

DISSOLVING STOCK DISCRETENESS WITH SATELLITE TRACKING: BOWHEAD WHALES IN BAFFIN BAY

M. P. HEIDE-JØRGENSEN

K. L. LAIDRE

Greenland Institute of Natural Resources,
c/o Danish Polar Center,
Strandgade 100H, DK-1401 Copenhagen K, Denmark
E-mail: mhj@dpc.dk

M. V. JENSEN

Mikkels Værksted,
Gislingevej 2, DK-4571 Grevinge, Denmark

L. DUECK

L. D. POSTMA

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

ABSTRACT

Nine bowhead whales (*Balaena mysticetus*) were instrumented with satellite transmitters in West Greenland in May 2002 and 2003. Transmitters were either encased in steel cans or imbedded in floats attached to wires. Transmitters mounted in steel cans had a high initial failure rate, yet those that were successful provided tracking durations up to seven months. Float tags had a low initial failure rate and initially provided large numbers of positions; however, they had deployment durations of only 2–33 d. All tracked whales departed from West Greenland and headed northwest towards Lancaster Sound in the end of May. Three tags with long tracking durations (197–217 d) recorded movements of whales (1♂, 2♀) into December in 2002 and 2003. All of these individuals remained within the Canadian High Arctic or along the east coast of Baffin Island in summer and early fall. By the end of October, all three whales moved rapidly south along the east coast of Baffin Island and entered Hudson Strait, an apparent wintering ground for the population. One of the whales did not visit Isabella Bay on east Baffin Island, the locality used for abundance estimation from photographic reidentification of individuals. The movements of whales tagged in this study raise critical questions about the assumed stock discreteness of bowhead whales in Foxe Basin, Hudson Strait, and Davis Strait and indicate current estimates of abundance are negatively biased.

Key words: bowhead whale, *Balaena mysticetus*, satellite tracking, stock identification, West Greenland, Canadian High Arctic.

Following the definition suggested by Ihssen (1981), a stock of cetaceans can be defined as a subpopulation or "an intraspecific group of randomly mating individuals with temporal or spatial integrity" that are subject to some level of exploitation. However, the delineation of stocks of large cetaceans remains a complicated and controversial issue. Assessment and management of cetaceans requires knowledge about population structure and, because little information is available for most large whale populations, with the possible exception of gray whales (*Eschrichtius robustus*) or North Atlantic humpback whales, (*Megaptera novaeangliae*), many management decisions with respect to stock identification are based on assumptions or limited genetic data. For some species obvious inferences can be made based on separation by continents or oceans; however, for most species stock boundaries are both irregular and difficult to discern either because whales occur in a continuum in the open oceans or because movements take place in complex coastal areas. One example of the latter is the bowhead whale (*Balaena mysticetus*) that ranges in the complex archipelago of the Canadian High Arctic, Foxe Basin, Hudson Bay, Hudson Strait, Baffin Bay, and Davis Strait.

Bowhead whales in the Northwest Atlantic are currently considered as two stocks: the Davis Strait-Baffin Bay stock and the Foxe Basin-Hudson Bay stock, recognized by the International Whaling Commission (IWC 1978, 1992). The main rationale behind the stock delineation was the separation of summering areas in Baffin Bay (and adjacent sounds in the High Arctic) and Foxe Basin, and the assumption that baleen whales, in general, make seasonal north-south movements rather than east-west movements, so exchange between summering populations was considered unlikely. This stock delineation was adopted despite the fact that information from historic whaling activities did not support a division into two stocks (Southwell 1898). No scientific evidence has been presented confirming the separation of these two stocks, yet photographic and satellite tracking studies link bowhead whales between West Greenland and the east coast of Baffin Island (Heide-Jørgensen and Finley 1991, Heide-Jørgensen *et al.* 2003a).

