observations from whalers and various expeditions, it was first noted by Southwell (1898) that bowhead whales in Baffin Bay-Hudson Bay exhibit considerable sex and age-class segregation across their geographic range. According to Southwell (op cit.) the bowhead whales were first encountered by whalers at the northern Labrador coast in winter. Later in April-May when the whales were found at the entrance to Hudson Strait, old males apparently headed for Disko Bay on the eastern side of Baffin Bay. Females and immature whales headed north along the east coast of Baffin Island through leads and cracks along the east coast of Baffin Island in May and June. Later in July, the old males from Disko Bay joined again with the females and immature whales at the entrance to Lancaster Sound, from where they moved west into the Canadian high-Arctic Archipelago, in particular to the Prince Regent Inlet when ice conditions permitted. Before fast-ice formed in the Canadian high-Arctic Archipelago the whales abandoned the area with the old whales heading south along the east coast of Baffin Island and females with young travelling through the Fury and Hecla Strait into Foxe Basin

and the Hudson Bay. The various segments of the population wintered in Hudson Strait and at the Labrador coast where also parturition was believed to occur.

The claim by Southwell (op. cit.) that it was primarily old males that headed towards Disko Bay in spring is not in agreement with the recordings of females with fetuses in Disko Bay documented by Eschricht and Reinhardt (1861). However, both Southwell (op. cit.) and Eschricht and Reinhardt (op. cit.) relied on second hand observations with sex and size only determined for whales that were killed. The observations by Southwell (op cit.) were largely ignored by the scientific community because of the lack of quantitative evidence of the sexual segregation. However, Southwell's (op. cit.) description of the movements of the bowhead whale is in good agreement with modern satellite tracking studies of whales in the Baffin Bay (Heide-Jørgensen et al. 2003, 2006). The recent increase in bowhead whale abundance in West Greenland and the development of genetic methods made it feasible to study in more detail the large scale sexual segregation of bowhead whales in this region. The understanding of the sexual segregation is important in relation to the understanding the population structure of bowhead whales in Eastern Canada and Western Greenland.

In this study we collected 710 skin biopsies from bowhead whales by use of crossbows with biopsy darts at five localities in the Eastern Canadian Arctic and in the Disko Bay, West Greenland, between 1995 and 2009 (Table 1). An additional seven samples were collected from the subsistence hunt in Canada and West Greenland. The majority of the samples were collected during field operations where bowhead whales were instrumented with satellite transmitters, but in some communities (Pelly Bay, Repulse Bay) biopsies were collected by local hunters. Since 2007 the sampling in Disko Bay was augmented by supplying a substantial reward (200 US \$) to the hunters for each biopsy that was collected. The majority of samples in Disko Bay were collected during April and May, and the samples from Nunavut, Canada, were collected between July and September. All samples were stored in salt saturated 20% DMSO and kept frozen until analysis in the laboratories.

Total DNA was extracted from the skin biopsy samples using commercially available DNA extraction kits (DNeasy®, Qiagen, E.Z.N.A. or GenElute™, Sigma-Aldrich). Molecular sex determination of all whales used a PCR-based approach as described by Berubé and Palsbøll (1996) or Shaw *et al.* (2003).

A stretch of the mitochondrial control region was amplified and sequenced as described by Rooney *et al.* (2001). The obtained nucleotide sequences were aligned and edited with the computer program Sequencher 4.1 (GeneCodes) and mitochondrial haplotypes were subsequently assigned to each individual. The obtained information on mitochondrial haplotype and sex allowed for a first prescreening of the sampled individuals with respect to potential recaptures. Same sex individuals with same haplotypes were furthermore compared with first four and then up to eight highly variable microsatellite loci (Heubinger *et al.* 2006) and alleles at all loci were compared for all samples to identify identical genotypes. Within year replicate samples were removed from further analysis.

RESULTS AND DISCUSSION

Sex was determined for 687 samples from a total of 710 biopsies collected from bowhead whales in Canada and Greenland from 1995 through 2009 (Table 1). A total of 110 re-identifications within the same year collected from Foxe Basin, Disko Bay and Cumberland Sound were removed from further analysis. Both the number of samples and the proportion of replicates increased dramatically after 2006 when the sampling in Disko Bay was stimulated by a reward given to the hunters.

Females made up 76% of the overall proportion of whales in Disko Bay when all years were combined and after removing within-year re-identifications. This was slightly lower than the estimate of 82% females for 2007 alone, the year with the largest sample size (n=93 biopsies). The most extreme case was 2006 when no males were detected out of 20 samples.

