NATURAL HISTORY MUSEUM OF DENMARK
FACULTY OF SCIENCE
The PhD School of Science
UNIVERSITY OF COPENHAGEN

Acoustic behaviour of bowhead whales *Balaena mysticetus* in Disko Bay, Western Greenland

PhD thesis by

Outi Tervo

Academic advisor: Prof. Reinhardt Møbjerg Kristensen D.Sc.

Submitted: April 2011

ARCTIC STATION
UNIVERSITY OF COPENHAGEN

Acoustic behaviour of bowhead whales *Balaena mysticetus* in Disko Bay, Western Greenland

PhD thesis

by

Outi Maria Tervo

Supervisors: Dr. Reinhardt Møbjerg Kristensen, PhD
Dr. Susan E. Parks, PhD

Arctic Station
Natural History Museum of Denmark
The PhD School of Science, Faculty of Science, University of Copenhagen, Denmark

Data sheet

Title: Acoustic behaviour of bowhead whales *Balaena mysticetus* in Disko Bay, Western Greenland

Subtitle: PhD Thesis

Author: Outi Maria Tervo

Affilitations: Arctic Station, Faculty of Science, University of Copenhagen, Denmark and Natural History Museum of Denmark, Faculty of Science, University of Copenhagen, Denmark

Supervisor: Reinhardt Møbjerg Kristensen, PhD; Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark and Susan E. Parks, PhD; Applied Research Laboratory, Pennsylvania State University, P.O. Box 30, State College, PA 16804-0030, USA

Key words: bowhead whale, bioacoustics, acoustic behaviour, song, mate choice, Disko Bay, Greenland

Frontpage photo: Peter Westy Henriksen

Chapter title photos: Qeqertarsuaq bowhead whale research group

Printed by: ASC-Grafisk, University of Copenhagen

Number of pages: 132

Circulation: 50

Internet version: Available in electronic format (pdf) at the Arctic Station website

CONTENT

Tervo, O.M., Christoffersen, M.F., Ilmoni, C.I. and Kristensen R.M.Rare sighting of a bowhead whale calf (*Balaena mysticetus*) in Disko Bay, Western Greenland. (manuscript in prep.)

Thesis overview

This thesis represents the partial fulfilment of the requirements for the degree of Doctor of Philosophy (Ph.D.) at the Faculty of Science, University of Copenhagen, Denmark.

The main goal of this thesis is to describe the acoustic behaviour of bowhead whales *Balaena mysticetus* in Disko Bay, Western Greenland, using passive acoustic recordings coupled with behavioural observations and biopsy to better determine the function of these sounds. The data is used to 1) describe the bowhead whale acoustic repertoire (Papers I and II); 2) describe seasonal and annual trends in sound use (Papers I and II); 3) document some of the vocalisation capabilities of singing bowhead whales (Paper III); 4) estimate the source level of the bowhead whale song and the active space of this display (Paper IV); and finally 5) determine the gender of the individual producing songs (Paper V).

This thesis consists of seven manuscripts of which two are published in peer reviewed journals (Papers I and II), two are in review in peer reviewed journals (Papers III and V) and one is prepared for submission (Paper IV). The last two unpublished manuscripts are a note (Appendix) and a review on the acoustic displays of baleen whales which puts my findings into a broader context.

I have collected acoustic, biopsy and behavioural data, analysed the acoustic and behavioural data, and I am the first author on all the manuscripts. I have functioned as an external supervisor for BSc student Louise Normann Jensen, University of Copenhagen, and held the position of the scientific leader at the Arctic Station, University of Copenhagen, during my PhD. This study was funded by A.P. Møller og Hustru Chastine Mc-Kinney Møllers Fond til almene Formaal, Oticon Fonden and Arctic Station, University of Copenhagen.

Qeqertarsuaq, the 25th of April 2011

Outi Tervo

Outi Maria Tervo

Summary

The bowhead whale is a large baleen whale species with a circumpolar distribution in the Arctic. They do not exhibit long migrations between low latitude breeding areas and high latitude feeding areas like some other baleen whale species but stay in the arctic waters throughout the year. Like in all baleen whale species, female bowhead whales are larger than males reaching a length of 18 meters. Research effort has been restricted due to this often inaccessible icy habitat and so very little is known about the biology of this species. Disko Bay in Western Greenland has been an aggregation area for bowhead whales for centuries from February to May each year but the reasons why bowhead whales gather in the bay during early winter are unknown. Marine mammals rely on sound as the primary mean for communication. The species-specific vocalisations can be used to detect species presence and these vocalisations can be used as a possible indicator of other behaviours.

Here I summarise the most important findings presented in this PhD dissertation. The behaviour of bowhead whales in Disko Bay was studied using passive acoustics (passive listening of the sounds that the animals produce) coupled with DNA analysis of biopsy samples collected from the whales. The singing behaviour of bowhead whales showed a clear seasonal variation in which singing activity and song complexity was highest during February and March. Bowhead whales produced multiple different songs in a season and the entire song repertoire changed annually. Although only one sound-producing organ is thought to be involved in the vocalisations of baleen whales, bowhead whales were found to produce two sounds simultaneously while singing increasing the potential for creating complex songs. Bowhead whales use higher frequencies than most other baleen whale species of similar size and despite the high source levels of these displays, greater attenuation at high frequencies results in songs having a small communication range of ~ 90 km. By aggregating in a restricted area like Disko Bay signallers can reach a large number of receivers while taking advantage of the broad frequency range for creating complex signals. The singers studied were found to be females, which presents a new finding of female singing behaviour in a mammalian species. Singing, contrary to simple calling, is considered to be part of sexual behaviour in baleen whales and due to the active singing and presence of complex songs in winter in Disko Bay, this area is likely a mating area for the Davis Strait – Baffin Bay population of bowhead whales.

This thesis contributes to new knowledge to the acoustic behaviour of bowhead whales and with the discovery of female song raises exciting questions to the mating strategy of this species.

Resume translated by Mads Fage Christoffersen

Grønlandshvalen er en stor bardehvalart som har udbredelse over hele det polare havområde. Grønlandshvaler tilbringer hele deres liv i det arktiske område i modsætning til mange andre bardehvaler, der tilbringer en del af året i det tropiske område, hvor de parrer sig for senere samme år at flytte sig til Arktis for at æde. Som hos alle bardehvaler er hunner større end hanner, hunnerne kan nå en kroplængde på 18 meter. De arktiske havområder er svært tilgængelige for forskere, hvilket har begrænset forskningen i grønlandshvaler. Som følge heraf findes der kun begrænset viden om grønlandshvalers biologi. Diskobugten i vest Grønland har i århundrede været samlingsområde for grønlandshvaler fra februar til maj, men årsagen til den høje koncentration i vintermånederne er ukendt. Havpattedyr bruger lyd som deres vigtigste kommunikationsform. De fleste arter har specifikke lyde, således at lyd optaget under vandet kan bruges til at fastslå hvilke arter, der er til stede. Samtidig er bestemte lyde ofte knyttet til en bestemt adfærd.

Her vil jeg kort beskrive de vigtigste resultater i denne PhD afhandling. Grønlandshvaler og deres adfærd i Diskobugten er beskrevet ved hjælp af passiv akustik (passiv lytning til hvalernes egne signaler) koblet med DNA analyse af biopsier fra hvalerne. Optagelser af sangadfærd viste en stærk sæson afhængig variation, hvor sangens kompleksitet og sangaktiviteten var højest i februar og marts. Grønlandshvalerne sang flere forskellige sange hver sæson, og hele sangrepertoiret skiftede hvert år. Selvom antagelsen er, at grønlandshvaler kun har et lydorgan, viste det sig, at de var i stand til at producere to lyde samtidig, hvilket øger muligheden for at producere komplekse sange. Grønlandshvaler benytter sig af højere frekvenser end de fleste andre bardehvaler i samme størrelse, og disse høje lyde dæmpes relativt hurtigt i vand. Derfor kan hvalerne på trods af en meget høj lydstyrke i sangen kun høre hinanden indenfor ca. 90 km. Når hvalerne samler sig i det relativt lille område i Diskobugten, opnår de at kunne kommunikere de højfrekvente og komplekse sange til mange individer. Sangerne i dette studie viste sig at være hunner, hvilket er et nyt eksempel på et syngende hunpattedyr. Sang, imodsætning til simple kald, regnes for at være en del af en seksuel adfærd hos bardehvaler, og den høje sangaktivitet og den store kompleksitet i sangen under vinterperioden i Diskobugten peger på området som et parringsområde for grønlandshval populationen i Davis Strædet og Baffin Bugten.

Dette studie tilføjer ny viden til den akustiske adfærd hos grønlandshvaler, og fundet af hunner, der synger, rejser spændende spørgsmål omkring strategi for parring og partner valg hos grønlandshvaler.

Eqikkaaneq translated by Anni Dahl

Arfivik arferuvoq soqqalik, issittup imartaani uumasuulluni. Arfivik uumanertik tamaat issittup imartaaniiginnartarput, arferit allat kiannerusunut nuliuartortartut, kingusinnerusukkullu issinnerusumut neriartortartut assiginagit, Arfivik nunat issittut imartaaniiginnartarput ukioq kaajallallugu. Arferit soqqallit arnaviartaat allat assingalugit angutivianiit anginerusarput, arnavissat 18 meterit angullugit angissusseqalersarput. Nunat issittut imartaanni ilisimatusarneq ajornakusoortuuvoq, tamassumalu Arfiviit pillugit ilisimatusarnissaq killilersimallugu, taamaalillunilu ilisimasat killeqarlutik. Qeqertarsuup tunua Kalaallit Nunaata kitaaniittumi ukiuni hudredelikkaani februarimiit majimut katersuuffiuvoq, ilisimaneqaranili suna pillugu ukiuunerani katersuuttarnersut. Uumasut imarmiut miluumasut nipitik atorlugit imminnut attaveqatigiinnerminnut pingaarnertut atungarivaat. Arferit amerlanerit nipit atukkatik immikkuullarissuunerminnut ilisarnaatigivaat, nipillu immami misissukkat atorlugit nipinillu immiussinermi arferit suunerinut immikkoortinneqarsinnaallutik. Nipillu tusaasat naapertorlugit arferit pissussaanut aaliangiisuusarlutik. Matumuuna naalisakkamik nassuiaateqarfigissavara ilisimatusaatima inernerinik pingaarnersiukkat. Immap iluatigut Arfiviit Qeqertarsuup tunuaniittut nipaatigut pissusilersuutaat aammalu ilanngarsivigineratigut timikkut sananeqaataat misissorneqarlutik. Arferit uinngialanerisa immiunneqarnerini paasinarsitippaa piffissami aaliangersimasumi nipit aaliangersimasut “atorneqartut”, minnerunngitsumillu qaammatini martsimi februarimilu annertunerpaaffissamiittut. Arfiviit ukiut tamaasa uinngialanitik allanngorartittarpaat, “erinnallu”assigiinngisitaartarlutik. Naak ilisimaneqarsorineqartoq Arfiviit ataasiinnarmik “nipiliuuteqartut”, paasinarsivoq nipit marluk ataatsikkut “anisittaraat”, taamaalillutillu uinngialanitik atasuusitissinnaasarlugit. Arfiviit uinngialaneri arferit soqqallit angeqqataanit allat qataannerupput, nipillu qataattut immap iluani nipaarukkiartupallattarput, tamannalu pillugu nippaarikkaluaqisut taamaallaat 90 km iluani imminnut tusaasinnaasarput. Arfiviit Qeqertarsuup tunuani piffimmi annertungisassaanngitsumi katersuukkaangamik imminnut uinngialanitik “atorlugit” ataaveqatigiittarput. Uinngialasut (erinarsortut immiussisarfianni) arnaviaasut paasineqarpoq , tassalu immami miluumasut arnaviartaasa “erinarsortartut” nutaartaat. Uinngialanerit erinnatut imminnut atasut, arferit soqqallit nuliunerannut ilisarnaataalluni, uinngialanerit “ataasiaannartunut” allaanerullutik, ukiuuneranilu “erinarsornerunermut”, “erinnallu” atasuinnaanerat Arfiviit nuliunerannut uppernarsaataavoq Qeqertarsuup tunuani, kingornalu Davis Strædemi Baffin Bugtimilu piaqqiorneranik kingunilimmik.

Arfiviit uinngialasarnerinut ilisimasat annertusipput uinngialanerisa misissuiffiginerini, arnavissallu “erinarsortuunerannut” paasisat nuliunermut ileqqut/periutsit “aappassarsiornermilu” periutsit apeqqutit pinngortut pissanganarsitippaat.

Tiivistelmä

Grönlanninvalas on suuri hetulavalaslaji, jonka levinneisyysalue käsittää pohjoisen pallonpuoliskon arktiset merialueet. Useista muista hetulavalaslajeista poiketen, grönlanninvalaat eivät muuta trooppisten lisääntymisalueiden ja arktisten ruokailualueiden välillä vaan pysyvät arktisilla alueilla ympäri vuoden. Kuten kaikissa hetulavalaslajeissa, naaraat ovat uroksia kookkaampia saavuttaen 18 metrin pituuden. Arktisten alueiden vaativat olosuhteet vaikeuttavat tutkimusta, minkä seurauksena grönlanninvalaiden biologiasta tiedetään hyvin vähän. Diskolahti Länsi-Grönlannissa on ollut grönlanninvalaiden kokoontumisalue helmikuusta toukokuuhun jo vuosisatoja mutta syyt, miksi valaat kokoontuvat lahdelle alkutalvesta, ovat olleet epäselviä. Äänteiy on merinisäkkäiden tärkein kommunikointimuoto. Joka lajille ominaisia ääntelyjä voidaan käyttää alueen lajirunsauden kartoittamiseen ja jotkut äänet antavat lisätietoa eläinten käyttäytymisestä.

Tässä tiivistelmässä esittelen tohtorin väitöskirjani tärkeimmät tulokset. Grönlanninvalaiden käyttäytymistä Diskolahdella tutkittiin passiivisen akustiikan (eläimen omien ääntelyjen kuuntelu) ja valaista kerättyjen kudosnäytteiden DNA analyysien avulla. Valaiden ääntelyssä havaittiin selvä vuodenajasta johtuva vaihtelu, jonka johdosta valaat lauloivat aktiivisemmin ja laulut olivat monimuotoisimpia helmi- ja maaliskuussa. Grönlanninvalaiden kausittaiseen ääntelyyn kuului useita erilaisia lauluja ja koko laulu repertuaari vaihtui vuosittain. Vaikka hetulavalailla oletetaan olevan vain yksi äänentuotantoelin, grönlanninvalaiden havaittiin tuottavan kaksi ääntä samanaikaisesti. Tämä kyky lisää mahdollisuutta monimutkaisten laulujen tuottamiseen. Grönlanninvalaat käyttävät lauluissaan korkeampia taajuuksia kuin useat muut samankokoiset hetulavalaat. Lauluilla on suuri äänenvoimakkuus, mutta korkeiden taajuuksien nopean vaimentumisen johdosta, nämä signaalit ovat muiden grönlanninvalaiden kuultavissa vain noin 90 km päähän. Kokoontumalla rajatulle alueelle, kuten Diskolahdelle, myös laulujen korkeat taajuudet ovat useiden valaiden kuultavissa ja koko laaja äänentaajuusalue on hyödynnettävissä monipuolisten signaalien tuottamiseen. Tämän tutkimuksen mukaan laulajien havaittiin olevan naaraita, mikä on uusi esimerkki nisäkäsnaaraiden laulukäyttäytymisestä. Laulamista pidetään osana hetulavalaiden lisääntymiskäyttäytymistä ja talvisen korkean ääntelyaktiivisuuden sekä monimutkaisten laulujen johdosta Diskolahti on todennäköisesti Davisinlahden ja Baffinlahden grönlanninvalaspopulaation lisääntymisalue.

Tämän väitöskirjan tulokset lisäävät tietoa grönlanninvalaiden ääntelystä ja käyttäytymisestä ja havainto, että naaraat laulavat, herättää mielenkiintoisia kysymyksiä tämän lajin lisääntymiskäyttäytymisestä ja puolisonvalinnasta.

Acknowledgements

Five days from now it is precisely 8 years ago since I landed with a BELL 212 helicopter in Qeqertarsuaq – one day ahead of schedule, slightly confused but still very excited, and terribly jet lagged. The bowhead whales were in the bay but remained silent the whole May 2003. However, this somewhat surprising, and at the time terribly disappointing result turned out to be a significant finding and was the start of a Master thesis project that lead to this PhD dissertation.

I am grateful to my supervisors Reinhardt Møbjerg Kristensen and Susan Parks, and last but not least to Mads Fage Christoffersen who believed in this project from the very start and never stopped doing so. You all have supported and helped me immensely with your own expertise, both in the office and out on the field.

I want to thank my co-authors, people involved in the data collection and the board and staff of the Arctic Station. Arctic Station has been an exciting and challenging place to work at and has provided me with a unique platform for studying an arctic marine mammal. My sincere thanks go to Lee Miller who never stopped being my supervisor but carried on helping and guiding. Thank you to my family in Finland for your support and for understanding that I had to stay here. Thank you to the lovely ladies of the sewing club, and John, Margrethe and Finn, Abel, Felix, Elisabeth and Poul, and many others in Qeqertarsuaq, for making me feel at home in here. Thank you Tina for your friendship, hospitality and for showing that it is possible to make a PhD.

It is now six and half years ago since I moved to Qeqertarsuaq and a lot has happened since then. I have truly loved living and working in Greenland and I am forever happy that this thesis made it all possible.

This study was funded by A .P. Møller og Hustru Chastine Mc-Kinney Møllers Fond til almene Formaal, Oticon Fonden and Arctic Station, University of Copenhagen.

1. Introduction

1. INTRODUCTION

1.1. Bowhead whales of Disko Bay

The bowhead whale *Balaena mysticetus* is a baleen whale belonging to the Right whale family *Balaenidae* together with the Southern right whale *Eubalaena australis*, Northern right whale *E. glacialis* and North Pacific right whale *E. japonica*. Bowhead whales reach a length of 18 m and a weight of 50 - 80 tons (Brownell and Ralls, 1986; Evans, 1987) as full grown and as in all baleen whale species, females are larger then males (Haldiman and Tarpley 1993). The coloration ranges from black to grey some individuals having light grey or even yellowish pigmentation on the ventral side and at the tail stock. In addition, bowhead whales have a distinct white chin patch. Bowhead whales are one of the longest living animals on earth. They have been documented to reach ages exceeding 100 years, the oldest individual so far studied being 211 years old (George et al. 1999).

Bowhead whale is a planktivorous baleen whale species. Baleen whales do not posses any teeth but a row of baleen plates which projects from the outer edges of the roof of the mouth forming a dense sieve (Berta and Sumich 1999). The baleen plates are made out of keratin-like substance resembling nails and hair of other mammals. Right whales such as the bowhead whale are characterised by arched upper jaw and extremely long and numerous baleen plates (Eschricht and Reinhardt 1861; Berta and Sumich 1999). These species use continuous ram filtration technique where they swim slowly through the water column with their mouths open and filter small zooplankton from the water that passes through the baleen plates (e.g. Würsig et al. 1985; Simon et al. 2009).

Figure 1. A) Bowhead whale breaking ice in Disko Bay (Photo: L. Jensen) B) A breathing hole made by a bowhead whale where (Photo: O. Tervo) C) the ice was 18 cm thick (Photo: E. Christoffersen).

Bowhead whale has a circumpolar distribution in the arctic waters (Evans 1987, Moore and Reeves 1993). They are highly adapted to the ice cold waters of the arctic

illustrated by the extremely thick blubber layer and the absence of a dorsal fin. Bowhead whales venture often under the sea ice and break the ice using the snorkel like dorsal ridge where the blowholes are situated (Figure 1). Disko Bay, situated in Western Greenland (Fig. 2), has long known to be an important aggregation area for the Davis Strait-Hudson Bay bowhead whales from January to May (Eschricht and Reinhardt 1861) although the reasons why bowhead whales gather in the area are less clear. The current estimate of the population size of bowhead whales in Western Greenland is 1476 individuals (95% CI: 818-2133) (Wiig et al. in press). Disko Bay is an aggregation area primarily for adult animals (Eschricht and Reinhardt 1861; Heide-Jørgensen et al. 2007a) where juvenile animals and calves are rarely seen (Appendix). In April and May the majority of the whales are females (105/130, 81 %) (Heide-Jørgensen et al. 2007b).

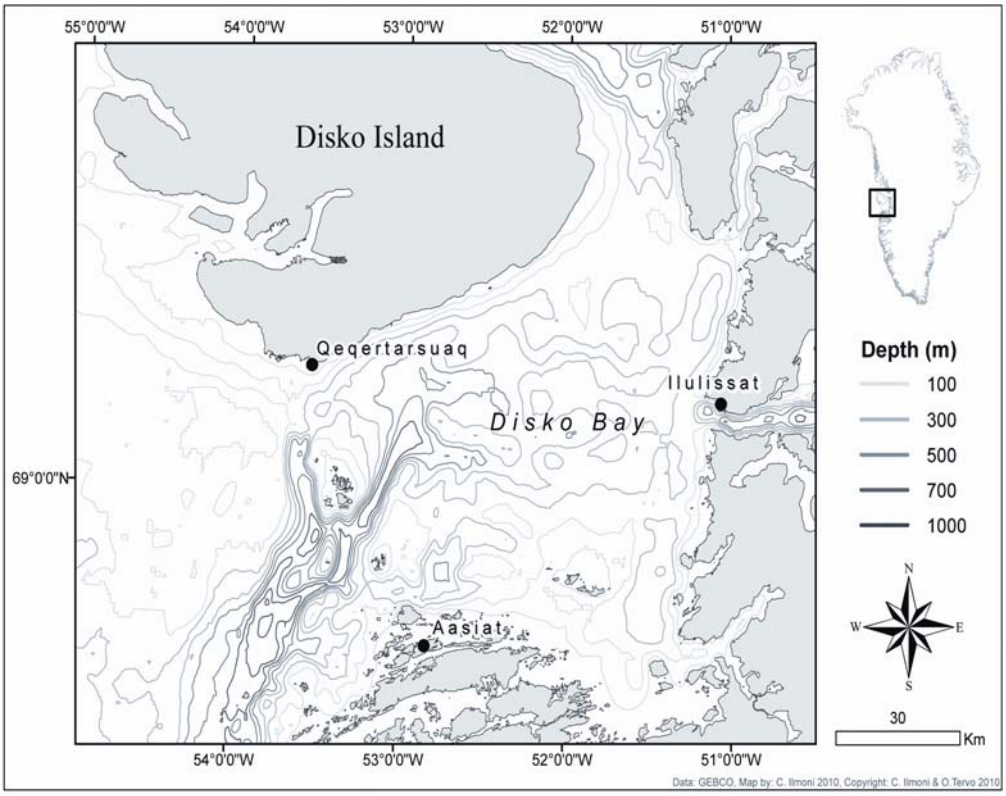

Figure 2. Map of Greenland showing the location of Disko Bay. Arctic Station, University of Copenhagen, is situated in Qeqertarsuaq on Disko Island. (map by C. Ilmoni).

Copepods of the genus *Calanus* dominate the mesozooplankton community in Disko Bay (Nielsen and Hansen 1995; Levinsen and Nielsen 2002) constituting an important prey resource for many marine fishes, birds and mammals, including the bowhead whale (Laidre et al. 2007; Simon et al. 2009). Bowhead whales feed on copepods in Disko Bay in April and May (Laidre et al. 2007; Simon et al. 2009) when the largest portion of the biomass of copepods is close to the surface

Figure 3. Bowhead whale skim feeding at the surface. The lower jaw is lowered exposing the baleen plates. The upper part of the baleen plates can be seen above the surface (Photo: J. Jakobsen).

(Madsen et al. 2001) (Fig. 3). There are no observations of bowhead whales feeding during the winter (Lowry 1993) but more data coupling the behaviour of bowhead whales with oceanography and prey distribution during the winter months are needed.

1.2 Aim of the study

The aim of this study was to describe the acoustic behaviour of bowhead whales in Disko Bay, Western Greenland, using passive acoustic recordings coupled with behavioural observations and biopsy to better determine the function of these sounds. Passive acoustic monitoring (PAM) is a non-invasive method for collecting acoustic recordings and has proven to be a powerful tool in studying marine mammals (e.g. Mellinger et al. 2007).

I divided the focus of this study into A) acoustic behaviour of bowhead whales on a population level, and B) singing behaviour of an individual. The aims of the population level investigation (A) included, 1) describing seasonal and diel variation in the singing activity, 2) describing seasonal and diel variation in the song repertoire, and 3) describing the level and sources of background noise in Disko Bay and determining the effects of man-made noise on the singing behaviour of bowhead whales. The aims of studying the singing behavior of bowhead whales on an individual level (B) comprised 1) determining the gender of the singing individual, 2) describing individual differences in song repertoire, and 3) describing the movements of the singing individual in an attempt to discover the displaying strategy or strategies utilised by this species.

In addition to the aims listed above, two more topics became part of this dissertation. A strike of luck in a form of simultaneous sound production by bowhead whales in 2008, made it possible to look into this subject as well. Another possibility rose from a co-operation with colleagues from the University of Århus and Institute of Natural Resources of Greenland to estimate source levels and active space of bowhead whale songs. This became an important part of my PhD research and enabled me to explore the physical properties of the vocal displays of bowhead whales.

In the next paragraph I will present the findings of this PhD study. I was not able to reach all the aims during the course of my PhD contrary to my plans, and these topics will be included in my plans for future research.

1.3 Results and discussion

A. Acoustic behaviour of bowhead whales on a population level

The applications of PAM include among others revealing presence of a species in area, estimating population sizes and describing the acoustic behavior of a species or individuals. I had considered deploying autonomous recording devices at the bottom to ensure a large data set with high temporal resolution but the year round presence of large icebergs in Disko Bay originating from Ilulissat icefjord made this approach too risky. Instead, the acoustic data was collected using one or two hydrophones deployed from R/V Porsild, a research vessel belonging to the Arctic Station situated in Qeqertarsuaq, from small 4 m open boats, from land (Fig. 4) or through holes in the ice. Due to the challenging weather conditions in the Arctic, the amount of data collected this way will always remain relatively small and explains partially why some of the goals of the study were not met.

Bowhead whales arrived in Disko Bay in average middle of February in the years 2005-2011 (n= 6) which is about 2 months later than in the late 1700 and mid 1800 centuries (n=35) (Fig. 5). The timing of departure of the whales from the bay at present is consistent with that 300 years ago (Eschricht and Reinhardt 1861) (Fig. 5). The singing activity of bowhead whales showed a sharp decline from February and March to April and May (Paper I). Although only data from 2005 has been analysed in detail the same pattern has been evident since 2003. The timing of decline in the singing activity seems to fluctuate between years (unpublished data) but every year bowhead whales in Disko Bay are silent from mid May onwards while still present in the bay. One explanation for the decline in the singing activity could be that bowhead whales shift from social and sexual behaviour during winter to foraging in spring making Disko Bay a potential breeding

area for the Davis Strait-Baffin Bay bowhead whales. The reasons for the observed fluctuations in the timing of the decline in singing activity could be explained by environmental factors such as annual variation in ice conditions, prey distribution and amount, and at this stage, variation in data collection effort.