Bowhead whales in Canada and eastern Baffin Bay are assumed to spend the winter in Hudson Strait, northern Hudson Bay, or along the pack-ice edge extending to coastal West Greenland (Reeves and Heide-Jørgensen 1996; Koski *et al.*, in press). Low numbers of bowhead whales may also be found in winter in the North Water and in polynyas along the east coast of Baffin Island (Richard *et al.* 1998; Koski *et al.*, in press). In spring, bowhead whales are found along the West Greenland coast (primarily Disko Bay), in Hudson Strait, Cumberland Sound, and the entrance to Lancaster Sound. Satellite tracking studies of bowhead whales instrumented in Disko Bay have revealed that at the end of May whales cross Baffin Bay from Disko Bay (at approximately 72°N) to Lancaster Sound (Heide-Jørgensen *et al.* 2003a), yet where they go after this spring migration has, up to this point, been unknown. During the summer, bowhead whales are known to be widely distributed in the fjords and bays of the Canadian High Arctic, in Hudson Bay, and in the shallow waters of Foxe Basin (Cosens *et al.* 1997, Cosens and Innes 2000). In fall, whales along Baffin Island have been thought to move south along the east coast of Baffin Island or cross over to the West Greenland coast, appearing there in September and October (Reeves *et al.* 1983), whereas whales in Foxe Basin are thought to move south and east and winter in Hudson Strait.

The stock identity of bowhead whales in Baffin Bay-Davis Strait and Foxe Basin-Hudson Bay is of particular interest because of renewed subsistence bowhead hunting in Canada where different quotas exist for each of the two areas (Finley 2001). For

effective management, there is a need for robust information that can be used to support or reject the current stock separation of bowhead whales in Baffin Bay-Davis Strait and Foxe Basin-Hudson Bay. This study presents evidence collected from satellite tracking data to provide insight into the stock discreteness of bowhead whales in these areas.

METHODS

Daily searches for whales were conducted from four small boats between 4–13 May 2002 and 4–18 May 2003 near the town of Qeqertarsuaq, Disko Island, West Greenland. When a whale was spotted, the boat moved toward it until the next dive. While it was underwater, two to four boats spread out to search for the next surfacing location. The process was repeated until the whale was surfacing in a predictable manner, which usually took less than half an hour. Then the whale was approached and instrumented with a satellite transmitter using an 8-m long fibreglass pole (within 4–5 m). A skin biopsy was taken for genetic studies either with the pole (using a 10-mm hollow cylinder, 28 mm in length with internal barbs) or a crossbow.

To test the performance of the tags, two different configurations of satellite-linked radio transmitters were deployed (SPOT2 and SPOT3 transmitters, Wildlife Computers, Redmond, WA). In one configuration, transmitters were mounted in a stainless steel can (referred to as “can tags”) with a bottom-mounted anchor device. The “can” dimensions were 45 × 32 mm and they had two lithium thianyl batteries. The anchor was a 33-cm titanium spear (diameter 8 mm) equipped with three foldable leaf-like barbs and a sharp pointed tip. In the second configuration the transmitter and lithium C-cell battery were imbedded in a torpedo-shaped float (referred to as “float tags,” 28 × 8 cm). The float tags were tethered to the whale with a 1.5-m stainless steel wire attached to the anchor. Two different types of anchoring systems were used for the float tags: a titanium anchor (similar to the one used for the can tags) or a flat stainless steel anchor configured into a harpoon head, imitating that traditionally used by Inuit hunters. The can tags were mounted on the tip of the pole secured by a nylon line in case of missed attempts. When the can tag was securely anchored in the whale, the nylon line was cut by a sharp edge on the pole. The float tags had an anchoring system at the tip of the pole and were held in a PVC tube-shaped housing on the side of the pole. The housing was designed to release the float after the anchor was placed on the whale and the tether pulled the tag from the housing. Tags were deployed only when the whale remained at the surface long enough to place the tag in a good position. The float tags had an expected longevity of 100,000 transmissions and were programmed to provide an unrestricted number of transmissions. The can tags had an expected longevity of 20,000 transmissions and were programmed to provide transmissions every other day.

Locations were collected using the Argos System (see Harris *et al.* 1990). Location qualities were provided by Service Argos and coded based on predicted accuracy. Location codes were LC B, A, and 0–3 in order of increasing accuracy of position. All location qualities were used to calculate an average daily position for each whale over the entire tracking period.