Northern Foxe Basin provided the largest sample size from Nunavut (n=214) with a sex ratio for all six years of 49% females. Smaller samples from Repulse Bay and Cumberland Sound had sex ratios of

44 and 45% females, respectively, and an even smaller sample from Pelly Bay (n=7) had a female proportion of 57% (Fig. 1).

The observed proportion of females in Disko Bay was significantly different from the expectation of equal proportions of males and females (G-test, $p < 0.001$, $G = 77.5$) but no significant differences from a 1:1 sex ratio were detected for Foxe Basin, Cumberland Sound, Pelly Bay or Repulse Bay ($p > 0.28$).

Despite the large number of whales that were taken along West Greenland in the 18th and 19th century, only two observations of newborns have been reported (Eschricht and Reinhardt 1861) indicating that this was not a major calving ground. In the 20th century there is only one reported observation of a mother and calf in Disko Bay from ca. 1920 (Knudsen 1983). During extensive aerial surveys conducted between 1981 and 2006 in West Greenland calves or immature whales have only been detected once on 25 April 2006 about 100 km west of the Greenland coast at 68°08'N 56°02'W (Heide-Jørgensen *et al.* 2007, David Boertmann, NERI, dmb@dmu.dk). Similarly observations made during field operations from 2000 to 2010 confirm that it is essentially adult whales (>14 m, with some whales >12 m) found in Disko Bay in spring (Heide-Jørgensen *et al.* 2002, 2006). A recent revival of Inuit subsistence hunting for bowhead whales in West Greenland in 2009-10 resulted in catches of five females and one male bowhead whale all >14 m confirming that it is primarily large mature females that are found in Disko Bay (Greenland Institute of Natural Resources, unpubl data).

Few calves have been reported from other areas of the Baffin Bay: Davis and Koski (1980) reported less than 3% (n=46 observations of whales) calves during fall aerial surveys of Lancaster Sound. In Isabella Bay (Fig. 1) Finley (1990) measured 83 bowhead whales with a mean length of 14.4 m on aerial photographs 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 confirm that mother-calf pairs and sub-adults were rarely seen along the east coast of Baffin Island in August. An aerial survey in September 2009 in Isabella Bay similarly revealed no sightings of immature whales (Hansen *et al.* in prep.). Results from

these studies strongly suggest that the bowhead whales occupying Baffin Bay and Davis Strait during summer and fall are mainly adults.

Disko Bay is an important feeding ground for bowhead whales (Laidre *et al.* 2007) but there are also indications from acoustic studies that Disko Bay, perhaps prior to when feeding begins, is also a mating ground. Intensive singing activity of bowhead whales with up to three unique songs were recorded in April 2007 (Stafford *et al.* 2008, Tervo *et al.* 2009). Singing is an activity that usually is attributed to male display in baleen whales and given most singing activity was recorded during spring it is plausible that mating between the relatively few males and the large fraction of females occurs in Disko Bay.

Disko Bay has a disproportionate number of adult female bowhead whales. This suggests that the whales observed in this area do not represent the whole stock. These whales are more likely a fraction of a larger population that temporarily segregates throughout the eastern Canadian high Arctic. With the increased abundance of bowhead whales in West Greenland (Heide-Jørgensen *et al.* 2007) it is also likely that a substantial number of whales must be migrants from other areas.

The main calf-producing fraction of the population can be found in the complex archipelago of the Canadian high Arctic. Historical whaling records clearly indicate that cows, calves, and sub-adult whales were taken in northwestern Hudson Bay from June through September (Reeves and Cosens 2003). Recent aerial photogrammetric and visual studies have shown that bowhead whales in Foxe Basin mainly consist of young-of-the-year calves and sub-adults, and the majority of adult individuals were believed to be cows with young-of-the-year calves (Cosens and Innes 2000, Cosens and Blouw 2003). Apparently there are few adult males and resting females in Foxe Basin and northwestern Hudson Bay, and no large assemblages of only adult whales have been reported within Hudson Bay and Foxe Basin. The biopsy samples from Foxe Basin shows an even sex ratio which is consistent with the assumption of a mixing ground for immature whales of both sexes and females with calves. The samples from Repulse

Bay suggest that this area is frequented by more males than females. The sample from Pelly Bay is too small to support the suggestion of the Gulf of Boothia being a nursing ground (Markham 1874, Southwell 1898, Finley 2001).