Figure 4. Qaqqaliaq, the lookout point on the southern tip of Qeqertarsuaq, has been used by hunters for centuries to spot whales. The 60 m tall cliffs provide an excellent platform for observing bowhead whales for research purposes too and due to the special bathymetry right off the cliffs where the bottom drops down to 50 m just 30 m from the shore, this site is also an ideal place to deploy a hydrophone (Photo: A. Foote).

Similarly, the complexity of song expressed as the amount of song notes present in the song repertoire was also observed to decline with advancing season (Paper I). However, this may or may not be true for all years because the method used only song notes, not whole songs, as an indicator of song complexity. There is variation in the song repertoire between years (Paper II) and this could cause that a song recorded early in the season would contain fewer different song notes than a song recorded in late April. For instance, in March 2009 a song composed of repetitions of a single song note type was recorded (Paper III) whereas in years 2006-2008 songs recorded in March contained in average 3 different song notes (Paper II) illustrating the annual variation in song composition and structure. The variation was so total that song notes recorded in 2005-2008 were found to be

specific to a year resulting in the song repertoire changing completely from year to year (Paper II). Multiple songs within a season were also recorded and the dominant song type, the type most often recorded, was shared by multiple individuals (Paper II). The same phenomenon has been evident in 2009-2011 (unpublished data).

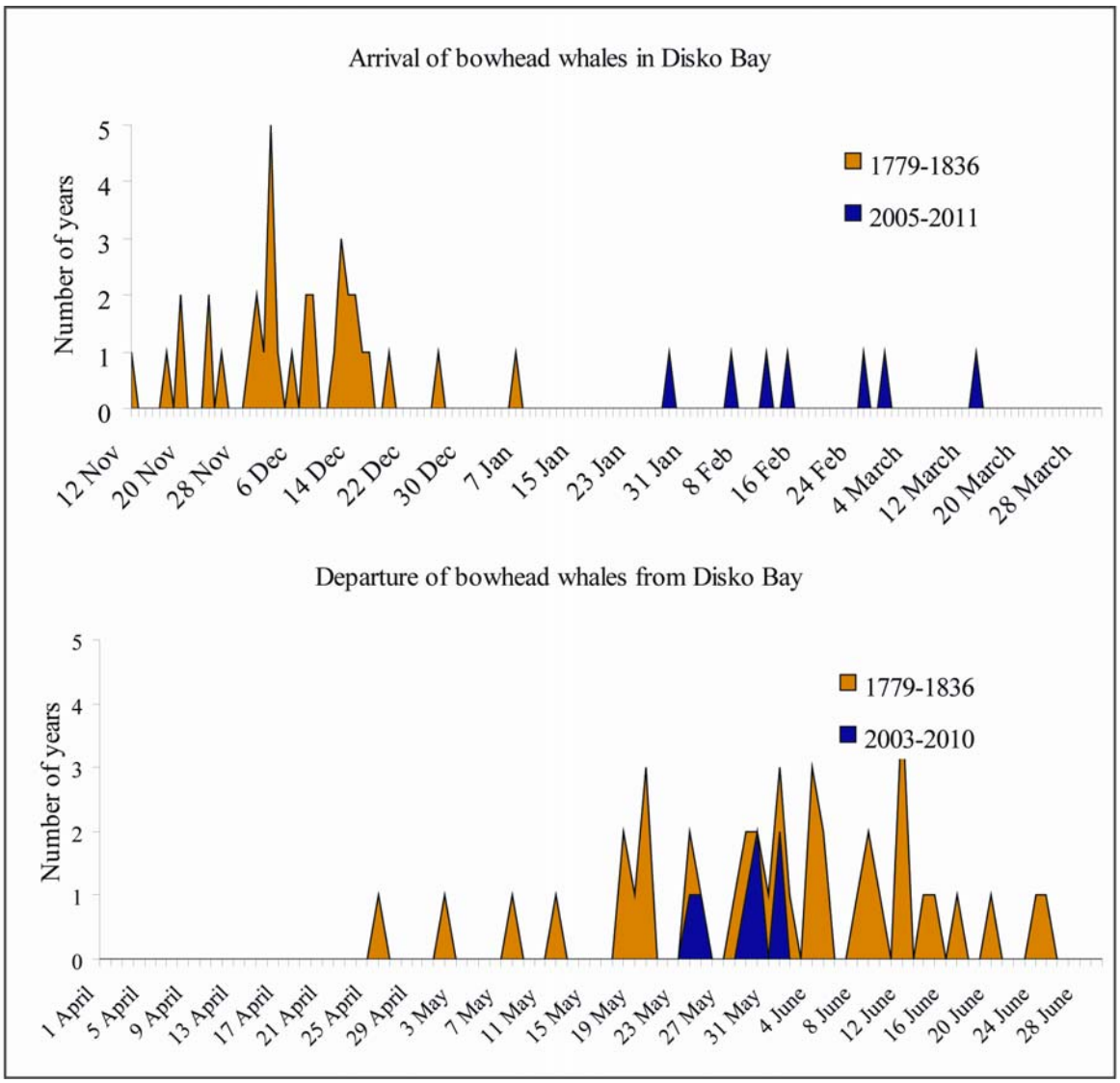

Figure 5. Timing of arrival and departure of bowhead whales into and from Disko Bay from 1779 to 1835 reported by Eschricht and Reinhardt in 1861 (yellow) compared with data from this study (blue).

The reasons for the described seasonal and annual changes in the song repertoire as well as the presence of multiple songs per season are unclear. The amount and site fidelity of individuals in February and March in Disko Bay are not known resulting that the seasonal changes in the song repertoire as well as the simultaneous existence of more than one type of song could be explained by new individuals arriving into the bay with individually specific song or songs. The annual

migration of bowhead whales in Davis Strait have only been partially described (Heide-Jørgensen et al. 2006) and recent genetic data suggests that the inter-annual recapture rate of bowhead whales in Disko Bay is highest after 8 years indicating a multi-year cycle (Wiig et al. in press.). These results do not, however, cancel the possibility that an individual could have seasonal and/or annual changes in its song repertoire.

B. Singing behaviour of bowhead whales on an individual level

Only very little is known about underwater vocal displays in marine mammals on an individual level. A challenge in studying marine mammals is that they spend most of their lives, if not their entire lives, out in the sea and typically come to the surface only to breath. In order to gain insight into the acoustic behaviour of an aquatic species on an individual level, the individual producing the vocalisation has to be positively identified. Because visual confirmation of the individual vocalising is often impossible, the identification of the signaller can be done by localising the vocalising animal with hydrophone arrays (e.g. Janik et al. 2000; Møhl et al. 2001) or by attaching acoustics tags to the animals (Johnson and Tyack 2003). The usage of these methods has increased the understanding of acoustic behaviour of marine mammals and has enabled studies targeting the functions of underwater vocal displays.

In this study, we have used hydrophone arrays to localise vocalising individuals (Papers III-V). Stereo hydrophone array allows the determination of a bearing to the sound source (used in Papers IV and V) whereas three or more hydrophones in an array can be used to position the vocalising individual (used in Paper III). The source level of bowhead whale song was estimated to be 178 dB re μPa (RMS) (Paper III). The bowhead whale song is subject to high frequency dependent absorption due to the high centroid frequency of 571 ± 83 Hz increasing the attenuation of this signal and this combined with the background noise level in Disko Bay at the time of the study resulted in an active space of approximately 90 km for this display (Paper III). The active space of an acoustic signal refers to the range from the sound source at which the sound level is just intense enough for a conspecific to detect/decode the signal (Brenowitz 1982; Janik 2000). Even if the active space of 90 km of bowhead whale song is smaller than that of blue whales and fin whales which can potentially communicate with each other over hundreds, maybe even thousands of kilometres (Payne and Webb 1971; Širović et al. 2007; Clark 1995), the range is sufficient for bowhead whales to be heard in the entire Disko Bay area. By aggregating in a small area such as Disko Bay, the high frequencies of the song, which are most subject to attenuation, will be audible for as many receivers as possible assuring that all the information encoded in the signal is available

for conspecifics. The broad frequency range available allows the production of a wide variety of song notes and the combination of these, gives rise to a large song repertoire. In addition, bowhead whales were observed to produce two sounds simultaneously (Paper IV) which further increases the potential for creating complex signals.

The last result presented in this PhD dissertation is that bowhead whale females were found to produce songs (Paper V). Female song is commonly reported for song birds (Langmore 1998) but is rare in mammals (Janik and Slater 1997). The suggested functions of female bird song include territorial defence, mate guarding, mate attraction and bonding within the breeding pair (reviewed in Langmore 1998). In the closely related Northern right whale, the female produces calls in sexual active groups that function for mate attraction (Parks 2003). The complexity of bowhead whale song could imply that sexual selection, either intrasexual within females or intersexual between females and males, is the driving force behind the song. Bowhead whale is an interesting mixture between balaenopterids and balaenids: they sing like humpback, fin, blue and minke whales from the balaenopterid family but like in Northern right whales, females produce the displays. In addition contrary to balaenopterids, bowhead whale males have large testes like the other balaenid males and these species form sexual active groups in which sperm competition is suggested to play a role (Brownell and Ralls 1986; Kraus and Hatch 2001).

1.4 Future directions

In this PhD study I aimed at describing the acoustic behaviour of bowhead whales in Disko Bay and describing some aspects of the singing behaviour of individuals. The results of this study provide new information on the topic and will be a platform to base future studies on.

Due to logistical difficulties (in other words a violent autumn storm that washed away our land based 4 hydrophone array just 5 days after deployment in October 2008) I was not able to collect enough data to study diel patterns in the acoustic activity of bowhead whales during my PhD. Now in spring 2011, we have managed to establish a permanent stereo recording station at Qaqqaliaq, Qeqertarsuaq, providing us with data that can be used for that purpose. The same data can be used to identify sources of background noise in the area. Changes in the background noise level can be monitored throughout the 4 month season when bowhead whales are in the Disko Bay; this is of special interest as ice often blocks ship traffic in the months of February and March. These

results could then be linked with the seasonal and the potential diel variation in the singing activity of bowhead whales, another topic that I aimed to investigate as a part of my PhD research.

In bowhead whales, none of the same song types have been recorded in multiple years but a larger data set covering a longer period of the year is needed to fully assess this question. Since bowhead whales of the Davis Strait – Baffin Bay population migrate between Greenland and Eastern-Canada (and maybe even further to Alaskan waters) cooperation between researchers for gathering temporally and spatially distributed data of the vocal behaviour would be essential. This kind of data set could also be used to study seasonal changes in the song activity throughout the year and coupled with ID-photography, on which our preliminary results are very promising, or biopsy the changes in song repertoire and singing activity could be linked to movements of individuals. Comparisons between songs from different populations will be an interesting topic to look at which I plan to do as next project together with my colleague studying the Bering Sea population of bowhead whales.

Adding more hydrophones to this existing recording setup at Qaqqaliaq could provide us with information of the movements of singers and that could shed light on the mating strategies used by this species as I intended to do already during the course of my PhD. The winter sea ice in the Arctic presents one more barrier between whales and their researchers, thus only few studies have attempted and succeeded in deploying archival tags on bowhead whales. Nevertheless, my colleagues and I have taken steps to pursue this line of research and aim to deploy acoustic tags on bowhead whales in the near future. Acoustic tags providing detailed information on the movements of the whale underwater will increase our understanding of the singing behaviour of bowhead whales tremendously. Coupled with hydrophone array data, acoustic tags are a powerful tool in studying individual variation in repertoire size and movements while singing, i.e. stationary or roaming, and these results again would provide us with more insight into the mating strategy of this species. In addition, acoustic data collected with a tag could help us to answer questions concerning sound production and vocalisation capabilities in this species as well.

Finally, the discovery of female song opens new and interesting directions for future research. Although it is not yet certain whether the song is solely a female display in this species, and a larger data set of biopsies from localised singers will be collected to answer this question, the fact that females do sing is an important factor for future studies. Playback experiments coupled with behavioural observations and biopsy collection will be a focus area for future research targeting the function of song.

Literature cited

Berta, A. and Sumich, J.L. 1999. Marine mammals: Evolutionary biology. Academic Press. 494 pp.

Brenowitz, E.A. 1982. The active space of red-winged blackbird song. J. Comp. Physiol. A. 147, 511-522. doi: 10.1007/BF00612017

Brownell, R.L. and Ralls, K. 1986. Potential for sperm competition in baleen whales. Rep. Int. Whal. Comm. Special Issue 8, 110-141.

Clark, C. W. 1995. Matters arising out of the discussion of blue whales. Rep. Int. Whal. Comm. 45, 210–212.

George, J.C., Bada, J.L., Zeh, J., Scott, L., Brown, S.E.,O`Hara, T. and Suydam, R. 1999. Age and growth estimates of bowhead whales (Balaena mysticetus) via aspartic acid razemization. Can. J. Zool. 77, 571-580.

Eschricht, D.F., and J. Reinhardt. 1861. Om Nordhvalen (Balæna Mysticetus L.) navnlig med Hensyn til dens Udbredning i Fortiden og Nutiden og til dens ydre og indre Særkjender. (The Northern Whale (Balaenoptera mysticetus L.) with especial reference to its geographical distribution in times past and present, and to its external and internal characteristics). Bianco Lunos Bogtrykkeri, Copenhagen, DK.

Evans, P.G.H. 1987. The Natural History of Whales and Dolphins. Christopher Helm Ltd, Bromley, Kent, UK.

Haldiman, J.T. and Tarpley, R.J. 1993. Anatomy and physiology. pp. 71-156. In: J.J. Burns, J.J. Montague and C.J. Cowles (Eds.) The bowhead whale. Special publication Number 2: The society of marine mammalogy. 787 p.

Heide-Jørgensen, M.P., Laidre, K., Jensen, M.V., Dueck, L. & Postma, L.D. 2006. Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay. Mar. Mamm. Sci. 22, 34-45.

Heide-Jørgensen, M.P., Laidre, K., Borchers, D., Samarra, F. and Stern, H. 2007a. Increasing abundance of bowhead whales in West Greenland. Biol. Lett. 3, 577-580.

Heide-Jørgensen, M.P., Laidre, K., Wiig, Ø., Bachmann, L., Lindqvist, C., Postma., L., Dueck, L., Lidsay, M. and Tenkula, D. 2007b. Segregation of sexes and plasticity in site selection of bowhead whales. Document number SC/60/BRG19, Rep. Int. Whal. Comm.

Janik, V. M. and Slater, P. J. B. 1997. Vocal learning in mammals. Adv. Stud. Behav. 26, 59–99.

Janik, V.M. 2000. Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. J. Comp. Physiol. A. **186**, 673-680.

Janik, V.M., Van Parijs, S.M., and Thompson, P.M. 2000. A two dimensional acoustic localization system for marine mammals. Mar. Mamm. Sci. 16, 437–447.

Johnson, M.P. and Tyack, P. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE (Inst. Electr. Electron. Eng.) Ocean Eng 28, 3–12.

Kraus, S.D. and Hatch, J.J 2001. Mating strategies in the North Atlantic right whale *(Eubalaena glacialis).* J. Cet. Res. Manage. 2, 2 37-244.

Laidre, K., Heide-Jørgensen, M.P. and Nielsen, T.G. 2007. Role of the bowhead whale as a predator in West Greenland. Mar. Ecol. Prog. Ser**.** 346, 285-297.

Langmore, N.E. 1998. Functions of duet and solo songs of female birds. Trends Ecol. Evol. 13, 136-140.

Levinsen, H. and Nielsen, T.G. 2002. The trophic role of marine pelagic ciliates and heterotrophic dinoflagellates in arctic and temperate coastal ecosystems: a cross-latitude comparison. Limnol. Oceanogr. 47, 427–439.

Lowry, L.F. 1993, Foods and feeding ecology. pp. 201-238. In: J.J. Burns, J.J. Montague and C.J. Cowles (Eds.) The bowhead whale. Special publication Number 2: The society of marine mammalogy. 787 p.

Madsen, S.D., Nielsen, T.G. and Hansen, B.W. 2001. Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, Western Greenland. Mar. Biol. 139, 75-93.

Mellinger, D.K., K.M. Stafford, S.E. Moore, R.P. Dziak, and H. Matsumoto. 2007. An overview of fixed passive acoustic observation methods for cetaceans. Oceanography 20, 36-45.

Moore, S.E and Reeves, R.R. 1993. Distribution and movements. pp. 313-386. In: J.J. Burns, J.J. Montague and C.J. Cowles (Eds.) The bowhead whale. Special publication Number 2: The society of marine mammalogy. 787 p.

Møhl, B., Wahlberg, M. and Heerfordt, A. 2001. A large-aperture array of non-linked receivers for acoustic positioning of biological sound sources. J. Acoust. Soc. Am. 109, 434 – 437.

Nielsen, T.G. and Hansen, B. 1995, Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. Mar. Ecol. Prog. Ser. 125, 239-257.

Parks, S. E. 2003. Response of North Atlantic right whales *(Eubalaena glacialis)* to playback of calls recorded from surface active groups in both the North and South Atlantic. Mar. Mamm. Sci. 19, 563-580.

Payne, R.S. and Webb, D. 1971. Orientation by means of long range acoustic signalling in baleen whales. Ann. NY. Acad. Sci. 188, 110-141. doi: 10.1111/j.1749-6632.1971.tb13093.x

Searcy, W.A. and Andersson, M. 1986. Sexual selection and the evolution of song. Ann. Rev. Ecol. Syst. 17, 507-533.

Širović, A., Hildebrand, J.A. and Wiggins, S.M. **2007**. Blue and fin whale call source levels and propagation range in the Southern Ocean. J. Acoust. Soc. Am. 122, 1208-1215.

Simon, M., Johnson, M., Tyack, P. and Madsen, P.T. 2009. Behaviour and kinematics of continuous ram filtration in bowhead whales (Balaena mysticetus). Proc. R. Soc. B 276, 3819–3828.

Wiig, Ø., Heide-Jørgensen, M.P., Lindqvist, C., Laidre, K.L., Postma, L.D., Dueck, L., Palsbøll, P.J. and Bachmann, L. in press. Recaptures of genotyped bowhead whales (*Balaena mysticetus*) in Eastern Canada and West Greenland. Endang. Spec. Res.

Würsig, B., Dorsey, E.M., Fraker, M.A., Payne, R.S. and Richardson, W.J. 1985. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: a description. Fish B-NOAA, U.S. 83: 357-377.

2. Vocal displays in baleen whales

Tervo, O. (unpublished manuscript)

2.1 Introduction

Communication is the signalling by one individual and the detection of that signal by a receiver. These informative stimuli can be divided into acoustic, visual, chemical and tactile signals. Acoustic signals are widely utilised across a variety of animal taxa (Bradbury and Vehrencamp 1998). The frequencies used in vocalisations range from the infrasonic signals of elephants and baleen whales (Payne and Webb 1971; Payne et al. 1986) to the ultrasonic signals of bats and toothed whales (Boughman and Moss 2003; Janik 2009). One taxonomic group of animals for which sound is thought to be an important modality for communication are marine mammals (Tyack 2000). The sea can be a very dark environment where light penetrates to shallow depths even in the clear waters of the open sea and even less in the murky nearshore waters, hence, few objects can be seen underwater at ranges of more than few tens of meters, in contrast, sound can be heard hundreds of kilometers away (Tyack 2000).

Acoustic communication includes vocal displays, a form of animal behaviour where an individual exhibits acoustically (Bradbury and Vehrencamp 1998). Vocal displays have been reported in a variety of taxa including frogs, reptiles, birds and mammals (e.g. Marcellini 1977; Wells and Schwartz 1984; Catchpole and Slater 1995; Tyack 2000). The best-studied example of vocal displays is bird song, from which many of the suggested functions of vocal displays originate (Catchpole and Slater 1995). Vocal displays can function for territorial or mate defence, bonding mechanism for a breeding pair and/or for courtship behaviour (Catchpole and Slater 1995). Vocal displays can also have significance in communicating activities such as travelling, feeding or socialising (Würsig and Clark 1993).

Studies on terrestrial mammals have provided insights into the potential functions of vocal displays. One of the best-studied terrestrial mammal species in terms of acoustic displays is the red deer Cervus elaphus (e.g. Reby and McComb, 2003a). The length of the vocal tract determines its resonance frequencies (formants) in some mammalian species (Fitch 1997) and hence vocalisations can be used as an honest signal for individual size in a mate choice context (Reby and McComb, 2003b). Red deer females can discriminate between roars produced by males of different sizes (Charlton et al. 2007a) and they prefer the vocal displays of large males (Charlton et al. 2007b).

In marine mammals, some airborne vocal displays are similar in form and function to the displays of terrestrial mammals mentioned above. For example, the roars of male Southern elephant seals *Mirounga leonina* carry honest information on the signaller's age and size and therefore can

be used as a cue for settling or invoking aggressive male-male interactions during the breeding season (Sanvito et al. 2007). However, many marine mammals, including pinnipeds and cetaceans produce vocal displays underwater. Unlike airborne vocalisations in which the resonance frequencies are dependent on the size of sound production organs, underwater vocalisations produced by diving mammals are subject to pressure changes at different depths. This has an effect on acoustic properties of the air filled cavities involved in sound production (Tyack 2000; Ridgway et al. 2001; Miller et al. 2007) making the resonance frequencies an unreliable cue for individual size. This makes investigating the function of underwater vocal displays and determining the cues used by receivers to discriminate between signalling rivals or mates a complex task for bioacousticians.

All seal species vocalise and some species produce acoustic displays underwater during their breeding season (ringed seal *Phoca hispida* Stirling 1973; Weddell seal *Leptonychotes weddelli* Thomas et al. 1983; bearded seal *Erignathus barbatus* Cleator et al. 1989; harbour seal *Phoca vitulina* Hanggi and Schustermann 1994; walrus *Odobenus rosmarus* Stirling et al. 1987). Two different displaying strategies have been identified where some individuals defend an acoustic territory, resembling a lek from the terrestrial world (e.g.Van Parijs et al. 2000; Van Parijs et al. 2003), and some males roam over a larger area (Van Parijs et al. 2003). All the singers for each species studied so far have proven to be males (Ray et al. 1968; Hanggi and Schustermann 1994; Thomas et al. 1983), but a connection between these male displays and female mate choice has not yet been confirmed.

Another marine mammal group that produces underwater vocal displays are the baleen whales (Mysticete) from the order Cetacea. Vocal displays in baleen whales include long and complex songs, the best known of which is that of the humpback whale, and other types of vocalisations such as short broadband sounds, e.g. the ‘gunshot’ sounds produced by Southern right whales (*Eubalaena australis*) (Clark 1983) and Northern right whales (*E. glacialis*) (e.g. Parks 2003). Toothed whales (Odontocete) from the same order Cetacea, are vocally highly active producing a large variety of calls but they have not been reported to sing as the baleen whales do (Janik 2009). Baleen whales are large mammals that use highly specialised baleen plates to filter small fish and crustaceans from the water. They live in loose social organisations and often exhibit long migrations between the feeding and breeding grounds (e.g. Tyack 1986). The songs of baleen whales have been the focus of much public and scientific attention resulting in numerous studies over the last 4 decades.

2.2 Types of vocalisations in baleen whales

There are fourteen currently recognised species of baleen whales in the seas of the world (Committee on Taxonomy 2009) and recordings of vocalisations exist from all of them. The sounds of baleen whales can be divided into non-vocal and vocal. Non-vocal sounds include blow sounds and percussive sounds such as tail slaps, whereas vocal sounds consist of calls and songs. Calls are short, discrete vocalisations. Clark (1990) divides the calls of baleen whales into three groups: simple calls, complex calls and variable calls, which include sounds described as clicks, pulses, knocks, and grunts. Simple calls refer to narrow bandwidth, frequency modulated signals with the main energy below 1000 Hz. Simple calls can contain harmonics and they can be to some extent amplitude modulated. Complex calls are broadband signals with a typical bandwidth of 500-5000 Hz. Complex calls are pulsed and can possess a frequency-modulated fundamental. Variable calls with wide variety of descriptive names refer to signals with short duration (<0.1 sec) and little or no frequency modulation.

Song differs from calls, as songs are composed of a series of discrete and stereotyped notes repeated in a pattern. Payne and McVay (1971) created a categorisation differentiating the components of the song in order to analyse it. They made a systematic as follows: (Subunit) → Unit → Phrase → Theme → Song → Song session (Fig. 1). The shortest continuous sound is called a unit (occasionally units are analysed further and named as subunits). A series of units is called a phrase and an unbroken sequence of similar phrases creates a theme. A song is composed of several distinct themes. A series of songs without a pause greater than 1 min is called a song session which in the case of humpback whales can last for hours (Winn and Winn 1978).

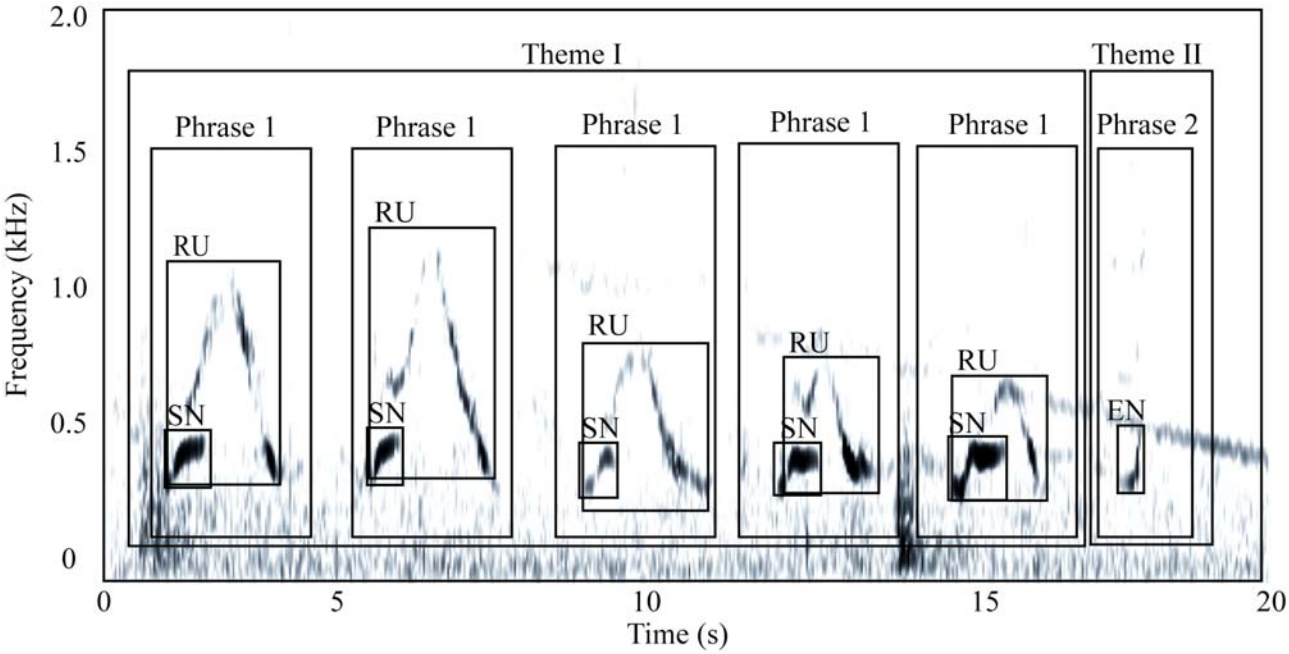

Figure 1. Song systematic created by Payne and McVay (1971) for humpback whale song applied for a bowhead whale song recorded in Disko Bay in 2008. This song is composed of two themes. The first theme I consists of five repetitions of phrase 1 whereas theme II comprises of one example of phrase 2. Song notes are labelled with capital letters. Notice the apparent, although not verified for this particular song, simultaneous production of song notes RU and SN.