Total DNA was extracted from the skin biopsy samples using a commercial tissue extraction kit (DNeasy, Qiagen). The sex of all whales was then determined using a PCR-based method for the identification of sex in cetaceans (Bérubé and Palsbøll 1996). This method amplifies ZFX- and ZFY-specific regions of nuclear DNA that

results in a product that corresponds to a portion of the X chromosome and a product specific to the Y chromosome (if present). Separation and visualization of these products on an agarose gel allows for the reliable assignment of sex.

RESULTS

Instrumentations

Between 4 and 13 May 2002, bowhead whales were observed on a daily basis in northwest Disko Bay. Six bowheads were tagged during this period and all whales were between 12 and 18 m long (Table 1). Four whales were instrumented with float tags and two were instrumented with can tags. Two additional float tags provided data for only 3–6 d and were therefore not included in the analysis. The average deployment time for the float tags with harpoon heads was 13 d ($n = 4$) and for the titanium spears 21 d ($n = 2$). The two can tags lasted 9 and 197 d, respectively. In a few cases the float tags continued to provide positions for an extended period after they came off the whales, and the date of attachment failure was determined by examining the number and quality of ARGOS positions each day. There was often a conspicuous increase in the frequency of good-quality positions when the tags were no longer attached to whales and were floating at the surface. Skin biopsies were collected from 10 whales (four males and six females) in 2002, including four of those that were instrumented with transmitters.

In May 2003 whales were sighted continuously between 4 and 18 May. Three whales (all > 15 m) were instrumented with can tags that were programmed to provide positions every other day. The can tags lasted between 81 and 217 d. Two of these lasted until 13 December 2003, or approximately 7 mo. Skin biopsies were collected from 11 whales in 2003 and all were determined to be females. No positive resightings of whales in any year allowed for examination of skin reactions to tag attachment.

Movement Patterns

After tagging, whales remained in Disko Bay until as late as 21 May. In both years, all tagged whales departed from Disko Bay at the end of May and travelled northwest across Baffin Bay. Some whales took a direct route from Disko Island towards Bylot Island while others took a route farther north; however all travelled in the same general NW direction within a relatively defined corridor (Fig. 1A). The whales reached the northern part of Baffin Bay in June and remained in a localized area northeast of Bylot Island. Contact was lost with all but three whales during this month.

Three tags lasted beyond June and provided the first documentation of movements of bowhead whales after arrival off the Bylot Island/Lancaster Sound area (Fig. 1B). In July the three whales headed south to latitude 71°N about 100 km off Baffin Island, perhaps avoiding heavy ice. One male whale tagged in 2002 turned north in August, and moved quickly north along the coast of Baffin Island. The whale reached Admiralty Inlet in the latter half of August and remained stationary in the southwestern part of the Inlet through to the end of August. The whale then moved north to Barrow Strait in mid-September and made localized movements near Cornwallis Island for three weeks, through 3 October. The whale moved east after