There is a slight preponderance of males (45%) in the Cumberland Sound samples that could account for the missing males in Disko Bay and that confirm Southwell's (op cit.) description of primarily males along east Baffin Island.

The bowhead whales exhibit large scale sexual segregation that is spatially defined rather than determined by behavioral or ecological factors. Traditionally sexual segregation in other vertebrates is explained by predation risk, forage selection or activity budgets (Ruckstuhl 2007). There are only few reports of killer whales in Disko Bay in winter and spring when bowhead whales are present in the bay and no other predators (aside from humans) could threaten bowhead calves in West Greenland. To a large extent different age and sex groups feed on the same types of prey (Calanoid copepods) and aside from migration patterns, that structures the sexual segregation, no obvious behavioral differences can convincingly explain why mature females choose to visit Disko Bay in spring and why mother and calves aggregate in Foxe Basin. From a habitat perspective Disko Bay differs from the other bowhead habitats by a much longer ice-free season (8 months vs. 2 months in Foxe Basin), much deeper water depths (400 m vs. <90m in Foxe Basin), and a more diverse marine production influenced by the warm West Greenland current of Atlantic origin. At the same time, the shallow and sheltered yet relatively unproductive waters of Foxe Basin may offer a refuge for young bowhead calves. The most parsimonious explanation for the seasonal occurrence of mature bowhead whales, most of which are females, in Disko Bay is the foraging opportunities offered by the rich production in the bay. Differences in seasonal feeding intensity of bowhead whales have also been observed in the Pacific population (Lee et al. 2005). The whales that visit Disko Bay in spring will benefit from a marine production and an abundance of copepods at the surface layers that exceeds what can be expected in other areas of the

range of bowhead whales (Laidre et al. 2007, Laidre et al. In Press). Post-lactating, pregnant or resting females will during short stays in the bay be able to regain fat depots that are otherwise difficult to maintain in the less productive Central Canadian Arctic Archipelago. Some of the females will be in estrous during their stay in the bay and some male bowhead whales follow these females. It is likely that the visits to Disko Bay are part of a multi-year reproductive cycle for the females where years with calving and nursing are spent in the Central Canadian Arctic Archipelago and where pregnant or post-lactating females feed intensively in the bay. That may explain the relatively low level of recaptures between years observed in Disko Bay (Wiig et al. in prep.).

In 1977, a two-stock hypothesis for bowhead whales occupying eastern Canadian and western Greenlandic waters was adopted as the working model of the IWC (Allen 1978). The stocks 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).

Given that bowhead whales from this stock 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 (IWC 2009), it is timely to re-assess the population structure of these whales in light of new information that has been collected. Heide-Jørgensen *et al.* (2006) suggested that the bowhead whales 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 individuals belonging to the two putative stocks.

The most reasonable explanation for the sex-segregation discussed in the present study is that bowhead whales summering in the eastern Canadian Arctic and wintering off the west coast of Greenland belong to just one population with those occupying Baffin Bay being mainly adult males and resting females and those in the Prince Regent, Gulf of Boothia, Foxe Basin and north-western Hudson Bay animals being nursing females, calves and sub-adults.

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Table 1. Sampling periods, number biopsies and fraction females in the samples without within-year re-identifications for each of 5 localities in West Greenland and Canada where bowhead whales were sampled.

Area/Year	Range of dates	Biopsies analyzed	Number with sex determinations	Re-identifications within year	Fraction females (re-identifications removed)
Disko Bay					
2000	22-28/4	7	7	1	0.17
2001	28/4-8/5	13	13	1	0.58
2002	4/5-13/5	10	10	0	0.60
2003	4/5-18/5	10	10	0	1.00
2004	6/5	1	1	0	1.00
2005	11/3-3/5	25	25	1	0.71
2006	15/4-6/5	24	24	4	1.00
2007	10/3-17/5	157	156	63	0.82
2008	20/4-3/6	65	61	16	0.78
2009	16/2-4/6	69	69	19	0.60
Sum		377	376	105	0.76
Pelly Bay					
2000	September	1	1	0	0.00
2001	September	1	1	0	1.00
2002	September	5	5	0	0.60
Sum		7	7	0	0.57
Foxe Basin					
1994	August	1	1	0	1.00
1995	August	11	11	0	0.73
1996	4-6/7	20	20	0	0.40
1997	August	2	2	0	1.00
2001	30 /6-6/7	41	41	1	0.43
2002	1-15/7	65	64	3	0.41
2003	August	32	32	0	0.69
2007	July	44	35	0	0.46
Sum		216	206	4	0.49
Repulse Bay					
1995	September	1	1	0	0.00
1997	Aug.-Sept.	5	5	2	0.67
1998	September	5	4	0	0.25
2000	September	4	4	0	0.75
2001	September	3	3	0	0.00
2005	September	1	1	0	1.00
Sum		19	18	2	0.44
Cumberland Sound					
1997	June to August	21	21	2	0.37
2002	June to August	9	8	0	0.63
2004	June to August	8	8	0	0.63
2005	June to August	17	17	0	0.47
2006	June to August	31	31	1	0.40
Sum		85	85	3	0.45