Five species of baleen whales so far are known to produce songs: blue whale *Balaenoptera musculus* (Cummings and Thompson 1971), humpback whale *Megaptera novaeangliae* (Payne and McVay 1971), bowhead whale (Ljungblad et al. 1982), fin whale *B. physalus* (Watkins et al. 1987) and minke whale *B. acutorostrata* (Mellinger et al. 2000; Gedamke et al. 2001).

2.3 Context of song

Songs of baleen whales have largely been assumed to occur during the breeding season and there appears to be a seasonal peak of singing at this time for these species. However, songs are also occasionally heard outside the mating period, and in some species throughout the year. This could indicate an alternative function for these displays or illustrate an extension of breeding behaviour to a longer time period than previously assumed (Clapham 1996; Clark and Clapham 2004).

Singing in humpback whales was originally reported during winter in the low-latitude breeding areas (Payne and McVay 1971, Winn and Winn 1978) but later on it has been demonstrated that songs of humpback whales can also been heard at the summer feeding areas as well as during migration (McSweeney *et al* 1989; Clapham and Mattila 1990; Clark and Clapham 2004). Bowhead whales exhibit a similar pattern to humpback whales in that singing is reported to

be most intense during winter (Paper I) when bowhead whales are presumed to mate (Nerini et al. 1984; Reese et al. 2001). However, bowhead whale song has also been recorded during autumn and spring outside the presumed breeding season (Ljungblad et al. 1982; Clark and Johnson 1984; Delarue et al. 2009). Singing outside the primary breeding season has been suggested to be a remnant from the mating season in bowhead whales (Würsig and Clark 1993) and in the case of humpback whale, an indication of a longer breeding season extending to the high latitude feeding areas (Clapham 1996; Clark and Clapham 2004).

Blue whales sing throughout the year (Širović et al. 2004; Oleson et al. 2007) with peaks in the singing activity in March and April and in October and November (Širović et al. 2004). Fin whales of the Southern hemisphere have been reported to sing in the winter from September to May (Watkins et al. 1987) and from February to June with a peak in the singing activity in May (Thompson and Richardson 1995; Širović et al. 2004). This coincides with the presumed breeding period for fin whales in the Southern hemisphere where most of the conceptions are thought to occur in May in the low latitude breeding areas (Boyd et al. 1999). Simon et al. (2010) showed that the peak in the singing activity of fin whales in Davis Strait was in November and December, just a few months before the estimated peak conception time of January for Northern hemisphere fin whales (Lockyer 1984).

Although singing in many of the species can also occur outside the presumed breeding season, songs have been assumed to be linked to courtship in baleen whales (e.g. Payne and Mcvay 1971; Tyack 1981; Clark 1990). Furthermore, only males in humpback, fin and blue whale have been documented to sing (Winn and Winn 1978; Croll et al. 2002; McDonald et al. 2001; Oleson et al. 2007) and the prevalence of this display in the one sex and lack of it in the other has lead to the conjecture that singing is a breeding display having significance in male breeding success (Tyack 1981; Tyack and Clark 2000). The sex of the singing individual in the bowhead whale has been assumed to be male as well (e.g. Würsig and Clark 1993; Stafford et al. 2008) but recent results show that at least some singers in bowhead whales are females (Paper V). The sex of the singing individual in minke whales is unknown.

The singers in humpback whales, fin whales and blue whales are typically alone (Tyack 1981; Watkins et al. 1987; Oleson et al. 2007). In humpback whale and fin whale, the singers are stationery, hanging in the water column at depths of 15-25 m (Au et al. 2006) and 50 m (Watkins et al. 1987), respectively. Blue whales have been reported to sing at depths of 20–30 m (Oleson et al. 2007). Some singers are stationery like in fin and humpback whales while others are travelling while singing (Oleson et al. 2007). Bowhead whales have been reported to sing during their spring

migration (Ljungblad et al. 1982; Clark and Johnson 1984) and some preliminary results suggest that singers are more or less stationery during winter singing (Papers III, IV and V). The depth that singing occurs in bowhead whales is unknown. The behaviour of singing minke whales is largely unknown.

2.4 Geographical and temporal variation in the song

Like many species of songbirds, some marine mammals exhibit clear geographical differences in their vocalisations (e.g. Winn et al. 1981; Ford 1989; Risch et al. 2007). Spatial variation in song structure can occur on microgeographical scale where interbreeding populations of the same species form their own distinct dialects or on macrogeographical scale where populations separated by a geographical barrier, produce vocalizations typical to only that particular area (e.g. Krebs and Kroodsma 1980). The formation of dialects is connected with the extent and accuracy of vocal learning abilities of the species in question whereas macrogeographical differences in the acoustic behaviour can more often be explained by a combination of ecological factors (e.g. properties of the soundscape/background noise, propagation and attenuation of sound in the habitat) and vocal learning (e.g. mimicry from other species present in the habitat) (e.g Krebs and Kroodsma 1980; Slater 1986).

Possibly the best known example of the existence of dialects in marine mammals are the vocalisations of resident killer whale *Orcinus orca* family groups (Ford 1989). The geographical variations of songs reported for humpback whales, fin whales and blue whales (e.g. Payne and Guinee 1983; Stafford et al. 2001; McDonald et al. 2006; Delarue et al. 2009a) could be argued to represent dialects as well. Oceans have few geographical barriers preventing the dispersal of individuals compared to the terrestrial world and the loud low frequency songs of baleen whales provide them with the potential of extreme long distance communication. The repetition rates of "boing" vocalisation of minke whales from different areas have also been shown to differ, illustrating a situation akin to the other singing baleen whales (Rankin and Barlow 2005). Although comparisons between recordings of bowhead whale songs from different areas have not yet been made, inspection of published spectrograms of songs seem to be unique to specific regions, however this needs to be confirmed by comparative studies.

Temporal variation in the vocal behaviour can be divided into diel, seasonal and annual variation. Fin whales, blue whales and humpback whales exhibit diel variation in their singing and calling activity where the proposed reasons for it include diel patterns in the movement of prey (e.g.

Stafford et al. 2005; Oleson et al. 2007; Simon et al. 2010), changes in the light conditions (Au et al. 2000; Simon et al. 2010) and changes in the behaviour of the whales (Au et al. 2000). Seasonal changes in the singing activity are often related to the breeding period as discussed above, but changes in the structure of the song and in the occurrence of different songs can also occur during one season as reported for humpback whales and bowhead whales. All humpback whale singers within an area perform the same songs at any point of time (Winn and Winn 1978) but the songs change gradually during the breeding season, and all males of the population incorporate the same changes into their songs (Payne et al. 1983; Payne and Guinee 1983; Payne and Payne 1985). The gradual changes in the song have been shown to occur at different rates in different years (Eriksen et al. 2005), but in all years the structure of the song normally stabilises after a short period early in the season (Payne et al. 1983; Eriksen et al. 2005). A significant change in the song of the humpbacks inhabiting the Pacific Ocean off Eastern Australia was discovered after they had been exposed to the song of the humpback whales from the Indian Ocean (Noad et al. 2000). A small number of individuals from the population off Western Australia migrated to the breeding areas normally belonging to the population off Eastern Australia and very rapidly the song of the humpback whales from Pacific Ocean was replaced by the new song from the immigrants suggesting that novelty drives changes in the humpback whale song (Noad et al. 2000). A temporal and macrogeographical change in the humpback whale song has also recently been documented in which multiple song types spread rapidly and repeatedly to different populations in the South Pacific within a decade (Garland et al. in press). Curiously, the transmission of these song types has been unidirectional, with song always spreading eastwards (Garland et al. in press).

The song composition of bowhead whales in an area goes through discrete changes during a season (Delarue et al. 2009b; Paper I). Multiple songs per season are recorded (Stafford et al. 2008; Delarue et al. 2009b; Paper I) and the relative occurrence of these songs changes within a season (Delarue et al. 2009b; Paper I). It is not yet known whether all the recorded songs within a season are produced by all singers, but at least one song every season is shared by multiple individuals (Paper II). Gradual changes in a song also occur, for example, in one song type recorded in Disko Bay in 2007 the end note T was deleted from the song in spring while the other units in the song remained unchanged (Tervo, O. unpublished data).

Annual changes in the song have been so far reported only for humpback whales and bowhead whales. In humpback whale songs the change between years is gradual but accumulative so that songs recorded furthest apart in time are most different (e.g. Payne et al. 1983; Eriksen et al. 2005). Bowhead whale songs seem to change completely from year to year, each year having a

unique repertoire of songs (Würsig and Clark 1993; Paper II). In Disko Bay, bowhead whale songs have been recorded since 2005 with new songs appearing each year (Paper II) (Fig. 2).

2.5 Physical properties of the song

Schewill and Lawrence in 1949 were the first to show that beluga whales *Delphinapterus leucas* have a rich vocal repertoire and in the past decades, numerous studies on both toothed whales and baleen whales have shown that cetaceans have extensive acoustic repertoires. Like songbirds (Fee et al. 1998), all toothed whales except for the sperm whales (Physeteridae) have a bilateral configuration for sound production (Cranford et al. 1996; Cranford 2000). In nonphyseterid toothed whales one of the two sound generating structures, the paired phonic lips, are located in each of the nasal passages of the spiracular cavity (Cranford et al. 1996; Cranford 2000). According to the current knowledge of baleen whale sound production it is assumed that sounds are produced in the larynx (Reidenberg and Laitman 1992; Reidenberg and Laitman 2007). The aretynoid cartilages in the lumen of the larynx support a U-shaped fold, which may function as a regulator of the airflow through the larynx much in the manner of true vocal folds (Reidenberg and Laitman 1992; Reidenberg and Laitman 2007). Vibrations in the edges of the U-fold are most likely responsible for generating sound and the laryngeal sack, which is a muscular and highly contractile construction, could function as an air reservoir, be responsible for providing pressurisation necessary for sound production and/or modify the frequency and amplitude of the generated sound (Reidenberg and Laitman 2007).

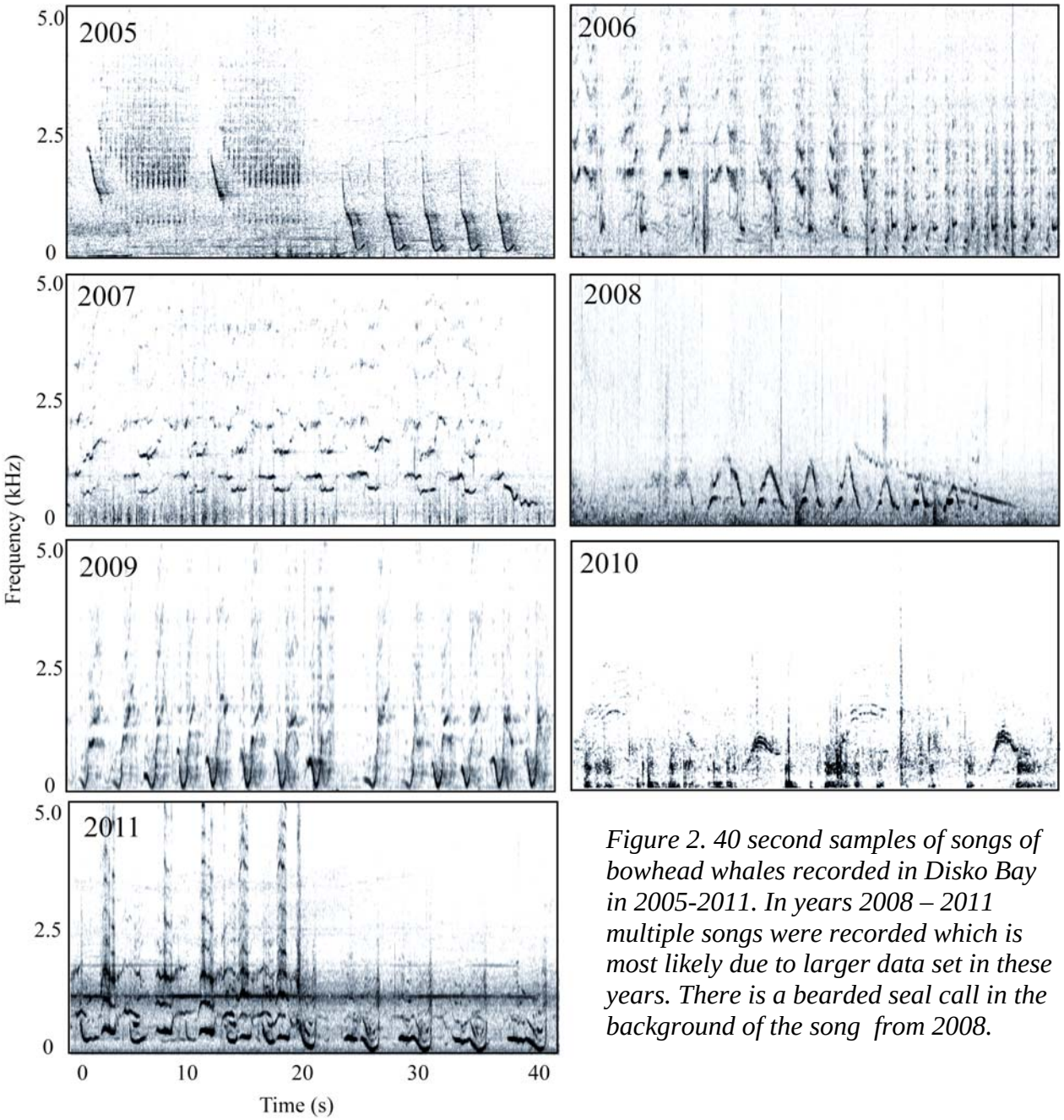

Figure 2. 40 second samples of songs of bowhead whales recorded in Disko Bay in 2005-2011. In years 2008 – 2011 multiple songs were recorded which is most likely due to larger data set in these years. There is a bearded seal call in the background of the song from 2008.

Nonlinear phenomena in vocalisations include biphonation, frequency jumps, subharmonics, side bands and deterministic chaos (Wilden et al. 1998). Due to the two-sided sound production organ constellation, toothed whales have the possibility to produce two sounds at the same time (Cranford et al. 1996) though this ability has only been documented for some species (Cranford et al. 2000; Tyson et al. 2007; Foote et al. 2008; Lammers and Castellote 2009; but see Madsen et al. 2010). However, nonlinear vocalisations have also been reported for a vide variety of mammals which seemingly have only one sound producing organ, the larynx. Examples of these from the terrestrial world include species of canids (Wilden et al. 1998; Riede et al. 2000), primates (Riede et

al. 2004) and even humans (Neubauer et al. 2004). Among marine mammals from taxonomic groups other than the odontocetes, nonlinear phenomena has been described for manatees (Mann et al. 2006), ringed seals (Rautio et al. 2009) and for three species of baleen whales; minke whale (Gedamke et al. 2001), Northern right whale (Tyson et al. 2007) and bowhead whale (Paper III).

There exists a general inverse relationship between body size and frequency according to which animals with small body size produce higher frequency sounds than animals with large body sizes (Fletcher 2004). Baleen whales are a good example of this rule in that they are capable of producing very low frequency sounds - the songs of blue whales and fin whales have fundamental frequencies ranging from 15 to 29 Hz (Cummings and Thompson 1971; Cummings and Thompson 1994; Watkins et al. 1987; Širović et al. 2007). The high source levels of 186 to 189 dB re 1μPa (root mean square, RMS) of these songs (Cummings and Thompson 1971; Watkins et al. 1987; Širović et al. 2007) and the fact that these low frequency displays are less affected by frequency dependent absorption (Urick 1983) results in a large active space allowing individuals to communicate potentially over thousands of kilometres (Payne and Webb 1971). The active space of a signal will though alter according the local conditions such as background noise levels, bathymetry of the area and the depth of the sender and receiver (discussed in Paper IV).

The fundamental frequencies of humpback whale song range from 30 to 4000 Hz (Payne and Payne 1985; Cerchio et al. 2001) and that of bowhead whales from 40 to 2000 Hz (Ljungblad et al. 1982; Cummings and Holliday 1987; Papers I and II). The broad frequency range of the songs of humpback and bowhead whales enables the production of highly complex and variable displays but due to the higher frequencies, these displays have a much lower active space than the songs of blue and fin whales. Bowhead whale song recorded in Disko Bay, Greenland had a source level of 178 re 1μPa (RMS) and an estimated active space of ~ 90 km (Paper IV). In similar background noise conditions and with the same source level, the 20 Hz song of fin whales was estimated to have an active space of 500 km (Paper IV). Due to these differences in the frequency ranges used for displays in the different species it seems evident that the displaying strategies have coevolved to facilitate the behavioural ecology of the species. Blue and fin whales live as single individuals most of the year and are not known to aggregate in specific breeding grounds (e.g. Connor et al. 2000). In contrast, individuals attracted by calls possibly over long distances will join feeding assemblies, where mating can occur (Croll et al. 2002; Delarue et al. 2009). Humpback whales and bowhead whales aggregate on designated areas at the time when singing is most intense most likely to breed (e.g. Clapham 1996; Paper I), enabling them to compensate spatially for their smaller

communication range and to exploit the advantages of a large frequency range in the form of a complex and dynamic acoustic display.

2.6 Function of the song

The purpose of the complex song of baleen whales has puzzled researchers ever since their discovery and a variety of suggestions have been made as to its function. It is generally hypothesised that singing is connected with the sexual behaviour of the species but the function of the song has never been unequivocally demonstrated. Since most of studies investigating songs and singing behaviour of baleen whales have concentrated on the humpback whale, also here the hypothesis as to the function of song stem from humpback whales research.

The current two main hypotheses of the function of the song are 1) song is an intersexual display in which females use the song as an honest indicator of male quality when choosing a mate (e.g. Winn and Winn 1978; Tyack 1981), or 2) song is an intrasexual display in which males communicate to each other the readiness to fight (e.g. Tyack and Whitehead 1983) and/or establishes social dominance between the males (e.g. Darling 1983; Clapham et al. 1992; Darling and Bérubé 2001).

Winn and Winn (1978) suggested that the song of humpback whales is used to attract females and that it appears to act as a spacing mechanism maintaining distance between singers. This could be interpreted as male-male interaction or as an indicator of lekking behaviour as suggested by Herman and Tavolga (1980). A lek refers to a communal display arena where males aggregate to display and females only attend to mate (e.g. Alatalo et al. 1992). Clapham (1996) introduced the term “floating lek” to encompass the idea of congregation of displayers where the different individuals are moving around although maintaining a distance in relation to each other (Tyack 1981). The idea of leks and intersexual selection is further supported by observations of female humpback whales joining singers (Medrano et al. 1994) although this result has not been able to be replicated in playback experiments (Tyack 1983, Mobley et al. 1988). A general concept in reproductive advertising by a display is that the displayer has to stand out from the rest of the displaying individuals in order to be chosen by the selecting sex and in lekking animals, females of many species show a strong tendency to mate only with a few males (e.g. Höglund et al. 1990).

Tyack (1981) suggested that the complexity and changes over time of the humpback whale song could be a result of female mate choice. In many songbird species mate choice by females is influenced by male singing behaviour (Catchpole and Slater 1995). Females of several songbird

species have been documented to prefer males that sing longer songs (Gentner and Hulse 2000) and increase their singing rate (Alatalo et al. 1990) possibly because these males are in better physical condition, more fit and possibly more motivated to mate (Beani and Dessi-Fulgheri 1995). The performance of males has also been observed to have an effect on the female response in songbirds: male birds that possess larger repertoires and males that perform challenging songs are preferred by females in some species (Searcy and Andersson 1986; Vallet et al. 1998; Ballentine et al. 2004). However, there is currently no evidence that humpback whale females use song to discriminate between males.

Observations supporting the second hypothesis of song functioning as an intrasexual display include males joining male singers (Darling and Bérubé 2001; Darling et al. 2006). Also, aggressive interactions (particularly between singers and known males) have been reported to be much more common than sexual interactions (particularly between singers and known females) (Tyack 1981, Darling 1983). Darling (1983) described agonistic encounters between singers and males that joined them, and suggested that song functions as an acoustic display that may determine dominance ranking. Subsequently, Darling and Bérubé (2001) reported males joining singers and suggested that these associations could lead to coalitions between males. On the breeding grounds, humpback whales form competitive groups, consisting typically one female and several males fighting for access to her (e.g. Tyack and Whitehead 1983). Coalitions of males could enhance the male's chances of gaining access to the females rather than working alone (Clapham et al. 1992).

Winn and Winn (1978) hypothesised that the high-frequency component of the song of humpback whales, referred as a cry, could carry signature information. Cries are distinctive, pure tonal frequency-modulated sounds lasting 0.2-2.85 s with frequencies ranging from 250 Hz to 4000 Hz (Hafner et al. 1979). All recorded individuals included in the study maintained a regular cry structure from one song to another, which has the potential to be the basis for individually distinctive signature information (Hafner et al. 1979). Even small samples rates of cries from each individual gave reliable discrimination indicating that the cries do posses such signature information although it has never demonstrated to be functional and used by receivers to discriminate amongst signallers in nature (Hafner et al. 1979).

The hypotheses concerning the function of humpback whale song discussed above could also be applicable to blue and fin whales, since only males have been reported to produce vocal displays in these species also. However, not enough is known about the sexual behaviour in these two species in order to assess these hypotheses. The right whale family Balaenidae, which includes the Southern and Northern right whale and the bowhead whale, differs in this context since females

have been documented to produce vocal displays (Parks 2003; Paper V). Bowhead whale song is complex and changes annually and these two features could have evolved through intersexual selection as Tyack (1981) suggested for the humpback whale song. However, complete courtship role reversal, in which females produce advertisement displays and males choose females, is only expected to occur when the parental investment of the selecting sex exceeds that of the selected sex (Emlen and Oring 1977). Complete courtship reversal is therefore very unlikely to occur in mammal species where the maternal investment is always higher than that of the male (with maybe *Homo sapiens* as an exception). Partial courtship reversal can however occur even when the maternal investment exceeds that of the paternal investment and the females are the limiting sex in reproduction (Gwynne 1991). In partial courtship role reversal both sexes engage in intrasexual competition for access to high quality mates (Gwynne 1991). The existence of intrasexual selection pressure could explain the complexity of female song in bowhead whales. However, it is not yet known whether song is solely a female display in this species.

In the closely related Northern right whale, females produce discrete scream calls which function to attract males into sexual active groups (Parks 2003). These groups are similar to humpback whale competitive groups (Tyack and Whitehead 1983) in which a single female is accompanied by several males that pursue to mate with her (e.g. Kraus and Hatch 2001). The males in Northern right whales posses long penises and very large testes (Brownell and Ralls 1986) and in sexual active groups they attempt to mate the females several times (Kraus and Hatch 2001) implying that the plausible sexual selection strategy of the males is sperm competition (Brownell and Ralls 1986; Kraus and Hatch 2001). Sexual active groups have also been described for bowhead whales (Würsig and Clark 1993) and it is possible that the function of the bowhead whale female song could be similar to that of the female northern right whale scream calls which in the case of bowhead whale, has gained complexity through intrasexual selection as discussed above. However, in Northern right whales males also produce what has been suggested to be male advertisement displays in the form of ‘gunshot’ sounds which are short broadband signals that sound like rifle fire (Parks et al. 2005). It is not known whether male bowhead whales also produce displays and in the lack of behavioural data we can only conclude that bowhead whales seem to share behavioural traits with both the rorqual whales and the right whales i.e. the song and that females produce displays.

2.7. Future directions

The research on acoustic displays of baleen whales has been concentrated on the humpback whale although there is an increasing amount of data available for fin whales, blue whales and bowhead whales. Acoustic tags, that can provide very detailed information on the movements and acoustic behaviour of an individual producing the display or on the reactions of a receiver to the display, have been successfully deployed on fin whales, blue whales and humpback whales (Goldbogen et al. 2006; Oleson et al. 2007; Stimpert et al. 2007). Applying this method on studies targeting singing individuals, also in other species such as bowhead whales and minke whales, would greatly expand our knowledge on acoustic displays in these species. Similarly, playback experiments on humpback whales (Tyack 1983), Southern right whales (Clark and Clark 1980) and Northern right whales (Parks 2003) have proven to be powerful tools in examining the reactions of other whales to the displays of conspecifics and could be applied to the other singing baleen whales as well. Acoustic tag deployments coupled with a morphological approach could greatly enhance our current knowledge on the sound production mechanism of baleen whales (e.g. see Samarra et al. 2011 for a similar approach in odontocetes). Here in particular, bowhead whales and minke whales seem very interesting due to reported non linear phenomena in the vocalizations. More data is needed in order to fully describe the extent of these phenomena.

Interestingly the most abundant and the smallest of all singing baleen whales, the minke whale, is the species for which we know least about its vocal displaying, highlighting the challenge of investigating this interesting and long-debated topic.

Acknowledgements

I want to thank Andy Foote and Mads Fage Christoffersen for their valuable comments to this manuscript.

Literature cited

Alatalo, R.V., Glynn, C. and Lundberg, A. 1990. Singing rate and female attraction in the pied flycatcher: an experiment. Animal Behav. 39, 601-603.

Alatalo, R.V., Höglund, J., Lundberg, A. and Sutherland, W.J. 1992. Evolution of black grouse leks: female preferences benefit males in larger leks. Behav. Ecol. 3(1), 53-59. doi: 10.1093/beheco/3.1.53

Au, W.W.L., Mobley, J., Burgess, W.C., Lammers, P.O. and Nachtigall, P.E. 2000. Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. Mar. Mam. Sci., 16, 530–544.

Au, W.W.L., Pack, A.A., Lammers, M.O., Herman, L.M., Deakos, M.H. and Andrews, K. 2006. Acoustic properties of humpback whale song. J. Acoust. Soc. Am. **120**, 1103-1110.

Ballentine, B., Hyman, J. and Novicki, S. 2004. Vocal performance influences female response to male bird song: an experimental test. Behav. Ecol. 15, 163-168.

Beani, L. and Dessi-Fulgheri, F. 1995. Mate choice in grey partridge, *Perdix perdix*: role of physical and behavioural male traits. Animal Behav. 49, 347-356.