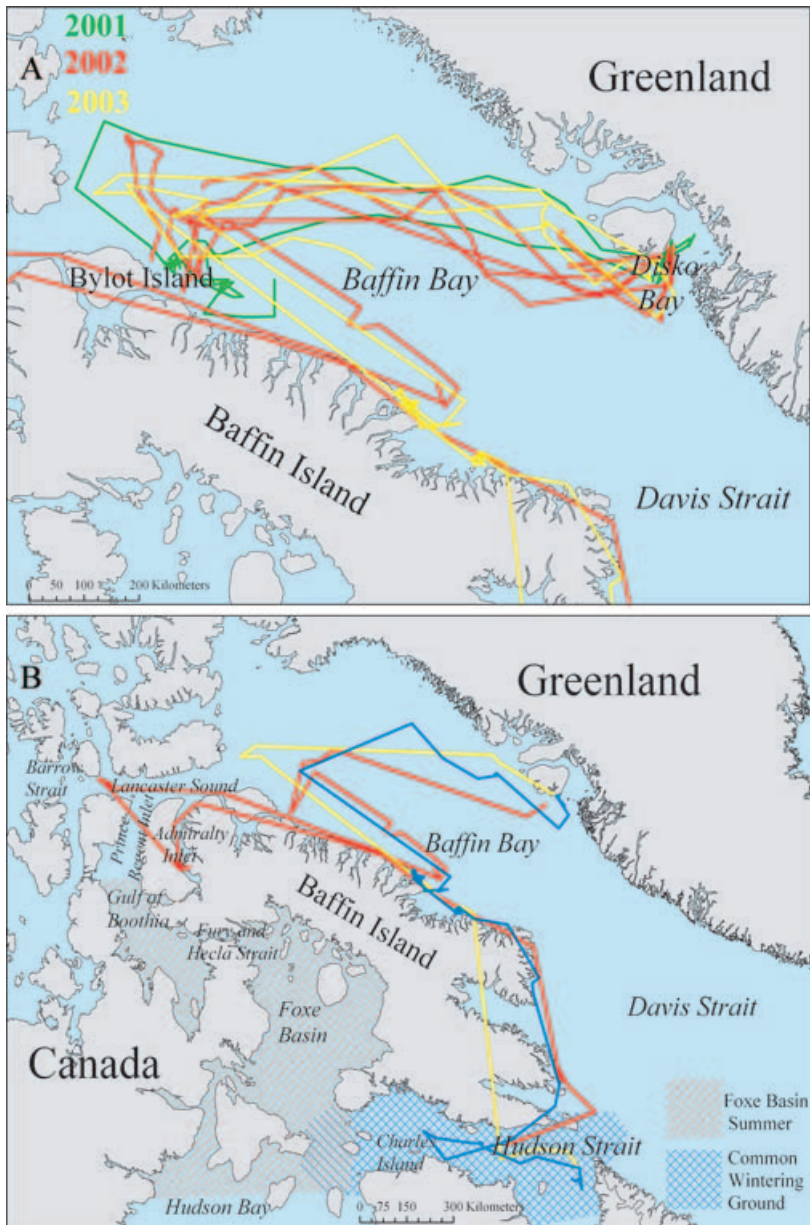


Figure 1. (A) Tracks of nine bowhead whales that were tagged in Disko Bay in May 2002 and 2003. Positions are based on daily averages of all quality classes. Data for two whales from 2001 are from Heide-Jørgensen *et al.* 2003a. (B) Tracks of three bowhead whales that provided positions through mid-November (red, whale 20160) and through mid-December (blue, whale 20688-03 and yellow, whale 20696). Distances travelled by one male bowhead whale (20160) tracked in 2002 was at least 5,888 km; travel distance of two females tagged in 2003 was 2,452 km (20688-03) and of 1,730 km (20696). The summering area in Foxe Basin and the common wintering ground in Hudson Strait are indicated. Gulf of Boothia is included in the summer range of bowhead whales from Foxe Basin based on recent data from satellite tracking (Dueck, unpublished data).

7 October and travelled out of Lancaster Sound and south along Baffin Island. During this time, the whale moved quickly, and there were no extended pauses in any region along the coast of Baffin Island. The whale reached the southeastern corner of Baffin Island on 31 October, and by 17 November moved into Hudson Strait one-third of the way to Hudson Bay where it remained until contact was lost. This individual travelled at least 5,888 km at an average speed of 38 km/d. Movement speed showed considerable variability depending on where the whale was located.

Between 1 and 10 August, after making localized movements off the coast of Bylot Island, two female bowhead whales tagged in 2003 moved into Isabella Bay on the east coast of Baffin Island. They spent about 50 d in this area before heading south in September to the southern part of Home Bay, where they spent two weeks (29 September to 15 October). These two individuals continued south to Hudson Strait where they arrived between 7 and 25 November. One of them moved as far west as Charles Island (11 November) in the western part of Hudson Strait. This whale later moved east to the eastern part of Ungava Bay where contact was lost on 13 December 2003. Using average daily positions the two whales travelled 1,730 and 2,452 km, respectively, over a period of 7 mo.