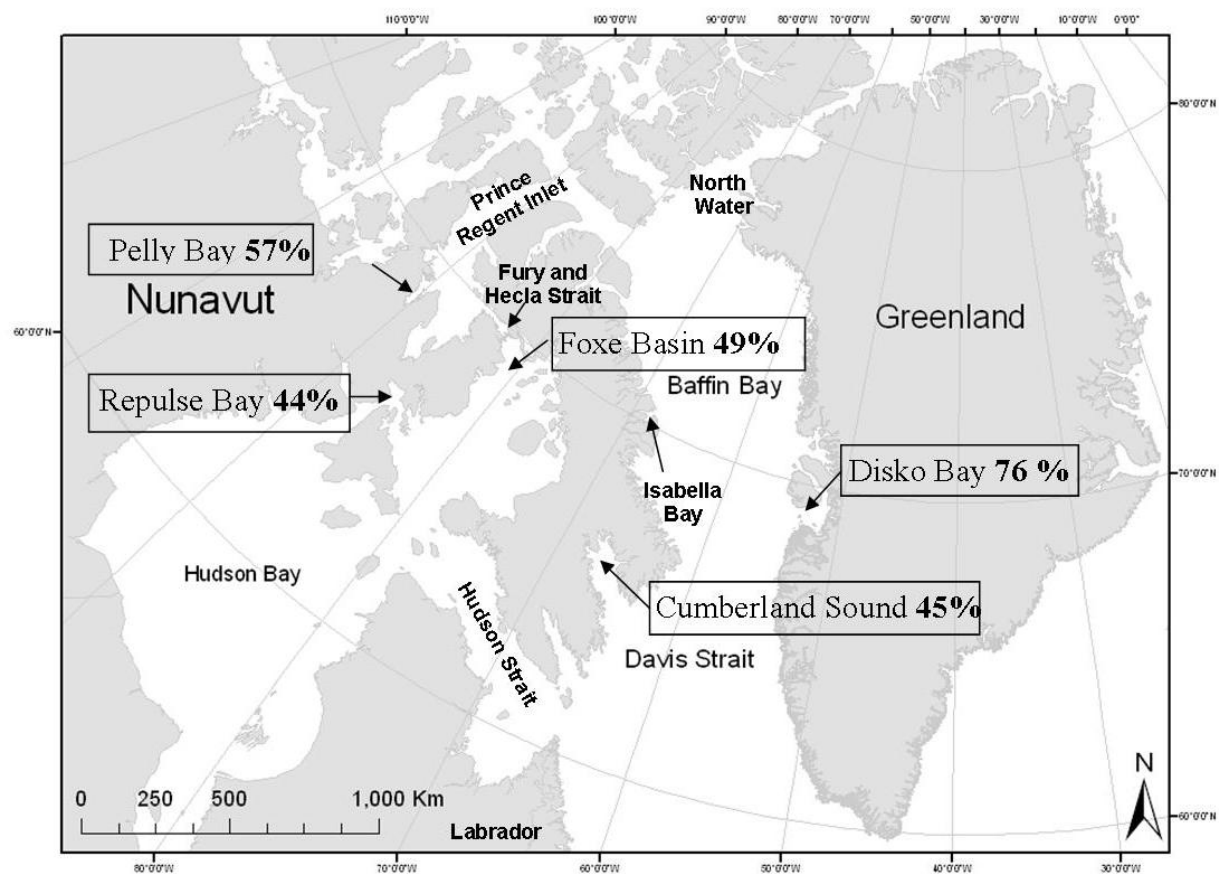


Fig. 1. Map of the localities where the bowhead whales were sampled and the percentage of females at each of these localities.