Boughmann, J. and Moss, C. 2003. Social Sounds: Vocal Learning and Development of Mammal and Bird Calls. Pp. 138-224. In: Acoustic Communication. Springer Handbook of Auditory Research, Volume 16. doi: 10.1007/0-387-22762-8

Boyd, I. L., C. Lockyer, and H. D. Marsh. 1999. Reproduction in marine mammals. Pp. 218–286 In: J. E. Reynolds and J. R. Twiss (Eds.). Marine mammals. Smithsonian Institution Press, Washington, D.C., USA.

Bradbury J.W. and Vehrencamp S.L. 1998. Principles of animal communication. Sinauer Associates.

Brownell, R.L. and Ralls, K. 1986. Potential for sperm competition in baleen whales. Rep. Int. Whal. Commn. Special Issue 8, 110-141.

Catchpole, C.K. and Slater, P.J.B. 1995. Bird song, Biological themes and variations. Cambridge: Cambridge University Press.

Cerchio, S., Jacobsen, J.K. and Norris, T.F. 2001. Temporal and geographical variation in songs of humpback whales, Megaptera novaeangliae: synchronous change in Hawaiian and Mexican breeding assemblages. Animal Behav. 62, 313–329.

Charlton, B.D., Reby, D. and McComb, K. 2007a. Female perception of size-related formant shifts in red deer, Cervus elaphus. Animal Behav. 74, 707-714- doi:10.1016/j.anbehav.2006.09.021

Charlton, B.D., Reby, D. and McComb, K. 2007b. Female red deer prefer the roars of larger males. Biol. Lett. 3, 382–385. doi:10.1098/rsbl.2007.0244

Clapham, P. J. and Mattila, D. K. 1990. Humpback whale songs as indicators of migration routes. Mar. Mam. Sci. 6, 155-160.

Clapham, P. J., Palsbøll, P. J., Mattila, D. K. and Vásquez, O.1992. Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour 122, 182–194.

Clapham, P. J. 1996. The social and reproductive biology of Humpback Whales: an ecological perspective. Mammal Rev. 26(1), 27-49.

Clapham, P. J. 2000. The humpback whale: seasonal feeding and breeding in a baleen whale. Pp. 173–196. In: J. Mann, P. L. Tyack, R. Connor and H. Whitehead (Eds.). Cetacean societies, Field studies of Dolphins and Whales. The University of Chicago Press, Chicago.

Clark C.W. and Clark, J.M. 1980. Sound playback experiments with southern right whales *(Eubalaena australis).* Science 207:663-665.

Clark C.W. 1983. Acoustic communication and behavior of the southern right whale. Pp. 163-198. In: R. S. Payne (Ed.). Communication and behavior in whales. Westview Press, Boulder, CO.

Clark, C.W. and J.H. Johnson. 1984. The sounds of the bowhead whale, *Balaena mysticetus*, during the spring migrations of 1979 and 1980. Can. J. Zool. 62, 1436-1441.

Clark, C.W. 1990. Acoustic behavior of mysticete whales. Pp. 571-583. In: J. Thomas and R. Kastelein (Eds.). Sensory Abilities of Cetaceans. Plenum Press, New York, NY.

Clark, C. W., and P.J. Clapham. 2004. Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. Proc. R. Soc. B. 271, 1051-1057.

Cleator, H. J., Stirling, I. and Smith, T. G. 1989. Underwater vocalizations of the bearded seal (Erignatus barbatus). – Can. J. Zool. 67, 1900-1910.

Committee on Taxonomy. 2009. List of marine mammal species and subspecies. Society for Marine Mammalogy, www.marinemammalscience.org, consulted on [4.4.2011].

Connor, R.C., Read, A.J. and Wrangham, R. 2000. Male reproductive strategies and social bonds. Pp. 247-270. In: J. Mann, P. L. Tyack, R. Connor and H. Whitehead (Eds.). Cetacean societies, Field studies of Dolphins and Whales. The University of Chicago Press, Chicago.

Cranford, T.W., Amundin, M. and Norris, K.S. 1996. Functional morphology and homology in the Odontocete nasal complex: Implication for sound generation. J. Morphology 282, 223-285.

Cranford, T.W. 2000. In search of impulse sound sources in Odontocetes. Pp. 109-165. In: W.W.L. Au, A.N. Popper and R.R. Fay (Eds.). Hearing by whales and dolphins. New York, Springer-Verlag.

Cranford, T.W., Elsberry, W.R., Blackwood, J.A., Kamolnick, T., Todd, M., Van Bonn, W.G., Carder, D.A., Ridgway, S.H., Bozlinski, D.M. and Decker, E.C. 2000. Physiological evidence for two independent sonar signal generators in the bottlenose dolphin. J. Acoust. Soc. Am. 108, 2613.

Croll, D.A., C.W. Clark, A. Acevedo, B.R. Tershy, S. Flores, J. Gedamke and J. Urban. 2002. Only male fin whales sing loud songs. Nature 417, 809.

Cummings W.C. and Thompson P.O. 1971. Underwater sounds from the blue whale, *balaenoptera musculus*. J. Acoust. Soc. Am. 50(4), 1193-1198.

Cummings, W.C. and D.V. Holliday. 1987. Sounds and source levels from bowhead whales off Pt. Barrow, Alaska. J. Acoust. Soc. Am. 83, 814-821.

Cummings, W.C. and Thompson ,D 1994. Characteristics and seasons of blue and finback whale sounds along the U.S. west coast as recorded at SOSUS stations. J. Acoust. Soc. Am. 95, 2853-2853.

Darling, J.D. 1983. Migrations, abundance and behaviour of Hawaiian humpback whales (*Megaptera novaeangliae*). PhD thesis, University of California, Santa Cruz, USA.

Darling, J. D. and Bérubé, M. 2001. Interactions of singing humpback whales with other males. Mar. Mam. Sci. 17, 570–584.

Darling, J.D., Jones, M.E. and Nicklin, C.P. 2006. Humpback whale songs: Do they organize males during the breeding season? Behaviour 143, 1051-1101

Delarue, J., Todd, S.K., Van Parijs, S.M. and Di Lorio, L. 2009a. Geographic variation in Northwest Atlantic fin whale (*Balaenoptera physalus*) song: Implications for stock structure assessment. J. Acoust. Soc. Am. 125(3), 1774-1782.

Delarue, J., M, Laurinolli and B. Mate. 2009b. Bowhead whale (*Balaena mysticetus*) songs in the Chukchi Sea between October 2007 and May 2008. J. Acoust. Soc. Am. 126, 3319-3328.

Emlen, S.T. and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 19, 215-223.

Eriksen, N., Miller, L.A., Tougaard, J. and Helweg, D.A. 2005. Cultural changes in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. Behaviour 142, 305-328.

Fee M.S., Shraiman, B., Pesaran, B. and Mitra, P.P. 1998. The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. Nature 395: 67–71.

Fitch, W.T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. J. Acoust. Soc. Am. 102, 1213–1222.

Fletcher, N.H. 2004. A simple frequency-scaling rule for animal communication. J. Acoust. Soc. Am. 115, 2334-2338.

Foote, A.D., Osborne, R.W. and Hoelzel, R. 2008. Temporal and Contextual Patterns of Killer Whale (*Orcinus orca*) Call Type Production. Ethology 114, 599–606.

Ford, J.K.B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia, Canada. Can. J. Zool. 67, 727–745.

Garland, E.C., Goldizen, A.E., Rekdahl, M.L., Constantine, R., Garrigue, C., Daeschler, N., Hauser, M., Poole, M., Robbins, J. and Noad, M.J. (in press). Dynamic Horizontal Cultural Transmission of Humpback Whale Song at the Ocean Basin Scale. Current Biol. 14 April 2011, 10.1016/j.cub.2011.03.019

Gedamke, J., D.P. Costa and A. Dustan. 2001. Localization and visual verification of a complex minke whale vocalization. J. Acoust. Soc. Am. 109, 3038-3047.

Gentner, T.Q. and Hulse, S.H. 2000. Female european starling preference and choice for variation in conspecific song. Animal Behav. 59, 443-458.

Goldbogen, J.A., Calambokidis J, Shadwick RE, Oleson EM, McDonald MA, Hildebrand JA. 2006. Kinematics of foraging dives and lunge-feeding in fin whales. J. Exp. Biol. 209, 1231-44.

Gwynne, D.T. 1991. Sexual competition among females: What causes courtship-role reversal. Trends Ecol. Evol. 6, 118-121.

Hafner, G.W., Hamilton, C.L., Steiner, W.W., Thompson, T.J. and Winn, H.E. 1979. Signature information in the song of the humpback whale. J. Acoust. Soc. Am. 66, l-6.

Hanggi, E.B. and Schusterman, R.J. 1994. Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*. Animal Behav. 48, 1275–1283.

Herman, L.M. and Tavolga, W.N. 1980. The communications systems of cetaceans. Pp. 149-209. In: Herman, L.M. (Ed.). Cetacean behaviour: Mechanisms and functions. Wiley & Sons, NY.

Höglund, J., Alatalo, R. V. and Lundberg, A. 1990. Copying the mate choice of others? Observations on female black grouse. Behaviour 114, 1–4.

Janik, V.M. 2009. Acoustic communication in delphinids. Adv. Stud. Behav. 40,123–157.

Kraus, S.D. and Hatch, J.J 2001. Mating strategies in the North Atlantic right whale *(Eubalaena glacialis).* J. Cet. Res. Manage. 2, 2 37-244.

Krebs, J. R. and Kroodsma, D. E. 1980. Repertoires and geographical variation in bird song. Adv. Stud. Behav. 11, 134–177.

Lammers, M.O and Castellote, M. 2009. The beluga whale produces two pulses to from its sonar signal. Biol. Lett. 5, 297-301. doi:10.1098/rsbl.2008.0782

Ljungblad, D.K., P.O. Thompson and S.E. Moore. 1982. Underwater sounds recorded from migrating bowhead whales, *Balaena mysticetus*, in 1979. J. Acoust. Soc. Am. 71, 477-482.

Lockyer, C. 1984. Review of baleen whale (Mysticeti) reproduction and implications for management. Rep. Int. Whal. Comm. 6, 27–50.

Madsen, P.T., Wisniewska, D. and Beedholm, K. 2010. Single source sound production and dynamic beam formation in echolocating harbour porpoises (Phocoena phocoena). J. Exp. Biol. 213, 3105-3110.

Mann, D.A., O'Shea, T.J. and Nowacek, D.P. 2006. Nonlinear dynamics in manatee vocalizations. Mar. Mam. Sci. 22, 548–555.

Marcellini, D. L. 1977. The function of a vocal display of the lizard *Hemidactylus frenatus* (Sauria: Gekkonidae). Anim. Behav. 15, 414-417.

McDonald, M. A., Calambokidis, J., Teranishi, A. M. and Hildebrand, J. A. 2001. The acoustic calls of blue whales off California with gender data. J. Acoust. Soc. Am. 109, 1728–1735.

McDonald, M.A., Hildebrand, J.A. and Mesnick, S.L. 2006. Biogeographic characterization of blue whale song worldwide: using song to identify populations. J. Cet. Res. Manage. 8, 55–65.

McSweeney, D. J., Chu, K. C., Dolphin, W. F. and Guinee, L. N. 1989. North Pacific humpback whale songs: a comparison of southeast Alaskan feeding ground songs and Hawaiian wintering ground songs. Mar. Mam. Sci. 5, 116–138.

Medrano, L., Salinas, I., Salas, P., Ladr6n de Guevara, P., Aguayo, A., Jacobsen, J. and Baker, C.S. 1994. Sex identification of humpback whales, *Megaptera novaeangliae,* on the wintering grounds of the Mexican Pacific Ocean. Can. J. Zool. 72, 1771-1774.

Mellinger, D. K., Carson, C. D., and Clark, C. W. 2000. Characteristics of minke whale (*Balaenoptera acutorostrata*) pulse trains recorded near Puerto Rico. Mar. Mam. Sci. 16, 739–756.

Miller, P. J. O., Samarra, F. I. P., and Perthuison, A. 2007. Caller sex and orientation influence spectra of two-voice stereotyped calls produced by free-ranging killer whales *Orcinus orca*. . Acoust. Soc. Am. 121, 3932–3937.

Mobley, J.R., Herman, L.M. and Frankel, A.S. 1988. Responses of wintering humpback whales *(Megaptera novaeangliae)* to playback of recordings of winter and summer vocalizations and of synthetic sound. Behav. Ecol. Sociobiol. 23, 211-223.

Nerini, M. D., Braham, H. W., Marquette, W. M. and Rugh, D. J. 1984. Life History of the bowhead whale, *Balaena mysticetus* Mammalia: Cetacea. J. Zool. 204, 443–468.

Neubauer, J., Edgerton, M. and Herzel, H. 2004. Nonlinear Phenomena in Contemporary Vocal Music. J. Voice 18: 1–12. doi:10.1016/S0892-1997(03)00073-0

Noad, M.J., D.H. Cato, M.M. Bryden, M-N. Jenner and K.C.S. Jenner. 2000. Cultural revolution in whale songs. Nature 408, 537.

Oleson, E. M., J. Calambokidis, W.C. Burgess, M.A. McDonald, C.A. LeDuc and J.A. Hildebrand. 2007. Behavioral context of call production by eastern North Pacific blue whales. Mar. Ecol. Prog. Ser. 330, 269-284.

Parks, S. E. 2003. Response of North Atlantic right whales *(Eubalaena glacialis)* to playback of calls recorded from surface active groups in both the North and South Atlantic. Mar. Mam. Sci. 19, 563-580.

Parks, S.E., Hamilton, P.K., Kraus, S.D. and Tyack, P.L. 2005. The gunshot sound produced by male North Atlantic right whales *(Eubalaena glacialis)* and its potential function in reproductive advertisement. Mar. Mam. Sci. 21, 458-475.

Payne, R.S. and McVay, S. 1971. Songs of Humpback Whales. Science 173, 585-597.

Payne, R.S. and Webb, D. 1971. Orientation by means of long range acoustic signalling in baleen whales. Ann. NY Acad. Sci. 188, 110-141. doi: 10.1111/j.1749-6632.1971.tb13093.x

Payne, K.B, Langbauer, W.R. and Thomas, E.M. 1986. Infrasonic calls of the Asian elephant (*Elephas maximus*). Behav. Ecol. Sociobiol. 18, 297-301. doi: 10.1007/BF00300007

Payne, R. and Guinee, L.N. 1983. Humpback whale songs as an indicator of 'stocks'. Pp. 333-358. In: R. Payne (Ed.). Communication and behaviour of whales. Westview Press, Boulder, Colorado.

Payne, K., Tyack, P. and Payne, R.S. 1983. Progressive change in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. Pp. 9-57. In: R. Payne (Ed.). Communication and behaviour of whales. Westview Press, Boulder, Colorado.

Payne, K. and Payne, P. 1985. Large scale changes over 19 years in songs of humpback whales in Bermuda. Z. Tierpsychol. 68, 89-114.

Rankin, S. and Barlow, J. 2005. Source of the North Pacific "boing" sound attributed to minke whales. J. Acoust. Soc. Am. 118, 3346–3351.

Rautio, A., Niemi, M., Kunnasranta, M., Holopainen, I. and Hyvärinen, H. 2009. Vocal repertoire of the Saimaa ringed seal (*Phoca hispida saimensis*) during the breeding season. Mar. Mam. Sci. 25, 920-930.

Ray, C., Watkins, W.A. and Burns, J.J. 1969. The underwater song of *Erignathus* (bearded seal). Zoologica 54, 79-83.

Reby, D. and McComb, K. 2003a. Vocal communication and reproduction in deer. Adv. Stud. Behav. 33, 231–264.

Reby, D. and McComb, K. 2003b. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim. Behav. 65, 519–530. doi:10.1006/anbe.2003.2078

Reese, C., Calvin, J. A., George, J. C. and Tarpley, R. J. 2001. Estimation of fetal growth and gestation in bowhead whales. J. Am. Stat. Assoc. 96, 915–938.

Reidenberg J.S. and Laitman J.T 1992. Anatomy of the vocal apparatus of humpback whales (*Megaptera novaeangliae*). Anat. Rec. 232: 73A

Reidenberg, J.S. and Laitman, J.T. 2007. Discovery of a low frequency sound source in Mysticeti (baleen whales): Anatomical establishment of a vocal fold homolog. Anat. Rec. 290, 745-759.

Riede, T., Herzel, H., Mehwald, D., Seidner, W., Trumler, E., Tembrock, G. and Böhme, G. (2000) Nonlinear phenomena and their anatomical basis in the natural howling of a female dog-wolf breed. J. Acoust. Soc. Am. 108, 1435–1442. doi:10.1121/1.1289208

Riede, T., Owren, M.J. and Arcadi, A.C. 2004. Nonlinear acoustics in pant hoots of common chimpanzees (Pan troglodytes): frequency jumps, subharmonics, biphonation, and deterministic chaos. Am. J. Primatol. 64, 277–291. doi:10.1002/ajp. 20078

Ridgway, S. H., Carder, D. A., Kamolnick, T., Smith, R. R., Schlundt, C. E. and Elsberry, W. R. 2001. Hearing and whistling in the deep sea: depth influences whistle spectra but does not attenuate hearing by white whales (*Delphinapterus leucas*) (Odontoceti, Cetacea). J. Exp. Biol. 204, 3829-3841.

Risch, D., Clark, C. W., Corkeron, P. J., Elepfandt, A., Kovacs, K. M., Lydersen, C., Stirling, I. and Van Parijs, S. M. 2007. Vocalizations of male bearded seals, Erignathus barbatus: classification and geographic variation. Anim. Behav. 73, 747-762.

Samarra, F.I.P., Deecke, V.B., Vinding, K., Rasmussen, M.H., Swift, R.J. and Miller, P.J.O. 2010. Killer whales (Orcinus orca) produce ultrasonic whistles. J. Acoust. Soc. Am. 128, 205-210.

Sanvito, S., Galimberti, F. and Miller, E.H. 2007. Vocal signalling of male southern elephant seals is honest but imprecise. Animal Behav. 73, 287-299. doi:10.1016/j.anbehav.2006.08.005

Schevill, W.E. and Lawrence, B. 1949. Underwater listening to the white porpoise (Delphinapterus leucas). Science 109, 143-144.

Searcy, W.A. and Andersson, M. 1986. Sexual selection and the evolution of song. Ann. Rev. Ecol. Syst. 17, 507-533.

Simon, M., Stafford, K.M., Beedholm, K., Lee, C.M. and Madsen, P.T. 2010. Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging. J. Acoust. Soc. Am. 128, 3200-3210.

Širović, A., Hildebrand, J. A., Wiggins, S. M., McDonald, M. A., Moore, S.E. and Thiele, D. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. Deep-Sea Res. 51, 2327–2344.

Širović, A., Hildebrand, J.A. and Wiggins, S.M. 2007. Blue and fin whale call source levels and propagation range in the Southern Ocean. J. Acoust. Soc. Am. 122, 1208-1215.

Slater, P.J.B. 1986. The cultural transmission of bird song. Trends Ecol. Evol. 1**,** 94-97.

Stafford, K.M., Nieukirk, S.L. and Fox, C.G. 2001. Geographic and seasonal variation of blue whale calls in the North Pacific. J. Cet. Res. Manage. 3, 65–76.

Stafford, K. M., Moore, S. E. and Fox, C. G. 2005. Diel variation in blue whale calls recorded in the eastern tropical Pacific. Anim. Behav. 69, 951–958.

Stafford, K.M., S.E. Moore, K.L. Laidre and M.P. Heide-Jørgensen. 2008. Bowhead whale springtime song off West Greenland. J. Acoust. Soc. Am. 124, 3315-3323.

Stimpert, A.K., Wiley, D.N., Au, W.W.L., Johnson, M. and Arsenault, R. 2007. Megapclicks: acoustic click trains and buzzes used during nighttime foraging of humpback whales (*Megaptera novaeangliae).* Biol. Lett. 3, 467-470.

Stirling, I. 1973. Vocalization in the ringed seal (*Phoca hispida*). J. Fish. Res. Can. 30, 107-153.

Stirling, I., Calvert, W. and Spencer, C. 1987. Evidence of stereotyped underwater vocalization of male Atlantic walruses (*Odobenus rosmarus rosmarus*). Can. J. Zool. 65, 2311-2321.

Thomas, J.A., Zinnel, K.C. and Ferm, L.M. 1983. Analysis of Weddell seal (*Leptonychotes weddelli*) vocalizations using underwater playbacks. Can. J. Zool. 61, 1448-1456.

Tyack, P.L. 1981. Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds. Behav. Ecol. Sociobiol. 13, 49-55.

Tyack, P.L. 1983. Differential response of humpback whales, *Megaptera novaeaghae,*to playback of song or social sounds. Behav. Ecol. Sociobiol 13, 49-55.

Tyack, P.L. and Whitehead, H. 1983. Male competition in large groups of wintering humpback whales. Behaviour 83, 132-154.

Tyack, P.L. 1986. Population biology, social behavior, and communication in whales and dolphins. Trends Ecol. Evol. 1, 144–150.

Tyack P.L. 2000. Functional aspects of cetacean communication. Pp.. 247-270. In: J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (Eds.) Cetacean societies, Field studies of Dolphins and Whales. The University of Chicago Press, Chicago.

Tyack P.L. and Clark C.W. 2000. Communication and Acoustic Behavior of Dolphins and Whales. Pp. 156-225. In: W.W.L. Au, A.N. Popper and R.R. Fay (Eds.). Hearing by whales and dolphins. New York, Springer-Verlag.

Tyson, R.B., Nowacek, D.P. and Miller, P.J.O. 2007. Nonlinear phenomena in the vocalizations of North Atlantic right whales (*Eubalaena glacialis*) and killer whales (*Orcinus orca*). J. Acoust. Soc. Am. 122, 1367-1373.

Urick, R.J. 1983. Principles of underwater sound. 3rd edition, New York: McGraw- Hill.

Vallet, E., Beme, I. and Kreutzer, M. 1998. Two-note syllables in canary songs elicit high levels of sexual display. Animal Behav. 55, 291-297.

Van Parijs, S. M., Janik, V. M. and Thompson, P. M. 2000. Display area size, tenure and site fidelity in the aquatic mating male harbour seal. Can. J. Zool. 78, 2209–2217.

Van Parijs, S. M., Lydersen, C. and Kovacs, K. 2003. Vocalizations and movements suggest alternative mating tactics in male bearded seals. Animal Behav. 65**,** 273-283. doi:10.1006/anbe.2003.2048

Wells, K.D. and Schwartz, J.J. 1984. Vocal communication in a neotropical frog, *Hyla ebraccata*: advertisement calls. Animal Behav. 32, 405-420.

Wilden, I., Herzel, H., Peters, G. and Tembrock, G. 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalizations. Bioacoustics 9, 171-196.

Winn, H. and Winn, L. 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. Mar. Biol. 47, 97-114.

Winn, H.E., Thompson, T.J., Cummings, W.C., Hain, J., Hudnall, J., Hays, H. and Steiner, W.W. 1981. Song of the Humpback Whale - Population Comparisons. Behav. Ecol. Sociobiol. 8, 41-46.

Watkins, W.A., Tyack, P., Moore, K.E. and Bird J.E. 1987. The 20-Hz signals of finback whales (*Balaenoptera physalus*). J. Acoust. Soc. Am. 82, 1901-1912.

Würsig, B. and C. Clark. 1993. Behavior. Pp. 157-200. In: J.J. Burns, J.J. Montague and C.J. Cowles (Eds.). The bowhead whale. Special publication Number 2: The society of Marine Mammalogy.

Paper I

Tervo, O. M., Parks, S. E. and Miller, L. A. (2009). Seasonal changes in the vocal behavior of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland. *Journal of the Acoustical Society of America* 126(3): 1570-1580.

Seasonal changes in the vocal behavior of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western-Greenland

Outi M. Tervo[a)]
Arctic Station, University of Copenhagen, P.O. Box 504, 3953 Qeqertarsuaq, Greenland

Susan E. Parks
Applied Research Laboratory, Pennsylvania State University, P.O. Box 30, State College, Pennsylvania 16804-0030

Lee A. Miller
Institute of Biology, University of Southern Denmark, DK 5230 Odense M, Denmark

(Received 17 December 2008; revised 19 May 2009; accepted 3 June 2009)

Singing behavior has been described from bowhead whales in the Bering Sea during their annual spring migration and from Davis Strait during their spring feeding season. It has been suggested that this spring singing behavior is a remnant of the singing during the winter breeding season, though no winter recordings are available. In this study, the authors describe recordings made during the winter and spring months of bowhead whales in Disko Bay, Western-Greenland. A total of 7091 bowhead whale sounds were analyzed to describe the vocal repertoire, the singing behavior, and the changes in vocal behavior from February to May. The vocal signals could be divided into simple (frequency-modulated) calls ($n=483$), complex (amplitude-modulated) calls ($n=635$), and song notes ($n=5973$). Recordings from the end of February to middle of March were characterized by higher call rates with a greater diversity of call types than recordings made later in the season. This study is the first description of bowhead song from the stock in Western-Greenland during both the winter and spring months, and provides support for the hypothesis that song during the winter months contains more song notes than song from the spring making the winter song more variable. © *2009 Acoustical Society of America.* [DOI: 10.1121/1.3158941]

PACS number(s): 43.80.Ka, 43.30.Sf [WWA] Pages: 1570–1580

I. INTRODUCTION

Bowhead whales, *Balaena mysticetus*, are found only in the arctic waters of the Northern Hemisphere (Moore and Reeves, 1993). The global population has traditionally been divided into five stocks: (1) Okhotsk Sea stock, (2) Bering Sea stock, (3) Hudson Bay stock, (4) Davis Strait stock, and (5) Spitsbergen stock. The Hudson Bay stock and Davis Strait stock have been treated separately due to historical whaling records, but in the light of modern satellite tag data and genetic data, it is likely that the two stocks form one population (Heide-Jørgensen *et al.*, 2003, 2006, 2007a). Disko Bay in Western-Greenland is known to be an important aggregation area for the Davis Strait–Hudson Bay bowhead whales (Eschricht and Reinhardt, 1861). Every year from February to May bowhead whales can be seen in a relatively small area in Disko Bay and in increasingly large numbers (Heide-Jørgensen *et al.*, 2006, 2007b). The current estimate of the population size of bowhead whales in Western-Greenland is ~1200 individuals (April–May) (Heide-Jørgensen *et al.*, 2007b). Disko Bay is an aggregation area primarily for adult animals; juvenile animals are rarely seen (Heide-Jørgensen *et al.*, 2007b). Furthermore, in the months of April and May, almost all of the whales (105/130, 81%) occupying the area of Disko Bay are female (Heide-Jørgensen *et al.*, 2007c). Disko Bay is an important feeding area for the bowhead whales in April and May (Laidre *et al.*, 2007), but the behavior, sex ratio, abundance, and movements of the whales earlier in the season are poorly documented. It is possible that more males are present in the area in February and March. Given the late winter presence of bowhead whales in the area, Disko Bay is a potential mating ground for the Davis Strait–Hudson Bay bowhead whale population (Würsig and Clark, 1993; Tyack and Clark, 2000). The few observations of sexual behavior of bowhead whales have been documented in January and February in Disko Bay (Eschricht and Reinhardt, 1861), and the extensive singing behavior of bowhead whales in February and March presented in this study further supports the hypothesis that Disko Bay acts as a mating ground for bowhead whales.