DISCUSSION

Performance of Tags

This was the first study to attach tethered float tags to cetaceans and the results were mixed. Positive aspects of the float tag method included a low initial failure rate and many more daily positions than can tags, ultimately providing more detail about the local movements of the whales. None of the float tags failed immediately after deployment, which was the case for some can tags. The float tags did, however, come off the whales relatively soon, after 3–33 d. This may have been due to the attachment system or greater vulnerability of the float tag to stress created by drag on the tethering system, perhaps in combination with social encounters or interactions with ice or the bottom.

Three can tags performed well and provided positions over 200 d, clearly exceeding the duration of all float tags and other similar instruments that have been deployed previously on bowhead whales (Mate *et al.* 2000, Heide-Jørgensen *et al.* 2003a). The three can tags most likely had drained their batteries by the time they stopped transmitting (after approximately 200 d voltage readings declined), and the end of tag transmissions did not appear to be due to attachment failure. Two can tags failed prematurely, because of poor implantation of the tag in the blubber, improper placement of the tag on the back of the whale (positioned too low for transmissions), or failure of the transmitter itself. It is assumed that all tags eventually came off the whales.

Spring Migration Schedule

Eschricht and Reinhardt (1861) collected information on the time of departure (latest spring observations) of bowhead whales from Qeqertarsuaq from 1780 to 1837. Their mean date for the last observations of whales in the area was 1 June, with a range from April 26 to June 25. The whales that were tracked in our study left Disko Bay between 10 and 21 May corresponding well with the >200-yr-old observations of

departure. Apparently the bowhead whales in Disko Bay still maintain their historical patterns of movement timing in spite of the severe reduction in numbers. This supports the idea that bowhead whales have a strict temporal migratory schedule, at least for part of the year, as this timing has been maintained over centuries perhaps in response to seasonal changes in ice cover and marine productivity.

A relatively good sample size of tracked animals from a small population collected over several years should ideally capture the overall movement patterns of the population, assuming individual variability is low. The relative consistency of movement patterns of the nine whales tracked in this study suggest that only a few individuals enable documentation of the timing and the route of the migration and are sufficient for identifying affinities to certain areas. Observed variation in departure dates and visited localities appeared to be related to gender. This, however, requires further study with larger and more evenly distributed sample sizes of each gender across several years.

Timing and Patterns of Movements

The initial data collected in this study confirm results from previous satellite tracking studies in Disko Bay, as whales tagged in 2001 also departed in late May and rapidly crossed the heavy pack-ice in central Baffin Bay (Heide-Jørgensen *et al.* 2003a). The traverse of Baffin Bay likely requires that whales move north along the West Greenland coast until they find a lead that intersects Baffin Bay running northwest to southeast, facilitating open water availability during the relatively short time span the whales cross to northern Canada.

Once the whales have crossed the Baffin Bay pack ice, open water is available in the North Water polynya or off Bylot Island, the area known by the whalers as “Ponds Bay” (*e.g.*, Markham 1874). Davis and Koski (1980) suggested that after the period in Ponds Bay, whales awaited the break up of fast ice in Lancaster Sound and then moved towards their summering grounds in the Canadian High Arctic. The data collected in this study did not support this hypothesis and instead demonstrated that whales stayed offshore and moved south along Baffin Island through July and into August. In August, the male from 2002 did indeed move into Lancaster Sound, yet was only in the vicinity of this area for <4 wk before moving south. In August the females tracked in 2003 remained along the coast of Baffin Island and used the well known bowhead whale locality of Isabella Bay (Finley 1990).

It is interesting to note that the male whale passed along the east coast of Baffin Island two times—in early summer and again in the autumn. On neither occasion did this individual visit Isabella Bay, identified as a “major congregation site” for Baffin Bay bowhead whales (Finley 1990). Isabella Bay also happens to be the area where bowhead population abundance estimates are obtained based on mark-recapture estimates from photo-identification (Zeh *et al.* 1993). If only a proportion of Baffin Bay bowhead whales visit Isabella Bay then abundance estimates in this area are negatively biased to an unknown extent.