The functions of bowhead whale sounds remain poorly understood despite recording efforts spanning over more than 20 years. Most descriptions of bowhead whale sounds are primarily from recordings of the Bering Sea population near Alaska (Ljungblad *et al.*, 1982, 1984; Clark and Johnson, 1984; Cummings and Holliday, 1987; Blackwell *et al.*, 2007), with a few studies recording sound from the Davis Strait–Hudson Bay population (Richardson and Finley, 1989; Richardson *et al.*, 1995; Tervo, 2006; Stafford *et al.*, 2008). The winter time acoustic behavior for the species is not known (Tyack and Clark, 2000). The migrating bowhead whales off Point Barrow, Alaska have been the subject of several acoustical studies (Ljungblad *et al.*, 1982; Clark and

[a)]Author to whom correspondence should be addressed. Electronic mail: ote@science.ku.dk

Johnson, 1984; Cummings and Holliday, 1987). The majority of the sounds recorded from the passing bowhead whales were low frequency-modulated (FM) calls (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Cummings and Holliday, 1987) with reported frequency ranges of 25–600 (Ljungblad *et al.*, 1982), 50–300 (Clark and Johnson, 1984), and 25–900 Hz (Cummings and Holliday, 1987). The sounds, or calls, were descending, ascending, constant, or inflecting in frequency (Clark and Johnson, 1984). The duration of all of these calls ranged from short 0.5 s signals to long and melodic 4–5 s tones (Clark and Johnson, 1984). Both song and singing behavior are considered to be advanced forms of vocalization in baleen whales (Clark, 1991). A song is composed of units, phrases, and themes. Units sung in a sequence form phrases, a repetition of a phrase is a theme, and several themes combined create a song (Payne and McVay, 1971). Songs have been recorded from bowhead whales during their spring migration in April–May off Point Barrow when the whales return from their breeding grounds and swim toward their feeding areas (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Cummings and Holliday, 1987) and in Disko Bay, Western-Greenland, during February through May (Tervo, 2006; Stafford *et al.*, 2008). Songs have been documented to change within and between seasons (Clark and Johnson, 1984; Würsig and Clark, 1993; Tervo *et al.*, 2007). It has been suggested that song recorded during the spring migration is a remnant from the winter breeding season and therefore may not represent the entire richness and complexity of the signals that are potentially present earlier in the winter when the bowhead whales are presumed to mate (Würsig and Clark, 1993; Tyack and Clark, 2000).

Song and singing behavior likely have significance in mate choice and sexual selection (Tyack, 1981; Tyack and Clark, 2000; Clark *et al.*, 2003). Four species of baleen whales produce songs: (1) the humpback whale (Payne and McVay, 1971) (*Megaptera novaeangliae*), (2) the blue whale (Cummings and Thompson, 1971) (*Balaenoptera musculus*), (3) the fin whale (Watkins *et al.*, 1987) (*Balaenoptera physalus*), and (4) the bowhead whale (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Cummings and Holliday, 1987). The best studied species is the humpback whale, which produces long and elaborate songs while in their winter grounds (Payne and McVay, 1971; Winn and Winn, 1978) where they breed and calve (Baker and Herman, 1984) and in late spring on their foraging grounds (Clark and Clapham, 2004). The singing behavior has been suggested to have significance in male breeding success (Tyack, 1981; Tyack and Clark, 2000) as only male humpback whales have been documented to sing (Glockner, 1983; Baker and Herman, 1984; Baker *et al.*, 1991). Humpback whale song has been suggested to function as an advertisement display (Tyack and Clark, 2000) and the same could be the case for bowhead whale song (Clark *et al.*, 2003) as well as for fin whale and blue whale song where only males have been observed to sing (McDonald *et al.*, 2001; Croll *et al.*, 2002; Oleson *et al.*, 2007). However, in right whales, a closely related species to bowhead, song has not been described (Clark, 1982; Parks and Tyack, 2005) and females produce the majority of sounds in social surface active groups (SAGs) (Parks and Tyack, 2005). The lack of song in right whales and the prevalence of female vocal behavior in social and sexual contexts make it unclear as to the sex of singing bowheads.

The goal of this study is to describe the changes in the singing behavior of the Davis Strait population of bowhead whales in Disko Bay from winter to spring. Disko Bay is an aggregation area for bowhead whales from January to May providing a unique opportunity to study the variability of vocal behavior of the same population throughout the winter and spring seasons. Understanding the singing behavior during winter is important since bowhead whales are presumed to mate at this time and the changes that occur in the singing behavior during a season can help to pinpoint the timing of sexual behavior of this population. The mating period is one of the most important time periods in the life cycle of a species and more information is needed to ensure that a potential key habitat such as Disko Bay remains accessible for the Davis Strait/Hudson Bay population of bowhead whales during this period.

II. METHODS

A. Collection of acoustic recordings

The study area was located in Disko Bay, Western-Greenland about 69°N and 54°W (Fig. 1). Acoustic recordings of bowhead whale vocalizations were made in Disko Bay offshore from Qeqertarsuaq between 25 February 2005 and 10 May 2005. A total of 890 min of recordings were made over 11 days during the 4 month study period (Table I).

The recordings were made using two hydrophones that were lowered into the water from each side of a dinghy or from R/V Porsild (a 49.5 ft, ice-strengthened, steel vessel) to a depth of ~8 m. One hydrophone (HELWEG, custom built) had a built-in 20 dB amplification and a flat frequency response to 50 kHz (±3 dB). The second hydrophone was a HS 150 (Sonar Research and Development Ltd., Beverley, UK) with a flat frequency response to 150 kHz, which was connected to an Etec amplifier (1 Hz–1 MHz) (Etec, Frederiksværk, Denmark) with high pass filter set at 10 Hz and 26 dB gain. The signals were recorded using a SONY DAT TDC-D8 tape recorder with a sampling frequency of 44.1 kHz. The DAT recorder was the frequency limiting instrument; thus the flat frequency response of the entire recording system was from 20 Hz to 22 kHz.

Simultaneous visual observations of the whales were made whenever possible. The number of individuals and their geographic position (latitude/longitude) were noted. All the recordings were made in the presence of bowhead whales during daylight hours between 8 a.m. and 5 p.m. in February and March and between 8 a.m. and 9 p.m. in April and May.

B. Data analysis

The audio data from the DAT tapes were digitized into standard wave files with BATSOUND software (Petterson Elektronik, Uppsala, Sweden). The acoustic data were analyzed using RAVEN 1.2.1 (Cornell Laboratory of Ornithology, Ithaca, NY) (Hann window, fast Fourier transform (FFT) size 512, with 50% overlap). The recorded signals were divided into the three main categories described by Clark (1991) using a

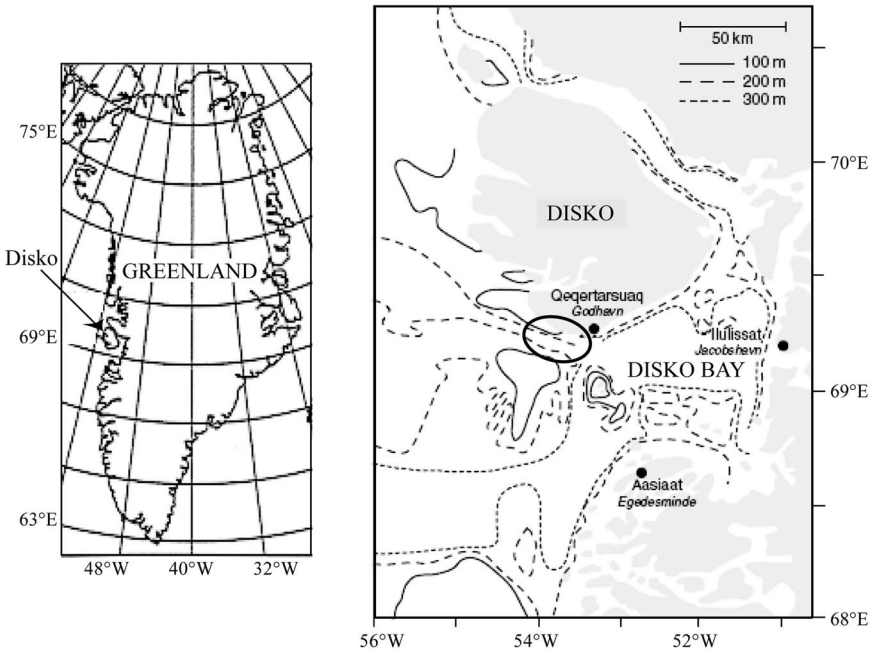

FIG. 1. Map of Greenland showing the location of Disko Bay (courtesy of Torkel Gissel Nielsen). The oval marks the general area where the recordings were made.

combination of spectral and audio qualities: simple FM calls, complex amplitude-modulated (AM) calls, and song notes. Eight variables were measured from simple FM calls and from song notes, including duration, maximum frequency, minimum frequency, frequency range, start frequency, end frequency, number of inflection points, and number of modulation points (Fig. 2). Only four of these parameters were measured for complex AM calls. These were duration, maximum frequency, minimum frequency, and frequency range. Duration of the signal was measured in seconds and was determined from the spectrogram or in some cases from the oscillogram. Maximum and minimum frequencies (Hz) were the highest and lowest frequency points in the signals and were measured from the spectrogram. Frequency range (Hz) refers to the difference between maximum and minimum frequencies of a signal. Start frequency (Hz) refers to the frequency at the start of the signal and end frequency (Hz) to that at the end of the signal. An inflection point refers to a point in the signal where the frequency contour changed from a positive slope to a negative slope or vice versa. A modulation point is a point in the signal showing a smaller degree of frequency modulation that was not strong enough to change the general direction of the signal in frequency and time. A change from a relative constant frequency to a positive or negative frequency slope was considered a modulation point (Fig. 2). Statistical analyses were done using S-PLUS 2000 (MathSoft. Inc., Seattle, WA) and SPSS 12.0.1 (SPSS Inc., Chicago, IL). A Hamming window and a FFT size of 1024 with 75% overlap were used to create the figures of the spectrograms in order to provide good resolution.

III. RESULTS

The bowhead whale was the only baleen whale species present in Disko Bay during the duration of the study and therefore the authors are confident that the acoustic signals

TABLE I. Distribution of sampling days into three time periods, number of different signal types recorded in each period, and the total amount of time in minutes recorded during each of the periods. Note that most singing occurred in the winter (time period 1).

			Simple calls		Complex calls		Song notes		Total	
	Time period	min	*n*	Signals/min	*n*	Signals/min	*n*	Signals/min	*n*	Signals/min
25 February 1 March 3 March 8 March	1	61	11	0.2	51	0.8	1090	17.9	1152	18.9
10 March 11 March 15 March	2	367	464	1.3	569	1.6	2849	7.8	3882	10.6
20 April 3 May 5 May 10 May	3	462	8	0.0	15	0.0	2034	4.4	2057	4.5

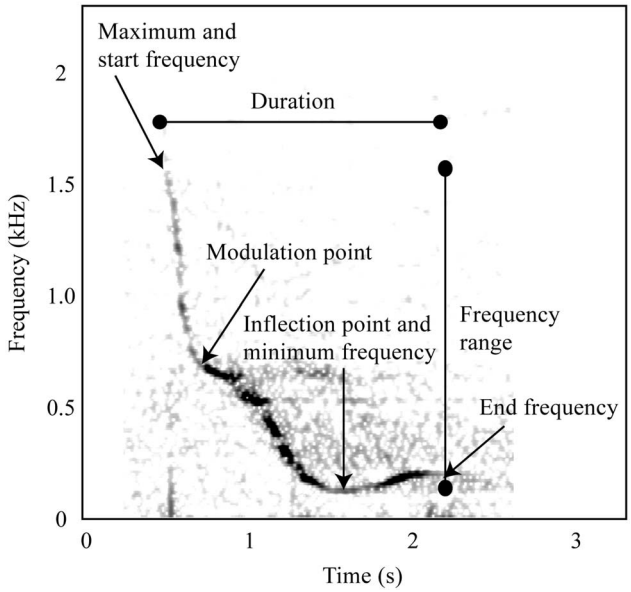

FIG. 2. A spectrogram of a type I song note together with a diagram illustrating the eight different variables measured for simple FM calls and song notes. (Hamming window, FFT size 1024, and 75% overlap).

described in this study were produced by bowhead whales. In addition to the bowhead whale there were two odontocete and five pinniped species inhabiting the study area at the time of the investigation. These were beluga whale *Delphinapterus leucas*, narwhal *Monodon monoceros*, hooded seal *Cystophora cristata*, bearded seal *Erignathus barbatus*, ringed seal *Phoca hispida*, harp seal *Phoca groenlandica*, and walrus *Odobenus rosmarus*. Bearded seal acoustic signals were recorded often from late March through May, but the other six species were not detected in any of the recordings.

Song notes were the most prevalent signal type ($n=5973$) followed by complex AM calls ($n=635$) and simple FM calls ($n=483$). Out of the 5973 song notes, 4115 song notes had a signal/noise ratio of ≥ 6 dB. These selected signals of high quality were analyzed in detail and used in the repertoire description. The remaining song notes ($n=1858$) had the distinctive qualities of song notes, but had signal/noise ratios <6 dB and were therefore used only in the signaling rate measurements.

A. Repertoire of bowhead whale vocalizations

1. Song notes

Songs were composed of song notes, which were narrow band FM signals. Song notes had an average duration of 1.32 ± 0.5 s (Table II). The average minimum and maximum frequencies of song notes were 390 and 982 Hz, respectively. The maximum frequency measured for song notes was 2638 Hz while the lowest frequency measured was 27 Hz. The number of inflection points ranged from 0 to 15, the average value being 1.1. The number of modulation points varied between 0 and 7, and the average value was 0.4. Song notes always appeared in the presence of another song note and in some cases the same song note type was repeated several times. Examples of song notes are shown in Fig. 3.

2. Complex AM calls

Complex calls included pulsative sounds comprised of short broadband pulses [Fig. 4(a)] as well as noisy bursts of sound [Fig. 4(b)] that did not have clear harmonic tonal structure. Complex AM calls had an average duration of 2.7 ± 1.1 s (Table II). The minimum frequency averaged at 91 Hz and maximum frequency at 495 Hz.

3. Simple FM calls and the constant frequency call

Simple calls were divided into three categories: the constant frequency call [Fig. 5(a)], the FM up call, which had an ascending frequency contour [Fig. 5(b)], and the FM down call, which had a descending contour [Fig. 5(c)]. The most common simple call type was by far the constant frequency

TABLE II. Time and frequency parameters of song notes and calls. See Fig. 2 for an illustration of the measured parameters.

		Duration (s)	Min (Hz)	Max (Hz)	Range (Hz)	Start (Hz)	End (Hz)	Inflections	Modulations
Song notes No.=4115	Average	1.3	390.2	981.5	591.2	962.5	466.2	1.1	0.4
	Median	1.3	335.7	952.3	530.8	907.3	404.0	1	0
	St. Dev.	0.5	263.4	282.2	381.0	288.2	281.1	1.5	0.7
	Min	0.2	26.6	125.7	35.9	83.0	26.6	0	0
	Max	7.0	1984.0	2636.4	2275.8	2636.4	2463.0	15	7
Simple FM calls No.=483	Average	1.4	155.9	208.3	52.4	196.6	169.1	0.1	0.0
	Median	171.0	31.2	163.7	131.5	28.6	0.0	0	0
	St. Dev.	0.9	111.0	143.1	68.7	133.2	127.9	0.3	0.3
	Min	0.2	41.0	70.1	7.0	41.0	54.1	0	0
	Max	6.6	1050.8	1263.3	682.5	1263.3	1050.8	2	5
Complex AM calls No.=635	Average	2.7	91.1	494.5	403.4				
	Median	2.8	88.6	432.8	346.1				
	St. Dev.	1.1	35.4	268.2	272.1				
	Min	0.5	20.1	128.7	31.2				
	Max	8.9	287.4	2222.5	2137.0				

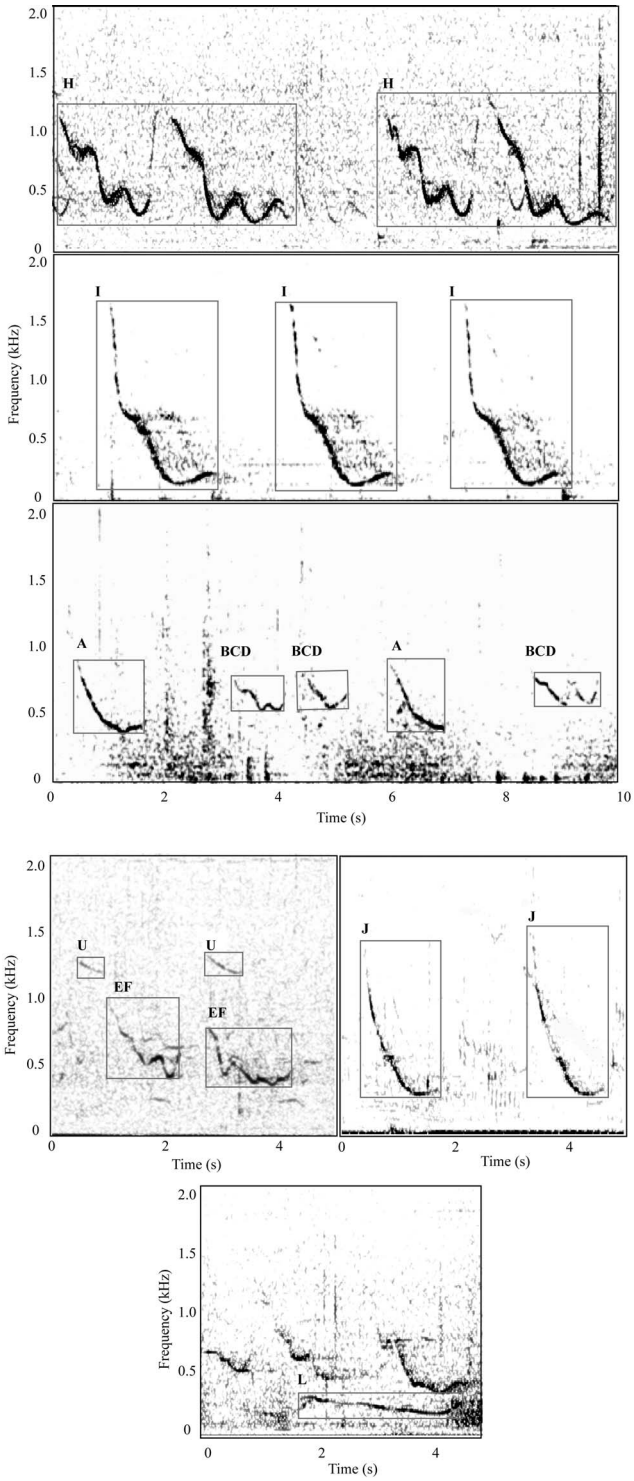

FIG. 3. Spectrograms of the eight song note types H, I, J, L, A, BCD, EF, and U (Hamming window, FFT size 1024, and 75% overlap).

call, which comprised 96.5% (n=466) of all simple calls. The FM up calls comprised 1.9% (n=9) and down calls 1.7% (n=8) of the data. Simple FM calls including the constant frequency call had an average duration of 1.4±0.9 s (Table II). The constant frequency calls had an average minimum frequency of 156 Hz and an average maximum frequency of 208 Hz. Harmonics were present in 24% (n=117) of the simple calls. The number of harmonics ranged from 1 to 13 averaging at 3±2. Harmonics could exceed 2000 Hz. Simple FM calls were not rich in inflection or in modulation points.

B. Classification of song notes

Using visual and audio qualities a classification of song notes was created and named A, B, C, D, E, F, H, I, J, L, and U. All the signals that did not fit into this categorization, but still had the distinctive qualities of a song note were named type x (n=48). The categorization was tested using multinomial log-linear regression analysis in S-PLUS 2000. The variables used in the analysis were duration, minimum frequency, maximum frequency, frequency range, start frequency, end frequency, number of inflection points, and number of modulation points. The results show that eight song note categories, instead of the original 11 categories, could be distinguished from each other using the variables measured (Table III). Using categorizations A, BCD, EF, H, I, J, L, and U the vast majority of the song notes (95.5%) were classified correctly by the multinomial log-linear regression model (Table III).

Each of the eight song note types had a characteristic frequency contour (Fig. 3) that was reflected in the number of inflection and modulation points and in the start and end frequencies of the signals (Table IV). Types BCD and U were short in duration (1.1 and 0.8 s) whereas type H had the longest average duration (3.6 s) (Table IV). Types I and L had both a low average minimum frequency (157 and 158 Hz), but type I had a broad frequency range (956 Hz) whereas type L had a narrow frequency range (237 Hz) (Table IV). Type J had the highest average maximum frequency (1337 Hz) even though the maximum frequency was measured for type I (2517 Hz) (Table IV).

By definition, song notes were always found in the presence of other song notes. Most of the type A song notes (76%, n=285) were encountered in the presence of one or more type BCD song notes. In 39.7% of these occasions (n=149) type A was followed by one type BCD song note. In 30.4% of the occasions (n=114) type A song note was followed by two BCD type song notes and in 5.1% (n=19) by three BCD song notes (Fig. 6). The least common combination consisted of a type A song note followed by four BCD notes, comprising only 0.8% (n=3) of the data. The remaining 24% of the A song notes (n=90) were observed following arbitrary song note types. Type BCD song notes were never observed without song note type A. Types EF, H, I, J, L, and U song notes were never observed singly; they were always observed with multiple copies of the same unit occurring in succession. For example, the following sequences would be observed: H, H or I, I, I (Fig. 3). Duration of song note combinations altered from a few seconds to a few minutes whereas the entire song session could last for hours.

C. Temporal changes in vocalizations

In order to investigate gradual changes in the vocal behavior in time, the study was divided into three time periods. Each period covers approximately 3 weeks of the season depending on the availability of the data. The time periods

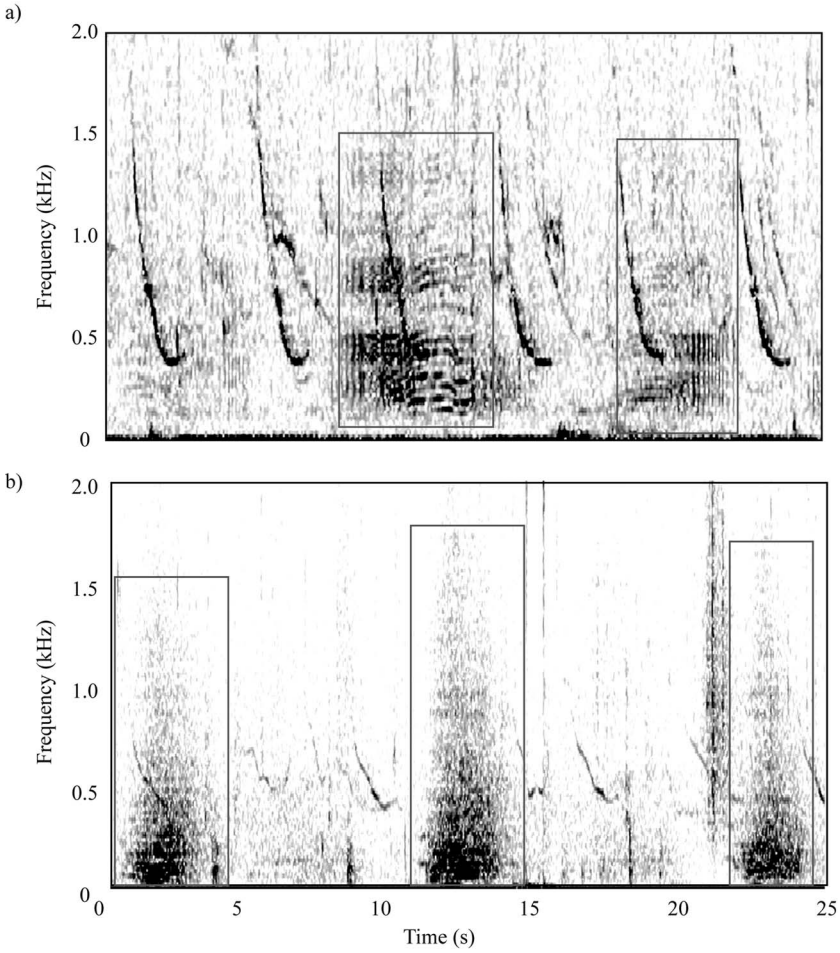

FIG. 4. Spectrograms of two pulsative complex AM calls. Those with harmonics (a) occur simultaneously with FM calls (see Fig. 5). Three complex AM calls with noisy burst-like appearances are shown in (b). All calls are inscribed in boxes (Hamming window, FFT size 1024, and 75% overlap).

were (1) 25 February–1 March 2005, (2) 3 March–15 March 2005, and (3) 20 April–10 May 2005. The overall signaling rate was the highest in the first time period when a total of 1152 signals were recorded in 61 min (18.9 signals min^{-1}) (Table I). The signaling rate decreased to 10.6 signals min^{-1} in the next time period and to 4.5 signals min^{-1} in the third time period. The entire study period was characterized by a high number of song notes per minute compared with the number of complex AM calls and simple FM calls per minute (Table I).

The types of song notes and rates of different song note types in the three time periods were distinctly different (Table V). There were five different types of song notes in the first winter time period and six different song note types in the second winter period. In contrast, only one song note, type I (see Fig. 3), was observed during the third time period, spring. This particular song note was not observed in the two winter time periods. Another difference in the singing between the first two time periods and the third time period was that in winter most of the song notes were emitted by two or

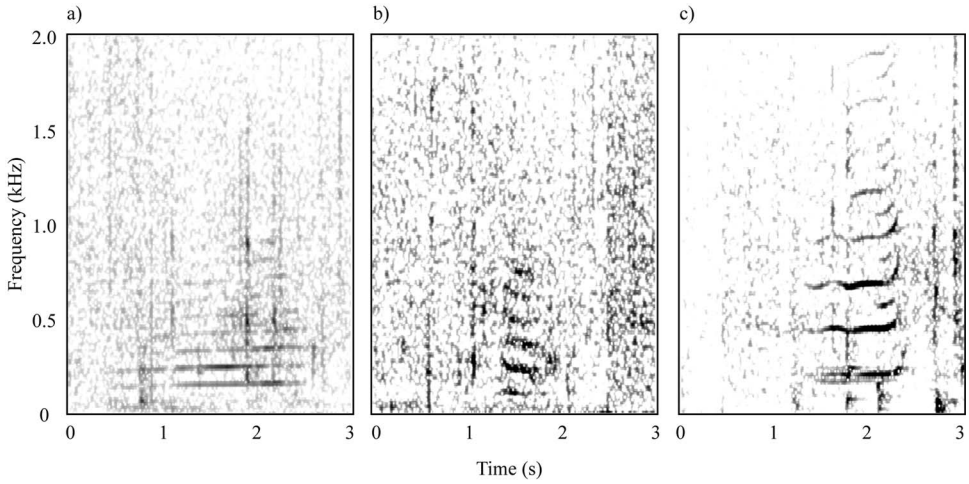

FIG. 5. Spectrogram of simple calls. A constant frequency call is shown in (a), a FM down call in (b), and a FM up call in (c). All have harmonics (Hamming window, FFT size 1024, and 75% overlap).

TABLE III. Multinomial log-linear regression analysis table for eight song note categories from lines to columns. The variables used were duration, minimum frequency, maximum frequency, frequency range, start frequency, end frequency, number of inflection points, and number of modulation points. The values are percentages. The values in bold indicate the percentage of signals that were classified to the type to which they were manually assigned. The numbers in bold print indicate the highest percentage score.

%		A	BCD	EF	H	I	J	L	U
A	(n=374)	**93.6**	2.1	0.5	0.0	1.1	2.7	0.0	0.0
BCD	(n=309)	2.6	**95.1**	1.9	0.0	0.0	0.0	0.0	0.3
EF	(n=347)	2.9	1.1	**93.4**	0.6	1.7	0.3	0.0	0.0
H	(n=46)	0.0	0.0	10.9	**89.1**	0.0	0.0	0.0	0.0
I	(n=2015)	0.7	0.0	0.1	0.0	**98.3**	0.8	0.0	0.0
J	(n=170)	8.2	0.6	0.6	0.0	35.9	**54.7**	0.0	0.0
L	(n=47)	0.0	0.0	0.0	0.0	0.0	0.0	**100.0**	0.0
U	(n=759)	0.1	0.3	0.0	0.0	0.0	0.0	0.0	**99.6**

more animals at the same time because some of the calls were overlapping in time (Fig. 6). In spring typically only one animal was singing at a time.

There were some indications of the existence of multiple songs (Fig. 6). In the recording made on the 25 February 2005 song notes of type A were associated with song notes of type BCD. During the same sequence, song notes of type EF were also present together with song notes of type H. Signals of types EF and H never overlapped in time, but they were often being produced at the same time as note types A and BCD. This suggests that one individual was singing a song composed of type A and type BCD song notes and another individual sang a song consisting of types EF and H song notes. Alternatively, these combinations may represent two separate phrases from the seasonal song.

IV. DISCUSSION

This study presents the first description of the vocal behavior of bowhead whales in Disko Bay during the winter. The vocal repertoire of bowhead whales in Disko Bay included simple FM calls, complex AM calls, and songs composed of song notes. Song notes were classified into eight distinctive types. The acoustic behavior of bowhead whales during winter was characterized by a broad repertoire of song note types and a high signaling rate. In contrast, the acoustic behavior of the bowhead whales in the spring consisted of only one song note type and a considerably lower signaling rate.

A. Song notes and singing behavior

Song notes were the most common signals recorded in this study. The frequency range, duration, and number of inflection and modulation points were consistent with the values reported in previous investigations (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Richardson and Finley, 1989; Tervo, 2006; Stafford *et al.*, 2008). Stafford *et al.* (2008) reported higher frequencies for two of the song notes in the "Screech" song recorded from bowhead whales in Disko Bay in 2007 than found in this study. The high interannual variability in the song note repertoire of bowhead whales (Clark and Johnson, 1984; Würsig and Clark, 1993; Tervo *et al.*, 2007) makes it difficult to compare results from studies made in different years. A total of eight different song note categories could be identified in this study. The song notes appeared in succession but without locating the vocalizing individuals it is impossible to determine whether the song notes were produced by a single or multiple individuals therefore making it difficult to judge the duration of a "song." Bowhead whales are known to counter call in song like successions of calls (Blackwell *et al.*, 2007). This study indicates that the Davis Strait stock of bowhead whales emits a rich repertoire of diverse song note types, similar to what has been described for the Bering Sea population.

There were clear differences in the singing behavior of bowhead whales between winter and spring illustrated by a decrease in the song note signaling rate and a change in the song note types that were present. As found in previous studies, there were multiple individuals singing at the same time during winter in contrast to spring where typically only one animal was singing at a time (Würsig and Clark 1993; Tervo, 2006; Stafford *et al.*, 2008). The existence of multiple songs during winter is consistent with the previous studies of the Davis Strait population (Tervo, 2006; Stafford *et al.*, 2008) but whether the multiple songs were due to differences between individuals or sexes is not known. Winter singing was characterized by the presence of many different song note types. During the first two time periods from 25 February to 15 March 2005 there were seven different song note types present. The winter song note type U appears similar to the two- and three-syllable bouts documented by Clark and Johnson (1984) (see Figs. 1 and 4 in Clark and Johnson, 1984). Only one song note type, type I, was present in the spring time period between 20 April and 10 May 2005. This is in sharp contrast with the diversity of song note types present earlier in the season described in this and in previous studies (Tervo, 2006; Stafford *et al.*, 2008), and supports the hypothesis that the song recorded in the spring does not represent the entire richness of the repertoire of singing bowhead whales.

Singing is an acoustic display typically performed by males having significance in mate choice and sexual selection (Searcy and Andersson, 1986). Using acoustic cues to advertise fitness is a behavior that has been described from a wide variety of species of insects, amphibians, birds, and whales (Searcy and Andersson, 1986; Payne and McVay, 1971). If the song of bowhead whales is associated with

TABLE IV. Time and frequency parameters of eight song notes. See Fig. 2 for an illustration of the measured parameters and Figs. 4 and 5 for illustrations of the different types of song notes.

		Duration (s)	Min (Hz)	Max (Hz)	Range (Hz)	Start (Hz)	End (Hz)	Inflections	Modulations
Type A, $n=374$	Average	1.5	375.9	877.1	501.2	875.9	417.9	0.4	0.3
	Median	1.5	364.3	878.7	497.5	877.5	410.0	0	0
	St. Dev.	0.3	55.7	141.6	129.3	142.5	75.5	0.5	0.7
	Min	0.6	218.6	482.7	174.7	482.7	218.6	0	0
	Max	2.5	560.5	1293.5	864.4	1293.5	992.7	2	5
Type BCD, $n=309$	Average	1.1	496.3	795.7	299.4	781.1	675.7	1.2	1.1
	Median	1.1	500.9	794.0	288.7	776.4	682.0	1	1
	St. Dev.	0.3	61.9	104.5	95.2	114.2	108.0	0.8	1.2
	Min	0.4	301.1	546.4	105.1	390.4	385.0	0	0
	Max	2.4	633.6	1187.0	681.7	1187.0	994.7	5	6
Type EF, $n=347$	Average	1.6	343.9	1078.0	733.2	1063.9	455.8	3.9	0.3
	Median	1.6	346.0	1079.6	719.5	1065.6	430.5	4	0
	St. Dev.	0.4	61.7	174.9	172.5	186.9	127.6	1.4	0.6
	Min	0.9	216.6	655.5	351.7	83.0	244.6	0	0
	Max	2.6	573.8	1875.6	1263.9	1875.6	1196.9	8	3
Type H, $n=46$	Average	3.6	312.8	1256.9	944.1	1142.2	420.4	8.2	1.0
	Median	3.7	303.3	1236.2	938.1	1148.0	384.0	8	1
	St. Dev.	0.7	55.0	163.7	176.1	195.6	111.6	2.3	0.8
	Min	1.9	232.4	775.1	421.4	707.0	278.4	2	0
	Max	5.6	517.6	1519.8	1221.1	1519.8	738.0	12	3
Type I, $n=2015$	Average	1.4	157.4	1114.9	957.5	1114.9	210.5	0.7	0.6
	Median	1.5	151.7	1053.1	893.5	1053.1	211.0	1	1
	St. Dev.	0.4	62.5	289.6	297.4	289.6	71.9	0.5	0.6
	Min	0.2	26.6	454.2	280.8	454.2	26.6	0	0
	Max	7.0	1552.8	2516.9	2275.8	2516.9	1861.0	3	7
Type J, $n=170$	Average	1.2	352.8	1336.4	983.6	1336.4	376.7	0.4	0.1
	Median	1.2	301.5	1299.3	926.6	1299.3	335.3	0	0
	St. Dev.	0.4	107.7	315.3	322.0	315.3	106.3	0.5	0.3
	Min	0.5	220.3	657.0	369.1	657.0	226.9	0	0
	Max	2.4	666.0	2010.6	1736.8	2010.6	666.0	2	1
Type L, $n=47$	Average	2.5	158.4	395.2	236.8	301.1	379.1	1.0	0.0
	Median	2.5	147.4	319.4	163.7	297.0	311.2	1	0
	St. Dev.	0.3	27.8	203.6	212.4	24.8	212.4	0.1	0.0
	Min	1.8	122.8	278.4	98.3	257.0	163.8	0	0
	Max	3.2	229.3	1002.6	866.2	376.7	1002.6	1	0
Type U, $n=759$	Average	0.8	946.2	1107.7	161.6	1014.9	1038.9	0.0	0.0
	Median	0.8	887.9	1037.8	159.7	893.3	1025.8	0	0
	St. Dev.	0.3	142.6	133.8	37.7	213.1	75.2	0.0	0.0
	Min	0.2	399.9	562.1	45.8	562.1	399.9	0	0
	Max	1.8	1324.6	1510.2	371.2	1457.6	1510.2	1	1

reproductive advertisement, then Disko Bay may be a mating area for the Davis Strait population of bowhead whales in the winter. Previous studies of the conception time of bowhead whales from the Bering Sea indicate that most conceptions take place between early March and mid-April (Reese *et al.*, 2001), which coincides with the timing of complex song found in this and in previous studies (Tervo, 2006; Stafford *et al.*, 2008). Sexual activity early in the season may shift into foraging behavior in the spring when waters off Disko Island are rich in copepods after the spring algae bloom (Madsen *et al.*, 2001; Laidre *et al.*, 2007). This shift in behavior could explain the low signaling rate and the presence of a less complex song in the spring months. The number of bowhead whales and the duration that individual whales reside in Disko Bay in February and March have not been studied. However, large numbers of bowhead whales are present in Disko Bay in April and May (Heide-Jørgensen *et al.*, 2003, 2007c), indicating that the decline in acoustic activity is not a result of a significant decrease in numbers of whales in the area.

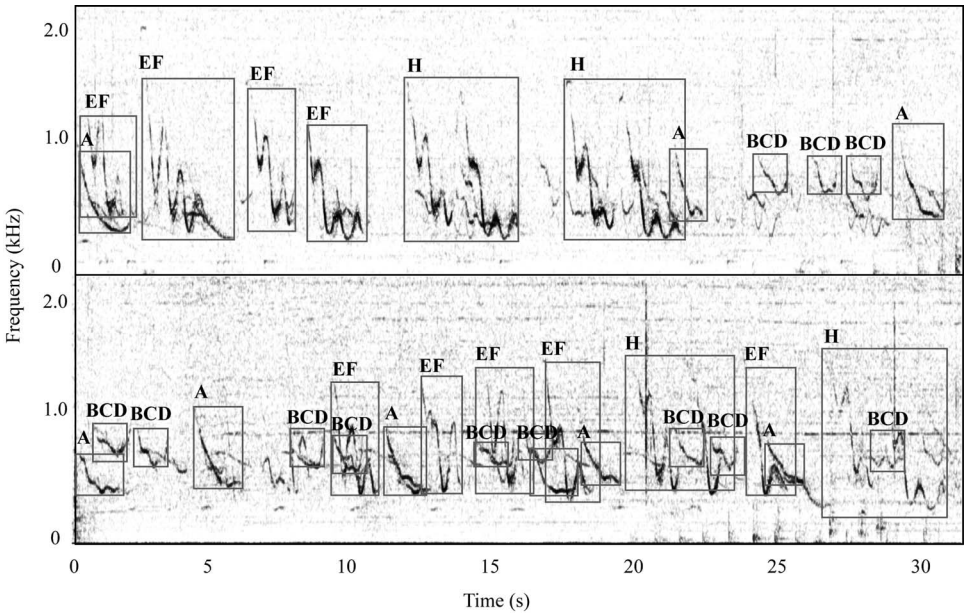

FIG. 6. A spectrogram showing a section of a recording where individual song note types are overlapping in time indicating more than one animal singing at the same time. Types A, BCD, and EF were the dominating song note types. The recording was made on 25 February 2005 (Hamming window, FFT size 1024, and 75% overlap).

B. Simple FM calls and complex AM calls

The simple FM call was the rarest of the three signal types recorded from bowhead whales in present study (Table II). This is in sharp contrast with some of the previous investigations where simple FM calls were the most numerous of the described signal types from the Bering Sea stock (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Ljungblad *et al.*, 1984). Furthermore, simple FM calls have been recorded in May in large number (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Ljungblad *et al.*, 1984; Cummings and Holliday, 1987) whereas the last time period from 20 April to 10 of May 2005 in the present study exhibited lowest signaling rate for simple calls compared with the two previous ones (Table I). However, these differences could be explained by diurnal variation in the signaling rate, which could not be captured in this study.

Simple calls have not been assigned to any particular behavior (Ljungblad *et al.*, 1984), but simple calls with ascending and descending frequencies, referred to as up and down calls (Richardson and Finley, 1989), have been recorded in the presence of socially and sometimes sexually active whales (Ljungblad *et al.*, 1984). The frequency range, duration, and number of inflection and modulation points of simple FM calls were consistent with previously documented values from the Bering Sea population in May (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Ljungblad *et al.*, 1984; Cummings and Holliday, 1987) and September–October (Ljungblad *et al.*, 1982) and from the Davis Strait population in Isabella Bay in August and September (Richardson and Finley, 1989). Simple calls have been also recorded from the Davis Strait population in April (Stafford *et al.*, 2008), but information on call parameters is lacking for comparison.

Complex AM calls were the second most commonly recorded signal type. The average duration measured for the signals in the present study was consistent with measurements from the same kinds of sounds emitted by bowhead whales from the Bering Sea population in May (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Ljungblad *et al.*, 1984; Cummings and Holliday, 1987) and September–October (Ljungblad *et al.*, 1982) and from the Davis Strait population in Isabella Bay in August and September (Richardson and Finley, 1989). A majority of the complex AM calls recorded in Disko Bay had a minimum frequency lower than 100 Hz and the lowest minimum frequency recorded was 20 Hz. Low complex AM calls with minimum frequencies at 25 Hz have been recorded from socially active bowhead whales from the Davis Strait stock in Isabella Bay in August and September (Richardson and Finley, 1989) and from migrating bowhead whales off Point Barrow, Alaska in May and September–October with minimum frequencies starting from 30 Hz (Ljungblad *et al.*, 1982). The average minimum frequency and maximum frequency of complex calls analyzed in this study were consistent with the documented values from the Bering Sea population (Ljungblad *et al.*, 1982; Clark and Johnson, 1984; Cummings and Holliday, 1987) and Davis Strait population (Richardson and Finley, 1989). Complex AM calls have been also recorded

TABLE V. Call rates (signals/min) of song note types A, BCD, EF, H, I, J, L, and U in the three time periods. The last column of the table indicates the number of different song note types recorded in each time period (see Table I). Note the markedly higher rates of calling in the winter time period 1.

Time period	A	BCD	EF	H	I	J	L	U	No. of note types
1	5.90	5.07	4.46	0.70	0	0	0	0.23	5
2	0.04	0	0.20	0.01	0	0.46	0.13	2.03	6
3	0	0	0	0	4.36	0	0	0	1

from the Davis Strait population in April (Stafford *et al.*, 2008), but information on call parameters was not presented for comparison.

Complex calls have not been positively associated with a particular behavior in bowhead whales (Ljungblad *et al.*, 1984; Würsig and Clark, 1993); however, they have been often recorded in the presence of mildly socializing (within a body length) or actively socializing (body contact) bowhead whales (Ljungblad *et al.*, 1984; Würsig *et al.*, 1984) and in the presence of sexually active whale groups (Richardson and Finley, 1989). Complex calls were also characteristic emissions of groups engaging in homosexual activity (Richardson and Finley, 1989). In the present study, complex calls had the highest signaling rate in the second time period from 3 March to 15 March (Table I). Since complex calls in previous studies were often recorded in the presence of socially and sexually active whales, the high signaling rate of complex calls in March observed in this study and the presence of AM calls in early April (Stafford *et al.*, 2008) further support the hypothesis of sexual activity in Disko Bay during winter.

Long-term studies of the acoustic behavior of the Davis Strait population are needed to describe inter-annual variation in the song of the bowhead whales in Disko Bay. Additional comparisons of the repertoires of the Davis Strait population with those of the Bering Sea population can be used to determine the similarities of the acoustic repertoires between the two stocks and furthermore evaluate stock connectivity. Similarities in the vocalizations between two stocks can indicate that the stocks are connected like in the case of humpback whales off Western and Eastern Australia (Noad *et al.*, 2000).

Determining the sex(es) of the singing individuals in this species will be very important to gain insight into the sexual behavior and mate choice strategy of bowhead whales. The bowhead whale is taxonomically closely related to the North Atlantic and southern right whales *Eubalaena glacialis* and *E. australis* (Reeves and Leatherwood, 1985). Males from all the three species possess disproportionately large testes suggesting that sperm competition plays a role in the sexual selection and mating strategy of the species (Brownell and Ralls, 1986). Southern and North Atlantic right whales exhibit signs of a polyandrous mating system where one female mates with multiple males in large mating groups referred to as SAGs (Kraus and Hatch, 2001). Right whales are not known to sing (Clark, 1982), instead, sexual selection pressure on males is thought to take place in the form of sperm competition (Kraus and Hatch, 2001; Mate *et al.*, 2005). Bowhead whales sing complex songs with high inter-annual variation (Clark and Johnson, 1984; Würsig and Clark, 1993; Tervo *et al.*, 2007) much in the manner of humpback whales (Winn and Winn, 1978). Male humpback whales produce long and elaborate songs as an advertisement display fulfilling the criteria of a lekking polygynous species where one male mates with multiple females (Clapham, 1996). Interestingly, bowhead whales seem to exhibit characteristics of both polyandrous and polygynous mating strategies—they have been seen in social groups similar to right whale SAGs (Würsig and Clark, 1993) and they produce songs such as humpback whales. Determining the sex and the size of the singers could greatly enhance the current understanding of the mating system of this species. If male bowhead whales produce songs, it would imply that males may have multiple mating strategies, including acoustic advertisement displays and sperm competition. Which of the two strategies is used could depend on the age and/or the social status of the males as suggested by Würsig and Clark (1993). However, it could be that both sexes produce songs independently or even simultaneously in the form of a duet known from various song bird species (Harcus, 1977; Hall, 2004). If so, this would be the first case of sex-role reversal in cetaceans, where females produce an advertisement display in the form of a complex song.

ACKNOWLEDGMENTS

This study was funded by DANCEA, the Danish Research Council for Natural Sciences (Grant No. 21-03-0171 to L.A.M. and Grant No. 21-04-0391 to Torkel Gissel Nielsen, National Environmental Research Institute, Roskilde, Denmark) and the Centre for Sound Communication, University of Southern Denmark supported by the Danish National Research Council. The Arctic Station of Qeqertarsuaq, University of Copenhagen provided an excellent working platform. The authors want to thank Abel Brandt, Tarfi Mølgaard, Kale Mølgaard, John Jakobsen, and the crew on RV Porsild for their help in data collection. Chris Clark provided valuable assistance in identifying bowhead whale acoustic signals. Rasmus Ejnærs was a great help in the data analysis and Mads Christoffersen gave valuable comments to this manuscript.

Baker, C. S., and Herman, L. M. (**1981**). "Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters," Can. J. Zool. **59**, 460–469.

Baker, C. S., Lambertsen, R. H., Weinrich, M. T., Calambodikis, J., Early, G., and O'Brien, S. J. (**1991**). "Molecular genetic identification of the sex of humpback whales (*Megaptera novaeangliae*)," Rep. Int. Whal. Comm. **13**, 105–111.

Blackwell, S. B., Richardson, W. J., Greene, C. R., Jr., and Streever, B. (**2007**). "Bowhead whale (*Balaena mysticetus*) migration and calling behaviour in the Alaskan Beaufort Sea, autumn 2001–04: An acoustic localization study," Arctic **60**, 255–270.

Brownell, R. L., and Ralls, K. (**1986**). "Potential for sperm competition in baleen whales," Rep. Int. Whal. Comm. **8**, 97–112.

Clapham, P. J. (**1996**). "The social and reproductive biology of humpback whales: An ecological perspective," Mammal Rev. **26**, 27–49.

Clark, C. V., Cortopassi, K. A., Ponirakis, D., Fowler, M. C., Fristrup, K. M., and George, J. C. (**2003**). "Seasonal variation in acoustic characteristics of bowhead whale (Balaena mysticetus) sounds during the spring 2001 migration of Pt. Barrow, Alaska," Document No. SC/56/BRG21, International Whaling Commission.

Clark, C. W. (**1982**). "The acoustic repertoire of the southern right whale, a quantitative analysis," Anim. Behav. **30**, 1060–1071.

Clark, C. W. (**1991**). "Acoustic behavior of mysticete whales," in *Sensory Abilities of Cetaceans*, edited by J. Thomas and R. Kastelein (Plenum, New York), pp. 571–583.

Clark, C. W., and Clapham, P. J. (**2004**). "Acoustic monitoring on a humpback whale (Megaptera novaeangliae) feeding ground shows continual singing into late spring," Proc. R. Soc. London, Ser. B, **271**, 1051–1057.

Clark, C. W., and Johnson, J. H. (**1984**). "The sounds of the bowhead whale, *Balaena mysticetus*, during the spring migrations of 1979 and 1980," Can. J. Zool. **62**, 1436–1441.

Croll, D. A., Clark, C. W., Acevedo, A., Tershy, B. R., Flores, S., Gedamke,

J., and Urban, J. (**2002**). "Only male fin whales sing loud songs," Nature (London) **417**, 809.

Cummings, W. C., and Holliday, D. V. (**1987**). "Sounds and source levels from bowhead whales off Pt. Barrow, Alaska," J. Acoust. Soc. Am. **82**, 814–821.

Cummings, W. C., and Thompson, D. (**1971**). "Underwater sounds from the blue whale, *Balaenoptera musculus*," J. Acoust. Soc. Am. **50**, 1193–1198.

Eschricht, D. F., and Reinhardt, J. (**1861**). *Om Nordhvalen (Balæna Mysticetus L.) Navnlig med Hensyn til Dens Udbredning i Fortiden og Nutiden og til Dens Ydre og Indre Særkjender (The Northern Whale (Balaena Mysticetus L.) with especial reference to its geographical distribution in times past and present, and to its external and internal characteristics)* (Bianco Lunos Bogtrykkeri, Copenhagen).

Glockner, D. A. (**1983**). "Determining the sex of humpback whales (Megaptera novaeangliae) in their natural environment," in *Communication and Behavior of Whales*, edited by R. S. Payne (American Association for the Advancement of Science, Westview, Boulder, CO), pp. 447–464.

Hall, M. L. (**2004**). "A review of hypotheses for the functions of avian duetting," Behav. Ecol. Sociobiol. **55**, 415–430.

Harcus, J. L. (**1977**). "The functions of vocal duetting in some African birds," Z. Tierpsychol **43**, 23–45.

Heide-Jørgensen, M. P., Cosens, S. E., Dueck, L. P., Laidre, K., and Postma, L. (**2007a**). "Baffin Bay–Davis Strait and Hudson Bay–Foxe Basin bowhead whales: A reassessment of the two-stock hypothesis," Document No. SC/60/BRG20, International Whaling Commission.

Heide-Jørgensen, M. P., Laidre, K., Borchers, D., Samarra, F., and Stern, H. (**2007b**). "Increasing abundance of bowhead whales in West Greenland," Biol. Lett. **3**, 577–580.

Heide-Jørgensen, M. P., Laidre, K., Jensen, M. V., Dueck, L., and Postma, L. D. (**2006**). "Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay," Marine Mammal Sci. **22**, 34–45.

Heide-Jørgensen, M. P., Laidre, K., Wiig, Ø., Bachmann, L., Lindqvist, C., Postma, L., Dueck, L., Lidsay, M., and Tenkula, D. (**2007c**). "Segregation of sexes and plasticity in site selection of bowhead whales," Document No. SC/60/BRG19, International Whaling Commission.

Heide-Jørgensen, M. P., Laidre, K. L., Wiig, Ø., Jensen, M. V., Dueck, L., Schmidt, H. C., and Hobbs, R. C. (**2003**). "First successful satellite tracking of bowhead whales, *Balaena mysticetus*, in Baffin Bay: From Greenland to Canada in ten days," Arctic **56**, 21–31.

Kraus, S. D., and Hatch, J. J. (**2001**). "Mating strategies in the North Atlantic Right whale (*Eubalaena glacialis*)," J. Cetacean Res. Manage. **2**, 237–244.

Laidre, K., Heide-Jørgensen, M. P., and Nielsen, T. G. (**2007**). "Role of the bowhead whale as a predator in West Greenland," Mar. Ecol.: Prog. Ser. **346**, 285–297.

Ljungblad, D. K., Moore, S. E., and Van Schoik, D. R. (**1984**). "Aerial surveys of endangered whales in the Northern Bering, Eastern Chukchi and Alaskan Beaufort seas, 1983: With a five year review, 1979–1983," Naval Ocean Systems Center Technical Report No. 955. Minerals Management Service, Alaska OCS Region, U.S. Department of Interior, San Diego, CA.

Ljungblad, D. K., Thompson, P. O., and Moore, S. E. (**1982**). "Underwater sounds recorded from migrating bowhead whales, *Balaena mysticetus*, in 1979," J. Acoust. Soc. Am. **71**, 477–482.

Madsen, S. D., Nielsen, T. G., and Hansen, B. W. (**2001**). "Annual population development and production by *Calanus finmarchicus, C. glacialis* and *C. hyperboreus* in Disko Bay, Western Greenland," Mar. Biol. (Berlin) **139**, 75–93.

Mate, B., Duley, P., Lagerquist, B., Wenzel, F., Stimpert, A., and Clapham, P. (**2005**). "Observation of a female North Atlantic Right Whale (*Eubalaena glacialis)* in simultaneous copulation with two males: Supporting evidence for sperm competition," Aquat. Mamm. **31**, 157–160.

McDonald, M. A., Calambokidis, J., Teranishi, A. M., and Hildebrand, J. A. (**2001**). "The acoustic calls of blue whales off California with gender data," J. Acoust. Soc. Am. **109**, 1728–1735.

Moore, S. E., and Reeves, R. R. (**1993**). "Distribution and movements," in *The Bowhead Whale*, edited by J. J. Burns, J. J. Montague, and C. J. Cowles (The Society of Marine Mammalogy, Lawrence, KS), Special Publication No. 2, pp. 313–386.

Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M. N., and Jenner, K. C. S. (**2000**). "Cultural revolution in whale songs," Nature (London) **408**, 537.

Oleson, E. M., Calambokidis, J., Burgess, W. C., McDonald, M. A., LeDuc, C. A., and Hildebrand, J. A. (**2007**). "Behavioral context of call production by eastern North Pacific blue whales," Mar. Ecol.: Prog. Ser. **330**, 269–284.