Implications for Stock Identification

Despite having chosen different summering locations, the three whales chose to winter in Hudson Strait at approximately the same time (mid-November). The fact that all three whales moved into this area in late fall suggests that this may be an important wintering ground for Baffin Bay bowhead whales. Southwell (1898) and

Brown (1868) indicated Hudson Strait was a wintering area for bowheads based on whaling records, and recent analysis of aerial surveys of Hudson Strait (conducted during March 1981) provided an abundance estimate of 1,272 (95% CI 484–3,346) whales, evidently the largest winter abundance of bowhead whales found in the Northwest Atlantic sector of the Arctic (Koski *et al.*, in press). Wintering bowhead whales have also been found at other localities in Baffin Bay, however, at lower densities which clearly do not constitute the bulk of the population.

It is important to note that Hudson Strait is also thought to be the wintering ground for bowhead whales from Foxe Basin and Hudson Bay. Thus, the identification of Hudson Strait as a wintering ground for Baffin Bay whales raises the question about the discreteness between these two areas. The distance to northern Foxe Basin from Hudson Strait is about 700 km, no more than a few days travel for a bowhead whale. In winter, bowhead whales are found throughout Hudson Strait and northern Hudson Bay (Reeves and Mitchell 1990), and in summer bowhead whales are observed in a continuum throughout Prince Regent Inlet, the Gulf of Boothia, Fury and Hecla Strait, Foxe Basin, and northern Hudson Bay (Cosens *et al.* 1997, Cosens and Innes 2000). Movements of bowhead whales from Foxe Basin have been recently documented by satellite tracking both northward into Prince Regent Inlet and southward to northern Hudson Bay (Dueck, unpublished data). Considering the wide-ranging capabilities of bowhead whales and this shared occurrence during winter, it seems plausible that bowhead whales from the two presumed stocks share a common wintering area with a high likelihood of genetic exchange. The significance of this result calls into question the discreteness of the presently defined stock separation between bowhead whales in Baffin Bay, Foxe Basin, and Hudson Bay.

The results of this study also demonstrate that bowhead whales found far west inside the northern Canadian High Arctic (up to 95°W) are the same whales found in Hudson Strait in winter. This suggests connectivity between bowhead whales at extreme distances across Arctic waters, with implications for bowhead whale populations elsewhere. Given the rapid travel speed across the dense Baffin Bay pack ice and the thousands of kilometres traversed by individuals over a mere 7 mo of tracking, bowhead whales apparently have the potential to cross stock boundaries perhaps not anticipated when they were established based on historic whaling data or the “conventional wisdom” of a mainly north-south migration of baleen whales (Gaskin 1982).

The whale that moved to 95°W in Barrow Strait was located at a position half-way between West Greenland and the Mackenzie Delta in the Beaufort Sea in September, the summering area for the Bering Sea stock of bowhead whales. The Northwest Passage that connects Baffin Bay with the Beaufort Sea is usually obstructed by dense pack ice. To date, there is no scientific evidence of bowhead whales traversing this ice, yet the potential for exchange between these areas is present. Historical evidence suggests that, in fact, whales have exchanged between these two areas (Clark 1887).

This study demonstrates the great potential for satellite tracking to address questions about cetacean stock identity. Genetic studies of mtDNA sequencing and nuclear DNA microsatellite analyses indicate a weak differentiation between bowhead sampled in Hudson Bay/Foxe Basin and Baffin Bay/Davis Strait (L. Postma, unpublished data). However, this picture is constantly evolving as sample sizes increase, introducing new patterns in mtDNA haplotypes and haplotype distributions. Interpreting genetic data is complicated by restriction of samples to spring and summer, clustering of groups of related individuals, segregation of sex and age classes, and lack of samples from Prince Regent Inlet, Lancaster Sound, or the east coast of Baffin

Island. Thus, strong arguments for stock identity based on molecular genetic data alone are difficult to make.