Parks, S. E., and Tyack, P. L. (**2005**). "Sound production by North Atlantic right whales (*Eubalaena mysticetus*) in surface active groups," J. Acoust. Soc. Am. **117**, 3297–3306.

Payne, R. S., and McVay, S. (**1971**). "Songs of Humpback Whales," Science **173**, 585–597.

Reese, S. C., Calvin, J. A., George, J. C., and Tarpley, R. J. (**2001**). "Estimation of fetal growth and gestation in bowhead whales," J. Am. Stat. Assoc. **96**, 915–938.

Reeves, R. R., and Leatherwood, S. (**1985**). "Bowhead whale," in *Handbook of Marine Mammals*, edited by S. H. Ridgway and R. Harrison (Academic, London), pp. 305–344.

Richardson, J. W., and Finley, K. J. (**1989**). "Comparison of behavior of bowhead whales of the Davis Strait and Bering/Beaufort Stocks," LGL Limited, Environmental Research Associates, prepared for Minerals Management Service, Alaska OCS Region, U.S. Department of Interior.

Richardson, W. J., Finley, K. J., Miller, G. W., Davis, R. A., and Koski, W. R. (**1995**). "Feeding, social and migration behavior of bowhead whales, *Balaena mysticetus*, in Baffin Bay vs. the Beaufort Sea: Regions with different amounts of human activity," Marine Mammal Sci. **11**, 1–45.

Searcy, W. A., and Andersson, M. (**1986**). "Sexual selection and the evolution of song," Annu. Rev. Ecol. Syst. **17**, 507–533.

Stafford, K. M., Moore, S. E., Laidre, K. L., and Heide-Jørgensen, M. P. (**2008**). "Bowhead whale springtime song off West Greenland," J. Acoust. Soc. Am. **124**, 3315–3323.

Tervo, O. M. (**2006**). "Vocalisation of bowhead whales (Balaena mysticetus) in Disko Bay, Western Greenland, in relation to oceanography and plankton distribution," MSc thesis, University of Southern Denmark, Denmark.

Tervo, O. M., Parks, S. E., and Miller, L. A. (**2007**). "Annual and seasonal changes in the song of the bowhead whale Balaena mysticetus in Disko Bay, Western Greenland," 17th Biennial Conference on the Biology of Marine Mammals, Cape Town, 29 November–3 December.

Tyack, P. L. (**1983**). "Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds," Behav. Ecol. Sociobiol. **13**, 49–55.

Tyack, P. L., and Clark, C. W. (**2000**). "Communication and acoustic behavior of dolphins and whales," in *Hearing by Whales and Dolphins*, edited by A. Whitlow, A. Popper, and R. Fay (Springer Handbook for Auditory Research, New York), pp. 156–224.

Watkins, W. A., Tyack, P., Moore, K. E., and Bird, J. E. (**1987**). "The 20-Hz signals of finback whales (*Balaenoptera physalus*)," J. Acoust. Soc. Am. **82**, 1901–1912.

Winn, H. E., and Winn, L. K. (**1978**). "The song of the humpback whale *Megaptera novaeangliae* in the West Indies," Mar. Biol. (Berlin) **47**, 97–114.

Würsig, B., and Clark, C. (**1993**). "Behavior," in *The Bowhead Whale*, edited by J. J. Burns, J. J. Montague, and C. J. Cowles (The Society of Marine Mammalogy, Lawrence, KS), Special Publication No. 2, pp. 157–200.

Würsig, B., Clark, C. W., Dorsey, E. M., Richardson, W. J., and Wells, R. S. (**1983**). "Normal behavior of bowheads 1982," in *Behavior, Disturbance Responses and Distribution of Bowhead Whales Balaena Mysticetus in the Eastern Beaufort Sea, 1982*, edited by W. J. Richardson (LGL Ecological Research Associates for U.S. Minerals Management Service, Reston, VA).

Paper II

Tervo, O. M., Parks, S. E., Christoffersen, M.F., Miller, L. A. and Kristensen, R. M. (2011). Annual changes in the winter song of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland. *Marine Mammal Science* doi: 10.1111/j.1748-7692.2010.00451.x

Marine Mammal Science

MARINE MAMMAL SCIENCE, **(*): ***–*** (*** 2011)

DOI: 10.1111/j.1748-7692.2010.00451.x

Annual changes in the winter song of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland

OUTI M. TERVO
Arctic Station, University of Copenhagen,
P.O. Box 504, 3953 Qeqertarsuaq, Greenland
E-mail: ote@science.ku.dk

SUSAN E. PARKS
Applied Research Laboratory,
Pennsylvania State University,
P.O. Box 30,
State College, Pennsylvania 16804-0030, U.S.A.

MADS FAGE CHRISTOFFERSEN
Arctic Station, University of Copenhagen,
P.O. Box 504,
3953 Qeqertarsuaq, Greenland

LEE A. MILLER
Institute of Biology,
University of Southern Denmark,
DK-5230 Odense M, Denmark

REINHARDT MØBJERG KRISTENSEN
Zoological Museum,
Natural History Museum of Denmark,
University of Copenhagen,
Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

Sexual selection through mate choice for elaborate displays usually requires that the selecting sex receive reliable information about the quality of the advertiser whether it is measured by health, body size, extravagant secondary sexual traits, or the ability to expend excessive energy on various displays (Zahavi 1975, Hamilton and Zuk 1982). These displays can be visual, kinetic, olfactory, or acoustic. Sound is of vital importance for reproductive advertisement in the marine environment where visual cues are limited, especially during winter in polar regions. Acoustic advertisement is used extensively in mating systems of several arctic seal species (Cleator *et al.* 1989, Sjare and Stirling 1996, Van Parijs *et al.* 2001). For example, male-bearded seals (*Erignathus barbatus*) produce long trill displays during the breeding season, and are most vocally active when females are present (Van Parijs *et al.* 2001). Bowhead whales (*Balaena mysticetus)* are known to use acoustic signals for communication (Clark 1990) and potentially receive information about their environment from echoes of their own vocalizations (Ellison *et al.* 1987, George *et al.* 1989). Bowhead whales produce a large variety of call types (Clark and Johnson 1984) and also produce elaborate

and complex songs that most likely function for intersexual selection and/or for intrasexual competition (Würsig and Clark 1993).

In studies of baleen whale bioacoustics, song is defined as stereotyped song notes that are repeated in a pattern, resembling singing behavior described in birds (Payne and McVay 1971, Catchpole 1980, Clapham 2000). Singing behavior is considered to be an advanced form of communication in baleen whales (Clark 1990). Out of the 14 currently recognized species of baleen whales, 6 are known to produce songs (Clark 1990, Gedamke *et al.* 2001, McDonald *et al.* 2006), including the bowhead whale. The singing behavior in baleen whales has been suggested to have significance in male breeding success (Tyack 1981, Tyack and Clark 2000) as only the males of at least three baleen whale species have been documented to sing (humpback whale, *Megaptera novaeangliae*, Winn and Winn 1978; fin whale, *Balaenoptera physalus*, Croll *et al.* 2002; blue whale, *B. musculus*, Oleson *et al.* 2007). The sex of the singing individual for the bowhead whale remains unknown.

Songs of bowhead whales have been described from the Bering-Chukchi-Beaufort Sea (BCB) population (Ljungblad *et al.* 1982, Clark and Johnson 1984, Cummings and Holliday 1987, Delarue *et al.* 2009) and from the Hudson Bay-Davis Strait population off Western Greenland (Tervo 2006, Stafford *et al.* 2008, Tervo *et al*. 2009). Bowhead whale songs recorded in spring off Alaska differ from year to year (Würsig and Clark 1993) and spring singing is thought to be a remnant from the winter breeding season (Würsig and Clark 1993, Tyack and Clark 2000). The song note repertoire of bowhead whales of the Hudson Bay-Davis Strait population is most complex during winter (Tervo *et al.* 2009).

Disko Bay has been an important aggregation area for Davis Strait-Hudson Bay bowhead whales for centuries (Eschricht and Reinhardt 1861). Bowhead whales arrive in Disko Bay in late January or early February (Eschricht and Reinhardt 1861, Tervo *et al.* 2009) and occupy a relatively small area offshore of Disko Island until late May (Heide-Jørgensen *et al.* 2006). This provides an excellent opportunity to study the acoustic behavior of these whales during the winter months when information about their basic biology is scarce due to the logistical challenges of studying an arctic species.

The aim of this study was to describe the annual changes in the winter song of the bowhead whales in Disko Bay, Western Greenland, during four consecutive years from 2005 to 2008. In this study, we found that the song repertoire of bowhead whales in Disko Bay changed completely from year to year. Detailed knowledge of the acoustic behavior of Western Greenland bowhead whales will shed light on the role song may play in mating strategies and, along with results from other studies, on the importance of the Disko Bay area for the ecology of this species.

The study area was located in Disko Bay, Western Greenland (69°N, 54°W; Fig. 1). Acoustic recordings of the winter song of bowhead whales were made in Disko Bay in the vicinity of Qeqertarsuaq from February to March in 2005–2008 (Table 1). The total recording time was 20 h and 50 min (see Table 1). The depth and position of the recorded whales relative to the hydrophones were unknown.

Two hydrophones were lowered 8–10 m into the water either (1) from each side of a dinghy, (2) from R/V *Porsild*, (3) through holes in the ice, or (4) from the shore.

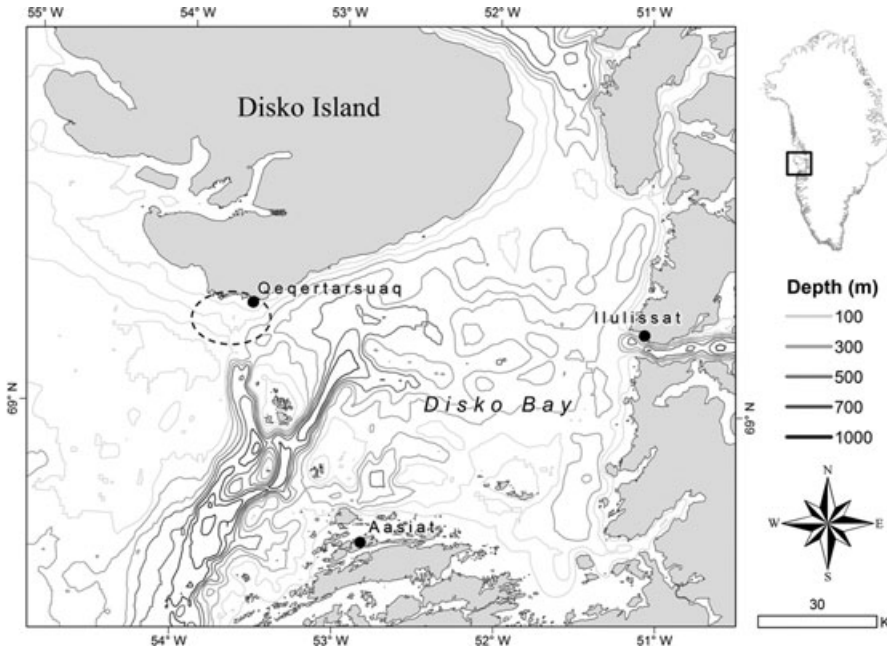

Figure 1. Map of Greenland showing the location of Disko Bay. The dotted circle shows the recording area (Data: GEBCO; map by C. Ilmoni).

We used two different recording systems. In 2005 and 2006, we deployed a custom-built hydrophone (−185 dB re: 1V/μPa; HELWEG, University of Auckland, New Zealand) and a HS 150 (−178 dB re: 1V/μPa; Sonar Research and Development Ltd., Beverley, U.K.). In 2007 and 2008, we used two HTI-94-SSQ hydrophones (−170 dB re: 1 V/μPa; High Tech, Inc., Gulfport, MS). All hydrophones had frequency ranges from at least 10 Hz to 30 kHz (±3 dB). In all four years the hydrophones were connected to amplifiers (maximum frequency 1 MHz) (custom built, Aarhus University, Denmark) with high pass filter set at 30 Hz. The signals were recorded using both channels of a SONY DAT TDC-D8 tape recorder with a sampling frequency of 44.1 kHz. Thus, the frequency band of the recording systems was from 30 Hz to 20 kHz.

The audio data were digitized at a sample rate of 44100 and 16-bit resolution into .wav files. Spectrograms of the acoustic recordings were produced with *Raven 1.2.1* and *Raven Pro 3* (Cornell Laboratory of Ornithology, Ithaca, NY) using a Fast Fourier Transform (FFT) size of 1,024 samples with Hamming windows having 50% or 75% overlap and a frequency resolution of 43 Hz (time resolution 23 ms).

The recorded signals were divided into the three main categories described by Clark (1990) using a combination of spectral and audio qualities: simple frequency-modulated (FM) calls, complex amplitude-modulated (AM) calls, and songs. In this study the songs were divided into themes, phrases, and units (song notes) according to the song systematic system created by Payne and McVay (1971) for humpback whale

Table 1. Summary of acoustic data collected in Disko Bay from 2005 to 2008. The total recording time was 20 hr and 50 min. Number of individuals was estimated from the presence or absence of overlapping song notes and songs. A 2+ indicates that at least two individual singers were noted, but that there could have been more than two.

Year	Date	Start	Recording time (min)	No. of song notes	Song note types	No. of individuals
2005	25 February	1320	45	821	A, BCD, EF, H, U	2+
	1 March	1255	15	4	A, BCD, EF, H	1
	3 March	1145	90	489	EF, H, U	2+
	8 March	1150	80	170	A, EF, H, U	2+
	10 March	1300	30	22	EF, J	1
	11 March	1215	85	103	EF, L, U	2+
	15 March	1305	80	430	EF, J, U	2+
2006	13 March	1155	35	37	Q, Y, S	2+
	15 March	1210	25	51	Q, Y, S	1
2007	15 February	1640	55	109	K, M, T	1
	17 February	1550	45	113	K, M, T	2+
2008	28 February	1130	125	18	BS, HI	2+
	4 March	1130	75	200	SN, RU, EN	1
	9 March	2130	25	59	BS, HI	2+
	10 March	1530	95	70	BS, HI	2+
	11 March	1330	135	44	BS, HI	2+
	12 March	1215	50	80	BS, HI	1
	19 March	2230	50	130	BS, HI	2+
	21 March	1400	65	31	BS, HI	2+
	26 March	1245	45	25	BS, HI, P, PY	2+

song. Songs were defined as a series of song notes repeated in a regular pattern. Song notes were defined as continuous frequency-modulated tones that had a definable contour and were the smallest discrete units in the song. Song notes could easily be categorized into different types. Only songs and song notes were included in our data analysis. In order to obtain reliable measurements, signals were chosen for analysis only if there was no signal overlap and if the peak-to-peak signal level was at least twice that of the overall background noise as measured from the waveform.

A priori categorization of song notes and songs was based on aural impression and visual inspection of spectrograms. Six variables were measured from each song note from 2005 to 2008, and eight variables were measured from each song from 2006 to 2008 (Fig. 2). The six variables measured from each song note were: (1) duration (s), (2) maximum frequency (Hz), (3) minimum frequency (Hz), (4) start frequency (Hz), (5) end frequency (Hz), and (6) number of inflection points. The eight variables measured from each song were: (1) duration of the song (s), (2) minimum frequency (Hz), (3) maximum frequency (Hz), (4) number of themes in the song, (5) number of phrases in the first theme, (6) number of phrases in the second theme, (7) number of song notes in the first phrase, and (8) the number of song notes in the second phrase. Only song notes were analyzed in the recordings from 2005 because the complexity and overlapping songs from multiple singers precluded a clear classification of complete songs. All variables were measured manually from

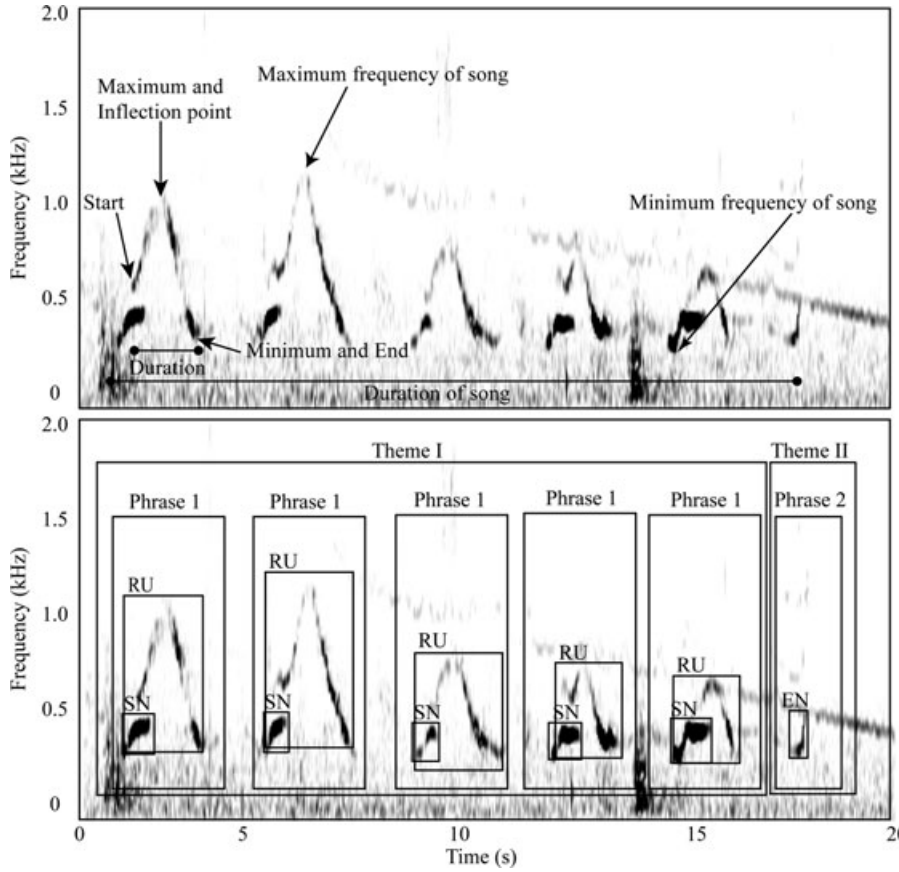

Figure 2. Analysis of bowhead whale song notes and song. The upper spectrogram shows song IV from 2008 illustrating the six different variables measured for song notes and the three frequency and time variables measured for the songs (Table 2). The lower spectrogram shows that this song is composed of two types of phrases and three types of song notes where SN and RU song notes form Phrase 1, which is repeated five times in Theme I. Song note EN comprises alone Phrase 2, which is repeated once in Theme II. There is a bearded seal call in the background. (Hamming window, FFT size 1,024, 50% overlap).

the spectrogram using the cursor tool in *Raven Pro*. The *a priori* categorization of song notes and songs were tested using discriminant analysis followed by Wilcoxon signed-rank test for matched pairs (Knörnschild and Von Helversen 2008). Statistical analyses were done using *S-PLUS 6.2* (TIBCO Software Inc, Palo Alto, CA).

Bowhead whale acoustic signals were present in all 2005–2008 recordings (Table 1). On most days there were multiple individuals singing the same song at the same time as indicated by overlapping songs and song notes (Table 1). A total of 3,006 song notes from the years 2005–2008 were analyzed (2005 $n = 2{,}039$, 2006 $n = 88$, 2007 $n = 222$, and 2008 $n = 657$). There were additional signals that fulfilled song note criteria but these were recorded infrequently and were not

included in the analyses. Other species detected in the recordings included bearded seals (Fig. 2, 3) and beluga whales (*Delphinapterus leucas*). The acoustic repertoires of both species have been described in various investigations, and they differ greatly from that of the bowhead whale (Schevill and Lawrence 1949, Cleator *et al.* 1989, Risch *et al.* 2007).

All song note categories could be distinguished from each other statistically based on the six measured variables. Discriminant analysis of the 3,006 song notes from 20 different categories classified 88.4% of all song notes to the correct category, which was significantly higher than expected by chance (chance = 5%, Wilcoxon signed-rank test for matched pairs: $T = 1$, $n = 20$, $P = 0.05$). Correct classification scores ranged from 28% (song note type EN) to 100% (song note type HI). In all, seven song note categories were identified for 2005, three for 2006, three for 2007, and seven for 2008.

In 2006 and 2007 a single, but different, song type was recorded in each year (Fig. 3, Table 2). In 2008 two separate songs were identified in our recordings (Fig. 3, Table 2). However, the single song types described in 2006 and 2007 could be due to a limited sample size as multiple song types within the same season have been described for several bowhead whale stocks (Stafford *et al*. 2008, Delarue *et al*. 2009). Song type I (song notes S, Y, and Q) was recorded in 2006 and song type II (song notes K, M, and T) was prevalent in 2007. In 2008 two song types, song type III (song notes HI and BS) and song type IV (song notes RU, SN, and EN), were recorded in the repertoire (Table 2). It is possible that song note types P and PY recorded on 26 March 2008 (Table 1) were part of a third song type from that year, but the song notes were not recorded often enough to confirm this conjecture.

Ten examples of complete songs of the same type could readily be identified in 2006. To match this, 10 songs of each type were randomly chosen from the 2007 and 2008 data sets using the RAND worksheet function in *Excel 2002* (Microsoft, Redmond, WA) giving 40 songs in all with 10 in each of the four types. Each of the four song types had a maximum of two themes and each theme included only one phrase that was repeated (Table 2). The song note composition within a song type was highly different from year to year. No song note type was present in multiple years hence song type(s) in each year were always composed of completely different song note types (Table 2). In addition, songs could be distinguished from each other statistically based on the eight variables measured for each song. Discriminant analysis with the 40 songs using all eight different variables classified 100% of songs to the correct type. Discriminant analysis using only time and frequency parameters (duration, minimum frequency, and maximum frequency) also correctly classified 100% of all songs.

We found year to year changes in the song of bowhead whales in the Davis Strait, as has been previously documented for the bowhead whales of the BCB population (Würsig and Clark 1993). We observed that multiple individuals were singing the same shared songs in all years from observed temporal overlap of song notes. However, we cannot state the degree of independence nor the amount of pseudoreplication in our recordings. Despite this, it is clear that new song notes appear each year and none carry over from one year to the next.

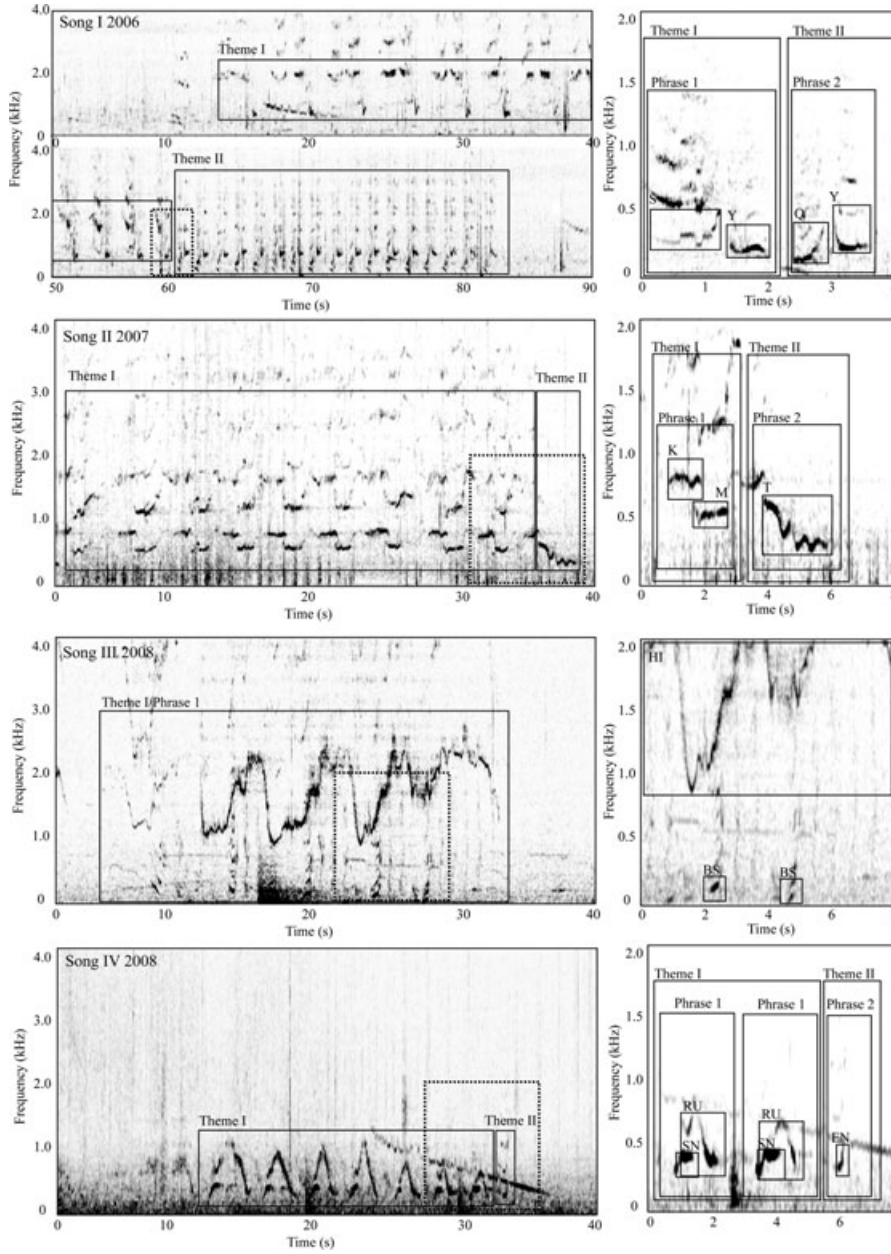

Figure 3. Spectrograms of the four song types as recorded in 2006–2008. The spectrograms on the right are an expanded section from the song spectrograms on the left as indicated with a dotted box. Notice the different x-axes for different songs and different y- and x-axes scales in the expanded spectrograms. In the spectrograms of song type I and song type IV there is a bearded seal call in the background. Notice the simultaneously produced song notes in song types III and IV (Hamming window, FFT size 1,024, 50% overlap).

Table 2. Time, frequency, and song structure parameters of the four different song types ($n = 10$) recorded in 2006, 2007, and 2008. The data from 2005 were not included in the analysis because songs could not be identified that season. Note that two types of songs were sung in 2008.