The stock division appears to have been originally proposed in IWC as a conservative measure (IWC 1978, 1992), despite the fact that no data supported the division except the simultaneous occurrence of bowhead whales in two different areas in summer. Furthermore, the catch history did not support this division (Woodby and Botkin 1993). Davis Strait and Baffin Bay bowhead whales were the first to be exploited in the late 17th century, and after 1860 whales in this region were depleted, forcing whalers to move to Hudson Bay and in the ice of southwestern Foxe Basin occasionally with steam powered vessels. What is exceptional about this switch is that relatively few catches were made when whalers moved to Hudson Bay/Foxe Basin after depleting whales in Baffin Bay, even though no whaling had ever occurred in Hudson Bay/Foxe Basin. Therefore, despite no direct effort in the Foxe Basin area, this region was somehow depleted to similar levels as those in Baffin Bay implying some connection between the two areas. If this was not the case, one would have expected whalers to find whales in higher densities and catch whales in larger numbers, or at least comparable numbers to the pristine conditions of Baffin Bay before depletion.

No other methods offer such direct insight into the movement patterns of cetaceans as satellite tracking of individual whales. Although genetic studies have been used to determine movement rates and exchange between populations, they have in the past been directly contradicted by satellite tracking studies of individuals from genetically differentiated populations (*e.g.*, Heide-Jørgensen *et al.* 2003*b*). One of the major challenges with satellite tracking is that in some cases, especially with large cetaceans, large sample sizes may be difficult to obtain over a short time frame. This is, however, compensated by the fact that documentation of movements of individuals is of lasting and cumulative value and can be used for a complete over-all picture of migration patterns over many years. Baleen whale migrations have evolved over millennia and have in several cases been documented to show limited variability for nearshore stocks. Consequently, there is no reason to expect higher variability in movement patterns of other offshore or unstudied populations. This study illustrates such a scenario for bowhead whales, a species in which individuals can live for more than two centuries (George *et al.* 1999), and one that has evidently followed the same movement patterns and migration timing as those observed centuries ago.

ACKNOWLEDGMENTS

We wish to thank K. Mølgård, A. Brandt, K. Heilmann, S. K. Broberg, and F. Broberg for their excellent help during the search, pursuit, and tagging of the bowhead whales. Tags were developed by Wildlife Computers and modified by M. V. Jensen. The field work benefited from the assistance of Y. Geyer, A. V. Jensen, and K. Krogh. The board of the Arktisk Station, University of Copenhagen, is acknowledged for providing the facilities at Arktisk Station including the research vessel *Porsild*. This study was funded by the Greenland Institute of Natural Resources, the Carlsberg Foundation, and the Department of Fisheries and Oceans, Canada. Comments and critiques on this report were kindly provided by Phil Clapham and an anonymous reviewer.

LITERATURE CITED

- BÉRUBÉ, M., AND P. PALSBOÛLL. 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. *Molecular Ecology* 5:283–287.

- BROWN, R. 1868. Notes on the history and geographical relations of the Cetacea frequenting Davis Strait and Baffin's Bay. *Proceedings Zoological Society of London* 1868:533–556.
- CLARK, H. 1887. The whale fishery. In G. B. Goode, ed. *The fisheries and fishery industries of the United States*. V. History and methods of the fisheries. Government Printing Office, Washington, DC.
- COSENS, S. E., AND S. INNES. 2000. Distribution and numbers of bowhead whales (*Balaena mysticetus*) in Northwestern Hudson Bay in August 1995. *Arctic* 53:36–41.
- COSENS, S. E., T. QAMUKAQ, B. PARKER, L. P. DUECK AND B. ANADJUAQ. 1997. The distribution and numbers of bowhead whales, *Balaena mysticetus*, in northern Foxe Basin in 1994. *Canadian Field-Naturalist* 111:381–388.
- DAVIS, R. A., AND W. R. KOSKI. 1980. Recent observations of the bowhead whale in the eastern Canadian High Arctic. Report of the International Whaling Commission 30:439–444.
- ESCHRICHT, D. F., AND J. REINHARDT. 1861. Om Nordhvalen (*Balaena mysticetus* L.) navnlig med Hensyn til dens Udbredning i Fortiden og Nutiden og til dens ydre og indre Saerkjender. K. Danske Videnskabernes Selskabs Skrifter. Series 5, naturvidenskabelig og matematisk Afdeling 5:433–590.
- 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.
- GASKIN, D. E. 1982. The ecology of whales and dolphins. Heinemann, London, UK.
- GEORGE, J. C., J. BADA, J. ZEH, L. SCOTT, S. E. BROWN, T. O'HARA AND R. SUYDAM. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Canadian Journal of Zoology* 77:571–580.
- HARRIS, R. B., S. G. FANCY, D. C. DOUGLAS, G. W. GARNER, S. C. AMSTRUP, T. R. MCCABE AND L. F. PANK. 1990. Tracking wildlife by satellite: Current systems and performance. United States Department of the Interior, Fish and Wildlife Service, Fish and Wildlife Technical Report 30. 52 pp.
- HEIDE-JØRGENSEN, M. P., AND K. J. FINLEY. 1991. Photographic reidentification of a bowhead whale in Davis Strait. *Arctic* 44:254–256.
- HEIDE-JØRGENSEN, M. P., K. LAIDRE, Ø. WIIG, M. V. JENSEN, L. DUECK, L. D. MAIERS, H. C. SCHMIDT AND R. C. HOBBS. 2003a. From Greenland to Canada in ten days: Tracks of bowhead whales, *Balaena mysticetus*, across Baffin Bay. *Arctic* 56:21–30.
- HEIDE-JØRGENSEN, M. P., P. RICHARD, R. DIETZ, K. L. LAIDRE AND J. ORR. 2003b. An estimate of the fraction of belugas (*Delphinapterus leucas*) in the Canadian High Arctic that winter in West Greenland. *Polar Biology* 23:318–326.
- IHSSEN, P. E., H. E. BOOKE, J. M. CASSELMAN, J. M. MCGLADE, N. R. PAYNE AND F. M. UTTER. 1981. Stock identification: Materials and methods. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1838–1855.
- IWC 1978. Report of the Scientific Committee. Report of the International Whaling Commission 28:38–92.
- IWC 1992. Report of the Scientific Committee. Report of the International whaling Commission 42:51–270.
- KOSKI, W. R., M. P. HEIDE-JØRGENSEN AND K. LAIDRE. In press. Winter abundance of bowhead whales, *Balaena mysticetus*, in Hudson Strait, March 1981. *The Journal of Cetacean Research and Management*.
- MARKHAM, A. H. 1874. A whaling cruise to Baffin's Bay and the Gulf of Boothia in the whaler *Arctic* commanded by Captain Adams. Low and Searle, London, UK.
- MATE, B. R., G. K. KRUTZIKOWSKY AND M. WINSOR. 2000. Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi seas during the late-summer feeding season and fall migration. *Canadian Journal of Zoology* 78:1168–1181.
- REEVES, R. R., AND M. P. HEIDE-JØRGENSEN. 1996. Recent status of bowhead whales, *Balaena mysticetus*, in the wintering grounds off West Greenland. *Polar Research* 15:115–125.

- REEVES, R. R., AND E. MITCHELL. 1990. Bowhead whales in Hudson Bay, Hudson Strait, and Foxe Basin: A review. *Canadian Field-Naturalist* 117:25–43.
- REEVES, R., E. MITCHELL, A. MANSFIELD AND M. MCLAUGHLIN. 1983. Distribution and migration of the bowhead whale, *Balaena mysticetus*, in the Eastern North American Arctic. *Arctic* 36:5–64.
- RICHARD, P. R., J. R. ORR, R. DIETZ AND L. DUECK. 1998. Sightings of belugas and other marine mammals in the North Water, late March 1993. *Arctic* 51:1–4.
- SOUTHWELL, T. 1898. The migration of the right whale (*Balaena mysticetus*). *Natural Science* 12:397–414.
- WOODBY, D. A., AND D. B. BOTKIN. 1993. Stock sizes prior to commercial whaling. Pages 387–407 in J. J. Burns, J. J. Montague and C. J. Cowles, eds. The bowhead whale. Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS.
- ZEH, J. E., C. W. CLARK, J. C. GEORGE, D. WITHROW, G. M. CARROLL AND W. R. KOSKI. 1993. Current population size and dynamics. Pages 409–489 in J. J. Burns, J. J. Montague and C. J. Cowles, eds. The bowhead whale. Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS.

Received: 26 November 2004

Accepted: 22 April 2005