Year	Song		Duration (s)	Min (Hz)	Max (Hz)	No. of themes	Theme 1 No. of phrases	Theme 2 No. of phrases	Phrase I		Phrase II	
									No. of units	Name of units	No. of units	Name of units
2006	I	Mean	61	134	2,294	2	10.7	14.8	1	S	2.0	Y, Q
		SD	6.4	69.2	81.1	0.0	2.0	3.7	0		0.0	
2007	II	Mean	25	261	1,904	2	6.4	2.0	6.4	K, M	1.0	T
		SD	5.4	58.0	212.5	0.0	1.8	0.0	1.8		0.0	
2008	III	Mean	15	120	2,395	1	1.0	0.0	5.0	HI, BS	0.0	–
		SD	1.2	23.6	203.9	0.0	0.0	0.0	0.0		0.0	
2008	IV	Mean	16	265	1,063	2	4.6	1.0	2.0	RU, SN	1.0	EN
		SD	5.5	29.2	163.6	0	1.4	0	0		0.0	

According to published literature (Würsig and Clark 1993, Delarue *et al* 2009), it appears that none of the documented song types from the Davis Strait population were shared by the BCB population although a more thorough comparison using the same procedure for analysis is needed to fully confirm this statement. Song type II from 2007 was described by Stafford *et al.* (2008) and named "warble song." They found three different songs in 2007, suggesting that the amount of data in our study is not sufficient enough to fully describe the song repertoire. The average duration of the bowhead whale songs found in our study ranged from 15 to 61 s depending on the song type. The durations of songs and the number of themes in a song found in our study are consistent with results from previous studies on bowhead whale songs where the singing individuals were localized with a hydrophone array (Cummings and Holliday 1987, Würsig and Clark 1993). This gives us reason to believe that the songs of bowhead whales described in our study are complete songs and not just parts of a longer, more complex song.

Not only does the song repertoire change completely from year to year, the song notes for each year are unique and not present in multiple years. This is in contrast with the humpback whale song where some sections of the old song from the previous season can usually be detected in the new song at the start of the next breeding season (Payne *et al.* 1983, Eriksen *et al.* 2005, but see Noad *et al.* 2000). Changes in the humpback whale song have been shown to occur at different rates in different years (Eriksen *et al.* 2005) and most changes in the song are presumed to occur during the singing season and not in the more silent periods between breeding seasons (Payne *et al.* 1983). Humpback whales have been reported to sing in high-latitude feeding areas outside the breeding season (Gabriele and Frankel 2002, Clark and Clapham 2004, Stafford *et al.* 2007), but this singing is considered to be a remnant from the breeding season performed by only a few males (Clark and Clapham 2004). Bowhead whale song can change rapidly within a season where a set of song notes is replaced by new ones or new songs are incorporated in the repertoire while the season progresses (Delarue *et al.* 2009, Tervo *et al.* 2009). However, we do not yet know whether the changes in bowhead whale song recorded within a season are due to individual variability in song repertoire or related to the progressive arrival of new individuals into the recording area (Delarue *et al*. 2009, Tervo *et al*. 2009).

It is not known whether all individual whales in Disko Bay have a repertoire of multiple songs within a season or whether different individuals sing different songs. The presence of a frequent song and less-frequent song within a season (Stafford *et al*. 2008, our study) could indicate that in addition to a shared song, which would be sung by all the individuals in the area, some bowhead whales could also have individually distinctive songs. Another possible explanation for the differences between song repertoires and the plethora of song notes recorded from bowhead whales in Disko Bay is that individuals from geographically separated groups aggregating in Disko Bay may have differences in their song structure. This has been observed for numerous song bird species (Krebs and Kroodsma 1980) and for some of the other singing baleen whale species (Payne and Guinee 1983, Thompson *et al.* 1992, Rivers 1997). However, bowhead whales in Davis Strait do not appear to be divided into discrete populations. On the contrary, results from satellite tag studies suggest that the

Hudson Bay-Davis Strait stock and the Foxe Basin-Hudson Bay stock should be treated as one (Heide-Jørgensen *et al.* 2007). Consequently, we believe that the changes in the repertoire we describe here are likely to be annual changes in the repertoire of a single population.

A general concept in reproductive advertisement is that the displayer must stand out from other displaying individuals in order to be chosen by the selecting sex. Calls of the advertising individual can be (1) very loud, (2) over a wide span in frequency, (3) very high in frequency, (4) very low in frequency, and/or (5) very complex. Furthermore, songs can be organized into repertoires that require cognitive skills for remembering songs, to learn new songs, and to perform these songs. Bowhead whale song is complex (Würsig and Clark 1993, Stafford *et al.* 2008, Delarue *et al.* 2009) and covers a wide range of frequencies (Würsig and Clark 1993, Tervo *et al.* 2009). In addition, bowhead whales have a highly variable song repertoire indicated by the presence of multiple songs within a season and annual changes in the repertoire between seasons. Thus, the songs we recorded could function as an advertisement display produced by males or by females where a large repertoire size could have significance in sexual selection.

Acknowledgments

We want to thank John Jakobsen, Abel Brandt, Tarfi Mølgaard, Kale Mølgaard, and the crew on R/V *Porsild* for their help in data collection. We thank Kerstin Wiklander, University of Gothenburg, and Anu Valtonen, University of Joensuu, for their help with the statistical analysis and Niels Kristiansen, University of Århus, for construction of some of the electronic equipment. Arctic Station, University of Copenhagen, Qeqertarsuaq, provided an excellent and well-equipped base for our studies. Nukissiorfiit, Greenland, is thanked for granting a research leave for Mads Christoffersen in order to conduct this study. We thank Peter Teglberg Madsen for helpful discussions on the study. Two anonymous reviewers and Associate Editor Dr. David Mellinger provided constructive criticism and valuable comments to improve the manuscript. This study was funded by A. P. Møller og Hustru Chastine Mc-Kinney Møllers Fond til almene Formaal (grant to Reinhardt Møbjerg Kristensen and Outi Tervo, Arctic Station, University of Copenhagen, 12.11.2008), the Danish Research Council for Natural Sciences (grant #21-03-0171) to Lee A. Miller, University of Southern Denmark, and grant #21-04-0391 to Torkel Gissel Nielsen, National Environmental Research Institute, Denmark). Last, we thank support from the Danish National Research Council through The Centre for Sound Communication, University of Southern Denmark.

Literature Cited

Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour 74:149–165.

Clapham, P. J. 2000. The humpback whale: Seasonal feeding and breeding in a baleen whale. Pages 173–196 *in* J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. The University of Chicago Press, Chicago, IL.

Clark, C. W. 1990. Acoustic behavior of mysticete whales. Pages 571–583 *in* J. Thomas and R. Kastelein, eds. Sensory abilities of cetaceans. Plenum Press, New York, NY.

Clark, C. W., and J. H. Johnson. 1984. The sounds of the bowhead whale, *Balaena mysticetus*, during the spring migrations of 1979 and 1980. Canadian Journal of Zoology 62:1436–1441.

Clark, C. W., and P. J. Clapham. 2004. Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. Proceedings of the Royal Society London, Part B: Biological Sciences 271:1051–1057.

Cleator, H. J., I. Stirling and T. G. Smith. 1989. Underwater vocalizations of the bearded seal (*Erignatus barbatus*). Canadian Journal of Zoology 67:1900–1910.

Croll, D. A., C. W. Clark, A. Acevedo, B. R. Tershy, S. Flores, J. Gedamke and J. Urban. 2002. Only male fin whales sing loud songs. Nature 417:809.

Cummings, W. C., and D. V. Holliday. 1987. Sounds and source levels from bowhead whales off Pt. Barrow, Alaska. Journal of the Acoustical Society of America 83:814–821.

Delarue, J., M. Laurinolli and B. Mate. 2009. Bowhead whale (*Balaena mysticetus*) songs in the Chukchi Sea between October 2007 and May 2008. Journal of the Acoustical Society of America 126:3319–3328.

Ellison, W. T., C. W. Clark and G. C. Bishop. 1987. Potential use of surface reverberation by bowhead whales, *Balaena mysticetus,* in under-ice navigation. Report of the International Whaling Commission 373:29–332.

Eriksen, N., L. A. Miller, J. Tougaard and D. A. Helweg. 2005. Cultural changes in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. Behaviour 142:305–328.

Eschricht, D. F., and J. Reinhardt. 1861. Om Nordhvalen (Balæna Mysticetus L.) navnlig med Hensyn til dens Udbredning i Fortiden og Nutiden og til dens ydre og indre Særkjender [The Northern Whale (*Balaenoptera mysticetus* L.) with especial reference to its geographical distribution in times past and present, and to its external and internal characteristics]. Bianco Lunos Bogtrykkeri, Copenhagen, Denmark.

Gabriele, C., and A. Frankel. 2002. The occurrence and significance of humpback whale songs in Glacier Bay, southeast Alaska. Arctic Research of the United States 16:42–47.

Gedamke, J., D. P. Costa and A. Dustan. 2001. Localization and visual verification of a complex minke whale vocalization. Journal of the Acoustical Society of America 109:3038–3047.

George, J. C., C. Clark, G. M. Carroll and W. T. Ellison. 1989. Observations on the icebreaking and ice navigating behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barow, Alaska, spring 1985. Arctic 42:24–30.

Hamilton, W., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218:384–387.

Heide-Jørgensen, M. P., K. Laidre, M. V. Jensen, L. Dueck and L. D. Postma. 2006. Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay. Marine Mammal Science 22:34–45.

Heide-Jørgensen, M. P., S. E. Cosens, L. P. Dueck, K. Laidre and L. Postma. 2007. Baffin Bay—Davis Strait and Hudson Bay–Foxe Basin bowhead whales: A reassessment of the two-stock hypothesis. Paper SC/60/BRG20 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 36 pp.

Knörnschild, M., and O. Von Helversen. 2008. Nonmutual vocal mother-pup recognition in the greater sac-winged bat. Animal Behaviour 76:1001–1009.

Krebs, J. R., and D. E. Kroodsma. 1980. Repertoires and geographical variation in bird song. Advances in the Study of Behaviour 11:143–177.

Ljungblad, D. K., P. O. Thompson and S. E. Moore. 1982. Underwater sounds recorded from migrating bowhead whales, *Balaena mysticetus*, in 1979. Journal of the Acoustical Society of America 71:477–482.

McDonald, M. A., J. A. Hildebrand and S. L. Mesnick. 2006. Biogeographic characterization of blue whale song worldwide: Using song to identify populations. Journal of Cetacean Research and Management 8:55–65.

Noad, M. J., D. H. Cato, M. M. Bryden, M.-N. Jenner and K. C. S. Jenner. 2000. Cultural revolution in whale songs. Nature 408:537.

Oleson, E. M., J. Calambokidis, W. C. Burgess, M. A. McDonald, C. A. LeDuc and J. A. Hildebrand. 2007. Behavioral context of call production by eastern North Pacific blue whales. Marine Ecology Progress Series 330:269–284.

Payne, R. S., and L. N. Guinee. 1983. Humpback whale (*Megaptera novaeangliae*) songs as an indicator of "stocks". Pages 333–358 *in* R. S. Payne, ed. Communication and behaviour

of whales. American Association for the Advancement of Science, Westview Press, Inc., Boulder, CO.

Payne, R. S., and S. McVay. 1971. Songs of humpback whales. Science 173:585–597.

Payne, K., P. Tyack and R. S. Payne. 1983. Progressive change in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. Pages 9–57 *in* R. S. Payne, ed. Communication and behaviour of whales. American Association for the Advancement of Science, Westview Press, Inc., Boulder, CO.

Risch, D., C. W. Clark, P. J. Corkeron, A. Elepfandt, K. M. Kovacs, C. Lydersen, I. Stirling and S. M. Van Parijs. 2007. Vocalizations of male bearded seals, *Erignathus barbatus*: Classification and geographical variation. Animal Behaviour 73:747–762.

Rivers, J. A. 1997. Blue whale, *Balaenoptera musculus*, vocalizations from the waters off Central California. Marine Mammal Science 13:186–195.

Schevill, W. E., and B. Lawrence. 1949. Underwater listening to the white porpoise (*Delphinapterus leucas*). Science 109:143–144.

Sjare, B., and I. Stirling. 1996. The breeding behavior of Atlantic walruses, *Odobenus rosmarus rosmarus*, in the Canadian High Arctic. Canadian Journal of Zoology 74:897–911.

Stafford, K. M., D. K. Mellinger, S. E. Moore and C. G. Fox. 2007. Seasonal variability and detection range modeling of baleen whale calls in the Gulf of Alaska, 1999–2002. Journal of the Acoustical Society of America 122:3378–3390.

Stafford, K. M., S. E. Moore, K. L. Laidre and M. P. Heide-Jørgensen. 2008. Bowhead whale springtime song off West Greenland. Journal of the Acoustical Society of America 124:3315–3323.

Tervo, O. M. 2006. Vocalisation of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland, in relation to oceanography and plankton distribution. M.Sc. thesis, University of Southern Denmark. 97 pp. Available at http://arktiskstation.ku.dk/Forskning/projekter/MSc_thesis_Outi_Tervo.pdf/.

Tervo, O. M., S. E. Parks and L. A. Miller. 2009. Seasonal changes in the vocal behavior of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland. Journal of the Acoustical Society of America 126:1570–1580.

Thompson, P. O., L. T. Findley and O. Vidal. 1992. 20-Hz pulses and other vocalizations of fin whales, *Balaenoptera physalus*, in the Gulf of California, Mexico. Journal of the Acoustical Society of America 92:3051–3057.

Tyack, P. L. 1981. Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds. Behavioral Ecology and Sociobiology 13:49–55.

Tyack, P. L., and C. W. Clark. 2000. Communication and acoustic behavior of dolphins and whales. Springer Handbook for Auditory Research 12:156–224.

Van Parijs, S. M., K. M. Kovacs and C. Lydersen. 2001. Spatial and temporal distribution of vocalising male bearded seals—implications for male mating strategies. Behaviour 138:905–922.

Winn, H. E., and L. K. Winn. 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. Marine Biology 47:97–114.

Würsig, B., and C. Clark. 1993. Behavior. Pages 157–200 *in* J. J. Burns, J. J. Montague and C. J. Cowles, eds. The bowhead whale. Special Publication Number 2, The Society for Marine Mammalogy.

Zahavi, A. 1975. Mate selection: A selection for a handicap. Journal of Theoretical Biology 53:205–214.

Received: 7 April 2010
Accepted: 29 October 2010

Paper III

Tervo, O. M., Christoffersen, M. F., Simon, M. J., Miller L. A., Jensen, F., Parks, S. E. and Madsen, P. T. Source level and active space of singing bowhead whales (*Balaena mysticetus). Journal of the Acoustical Society of America*, (manuscript in prep.).

Source level and active space of singing bowhead whales (*Balaena mysticetus*).

Tervo, Outi M. [1*]; Christoffersen, Mads F.[1]; Simon, Malene[2,3]; Miller Lee A.[4]; Jensen, Frants H.[2]; Parks, Susan E.[5] and Madsen, Peter T.[2]

(1) Arctic Station, University of Copenhagen, P.O. Box 504, 3953 Qeqertarsuaq, Greenland

(2) Zoophysiology, Department of Biological Sciences, Aarhus University, Build. 1131, C. F. Møllers Allé 3, 8000 Aarhus C, Denmark

(3) Greenland Institute of Natural Resources, P.O. Box 570, Kivioq 2, 3900 Nuuk, Greenland

(4) Institute of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark

(5) The Pennsylvania State University, Applied Research Laboratory, P.O. Box 30, State College, PA 16804-0030, USA

* Telephone: +299 921384

Fax: +299 921385

Email: ote@science.ku.dk

Keywords: source level, active space, acoustic display, mating strategy, bowhead whale, *Balaena mysticetus*

ABSTRACT

The low-frequency songs of large balaenopterids whales such as blue and fin whales have the potential to be heard across entire ocean basins. In contrast, humpback whales and bowhead whales produce complex songs composed of higher frequencies that attenuate much faster. Here we evaluate the consequences of frequency range on the active space of bowhead whale song in Disko Bay, Western Greenland, and discuss our findings in the light of song evolution and mating behaviour in baleen whales. Four independent GPS-synchronized hydrophones, deployed through holes in the ice enabled localization and source level estimates of singing bowhead whales, and were used to record ambient noise level in the area. Bowhead whale song had a mean source level of 178 ± 3 dB re 1µPa (RMS). Due to a high mean centroid frequency of 571 Hz, this acoustic display has an estimated active space of less than 90 km, about an order of magnitude smaller than that of the low frequency songs of blue and fin whales produced at a similar source level. We propose that bowhead whales spatially compensate for their much smaller communication range through mating aggregations that co-evolved with a broad bandwidth song to form a complex and dynamic acoustic display.

I. INTRODUCTION

Whales rely on sound as the primary modality for communication (Tyack and Clark, 2000). The source properties of a signal in terms of source level, directionality, frequency, bandwidth and duration will greatly influence the information that can be communicated and the ranges over which such information can be decoded (Bradbury and Vehrencamp, 1998). Thus, source properties of vocalizations, and the background noise level play a significant role in the social structure and behaviour of communicating animals. The active space of an acoustic signal is defined as the range from the sound source at which the sound level is just intense enough for a conspecific to detect/decode the signal (Brenowitz, 1982a; Janik, 2000). In order to estimate the active space for a particular communication signal it is necessary to know the source level of the sound source, frequency range of the signal due to a close correlations between frequency and signal attenuation, hearing capabilities of the receiver and the ambient noise level in the habitat (Brenowitz, 1982a; Janik, 2000).

Vocalisations produced by species within the Cetacea order show some of the greatest diversity of source levels and frequency range for a single taxonomic group. For example, harbour porpoises (*Phocoena phocoena*) send out signals of more than 150 kHz (Møhl and Andersen, 1973) whereas blue whales (*Balaenoptera musculus*) use frequencies as low as 15 Hz (Cummings and Thompson, 1971) and these differences result in very different communication ranges. Blue whales and fin whales (*B. physalus)* in particular represent the extreme in terms of large active spaces in that they produce narrow banded communication signals with the low frequencies and great energy content. The dominant frequencies of their calls are reported to range from 15 to 29 Hz (Cummings and Thompson, 1971; Cummings and Thompson, 1994; Watkins *et al.,* 1987; Širović *et al.,* 2007) and source levels from 186 to 189 dB re 1μPa (root mean square, RMS) (Cummings and Thompson, 1971; Watkins *et al.,* 1987; Širović *et al.,* 2007). The combination of these low frequencies, where the absorption is negligible, and high source levels render a very large active space (Payne and Webb, 1971) ranging from hundreds of kilometres even to thousands (Širović *et al.,* 2007; Clark 1995).

From a meta-analysis of published data, Fletcher (2004) presented convincing evidence for an inverse relationship between animal size and the spectral peaks of sound production, so that larger animals produce lower frequencies than small animals. Hence large animals will all other things equal have a larger active space than small animals. Large balaenopterid whales such as fin and

blue whales fit such scaling predictions by being the largest marine mammal and together with the large terrestrial mammal African elephant *Loxodonta africana*, produce the lowest frequency signals of any animal (Cummings and Thompson, 1971; Watkins *et al.,* 1987; Poole *et al.,* 1988) (Fig. 1). However, not all whale species follow these scaling predictions; humpback whales (*Megaptera novaeangliae*) with a body mass of 40 tons (Brownell and Ralls 1986) produce high frequency songs with fundamental frequencies ranging from 30 to 4000 Hz (Payne and Payne, 1985; Cerchio *et al.,* 2001) and bowhead whales (*Balaena mysticetus*) with a body mass of 50 - 80 tons (Brownell and Ralls, 1986; Evans, 1987), comparable to that of fin whales, produce high frequency songs with fundamental frequencies ranging from 40 to 2000 Hz, (Ljungblad *et al.,* 1982; Cummings and Holliday, 1987) (Fig. 1). Thus bowhead whales sing at much higher frequencies and over much broader bandwidths compared to similar sized balaenopterids. Here we explore the consequences of such high pitched singing for the active space and discuss implications for the evolution of acoustic and mating behaviour in baleen whales.

II MATERIAL AND METHODS

The acoustic data were collected in Disko Bay, Western Greenland, near the Arctic Station (University of Copenhagen) from March 5 to March 9, 2009. Disko Bay is a large bay in Western Greenland located at the border of the sub-Arctic and high-Arctic regions north of the Polar Circle. The bay has an average depth of 200 m with a trench in the middle of the bay extending to over 800 m depth (see Fig. 6). The average air temperature between February 15 and March 9 2009 was -17.1 ± 4.0 °C resulting in extensive ice cover during the time of the study. Disko Bay has been known to be an aggregation area for bowhead whales for centuries (Eschricht and Reinhardt, 1861). Every year bowhead whales can be observed close to the shores of Disko Island from mid-February to late May. The area is visited by ~1200 individuals annually in April and May (Heide-Jørgensen *et al.,* 2007), of which 78% are females (Heide-Jørgensen *et al.,* 2010). The number of whales in the bay earlier in the season (February and March) is unknown.

A hydrophone array of four independent receivers was used to record bowhead whale song and ambient noise levels. The receivers were synchronized by using a GPS system generated timing pulse with 50 µs accuracy (Møhl *et al.,* 2001). A hydrophone was deployed through sea ice to a depth of 25 m at each recording station and the sea bottom was at a depth of more than 200 m. Recording stations were spaced about 500 m apart in a quasi-linear array (Fig. 2). Each recording

station consisted of a B&K 8101 hydrophone (Brüel & Kjær, Nærum, Denmark, sensitivity of -184 dBV re 1μPa) connected *via* a custom-built low noise amplifier (40 dB gain) to one channel of an M-Audio Microtrack II 24/96 digital recorder sampling at 96 kHz (16 bit). All recording chains were calibrated before and after the recordings using a Brüel & Kjær 4228 pistonphone. The GPS timing signal from a frequency shift-keying (FSK) device (see Møhl *et al.,* 2001 for details) was recorded simultaneously on the second audio channel allowing for post-recording derivation of position and absolute timing every second. Due to low temperatures, all equipment was run on lithium-ion cells.

In order to estimate a sound velocity profile in the water column at the time of the recordings, we obtained salinity, temperature and depth values to 187 m at 1 m intervals using a Seabird SBE-25-01-CTD (Sea-bird Electronics, Inc., WA, USA). The acoustical analyses were done with custom-written scripts in *MatLab 7.5* (The Mathworks, Inc. Natick, MA, USA).

Only clear signals that did not temporally overlap with other signals were chosen for the analysis. The location of the sound source was estimated (in two dimensions) by the time-of-arrival differences of the same signal on the four receivers of the array (Spiesberger and Fristrup, 1990, Wahlberg *et al.,* 2001). The time-of-arrival difference was determined by cross-correlating the signals on three receivers with that on a reference hydrophone (recording station 1, Fig. 2). For each pair of receivers, the source location was located along a hyperbolic line derived from the time-of-arrival difference between the receivers and their spatial geometry (Spiesberger and Fristrup, 1990). With four receivers, this resulted in three independent hyperbolic lines (Wahlberg *et al.,* 2001). The position of the sound source relative to the hydrophone array was estimated by solving the three hyperbolic equations with the method of least-squares (Spiesberger and Fristrup, 1990; Madsen and Wahlberg, 2007). An example of localization is shown in figure 2. The apparent source level (ASL) was determined as the back-calculated sound pressure level at 1 m from the source at an unknown angle from the acoustic axis (Møhl *et al.,* 2001). ASL can be calculated from dB values by adding the received level (RL) and the transmission loss (TL) where the transmission loss (TL) is estimated from the geometrical spreading loss and frequency dependent absorption in the medium. The ASL's were calculated as peak-to-peak (PP), root-mean-squared (RMS) and energy flux density (EFD) values (Au, 1993). In addition to sound pressure level measurements the duration (s), maximum frequency (Hz), minimum frequency (Hz), centroid frequency (Hz) and rms bandwidth (Hz) were calculated. The centroid frequency (F_c) divides the signal into two parts of equal energy on a linear

scale. Bandwidth (BW_{rms}) of the signals was calculated as the centralized rms bandwidth, which expresses the spectral standard deviation around the centroid frequency.

The ambient noise level was measured using custom-written routines in *MatLab 7.5* (The Mathworks, Inc. Natick, MA, USA) where sections of noise with a duration of 1.5 s were analysed. Noise was measured from the entire frequency range of the recordings. Noise sections were identified in all of the recordings and selected on the basis that no strong whale calls or iceberg break ups were present. A total of 14 min of ambient noise from two different days were included in the analysis. Six minutes of this was measured from background noise only, excluding the faintest bowhead whale song, and 8 minutes was measured including the distant bowhead whale song in order to examine the masking effect resulting from other singing individuals. Frequency dependent absorption was estimated from the equations of Kinsler et al. (2000) using a temperature of -1.7 C and a depth of 25 meters.

III RESULTS

The bowhead whale was the only baleen whale species present in Disko Bay during our recordings. Bearded seals (*Erignathus barbatus*) were the only other species recorded. Out of 12h 10min of acoustic data recorded on March 6 and March 9 2010, 6h 21min recorded simultaneously on three or four recording stations were analysed for this study. The data contained two song types but analysis concentrated only on the dominating song type. The other song type was recorded only on one day with a poor signal to noise ratio. The dominant song type was composed of one stereotyped song note that was repeated 7 - 25 times in a song (Fig. 3) and 142 song notes of this type were analyzed. Of those 35 song notes recorded on March 6 on all four recording stations could be localized with high accuracy and be used for estimation of source level (Table 1). The mean ASL_{PP} was calculated to be 197 ± 2 dB re 1 µPa while the mean ASL_{RMS} and the mean ASL_{EFD} were 178 ± 2 dB re 1 µPa and 180 ± 2 dB re 1 $\mu Pa^2 s$, respectively (Table 1). The frequency of these song notes ranged from 105 ± 12 Hz to 1380 ± 97 Hz (Table 1). The remaining 107 song notes were analyzed to address whether the subset of 35 song notes was representative of the entire data set. The acoustic characteristics (Table 1) of the localized song notes (n=35) were similar to the remaining song notes (N= 107) and we thus argue that this subset of the data is representative of the entire data set even if the localized song notes were probably produced by the same individual (Table 1). The individual was localized to an average distance of 5041± 295 m from the array (Fig. 2).

Figure 4 shows the back calculated apparent source level (ASL_{RMS}) of the localized song notes measured at all the four stations in time. As shown in Figure 4, the source level is fluctuating over time, however, these fluctuations are almost synchronised between stations. The received levels are consistently higher at stations 2 and 3 at the centre of the array compared with stations 1 and 4 situated in the far ends of the array (Fig. 4). Given that the array from station 1 to station 4 is covering approximately 18 degrees of the full circle around the sound source/whale the difference in received level is most likely not the result of directionality, but rather due to an obstacle (iceberg) possibly blocking the direct path of the sound for stations 1 and 4. We therefore argue that the true source levels are likely best represented by stations 2 and 3.

To estimate the detection threshold for bowhead whale calls, we assumed that the whales are limited by background noise and not by their hearing threshold. To estimate the masking noise level setting for the detection threshold, we summed the spectral noise over the mean BW_{RMS} of 365 ± 77 Hz around the mean centroid frequency of 571 ± 83 Hz. The mean spectral noise levels in that band were 38 and 45 dB re 1 $\mu Pa^2/Hz$ with the greater value including faint bowhead whale singing in the background (Fig. 5). When integrated over the BW_{RMS}, that results in a detection threshold of 71 dB re 1µPa (RMS) at 45 dB re 1 $\mu Pa^2/Hz$ assuming an SNR of 0 dB for detection.

The sound velocity profile calculated from CTD data revealed a discontinuity starting at about a depth of 55 m producing a sound duct near the surface. The sound velocity stayed constant at about 1440 ms^{-1} until 55 m of depth after which it started to increase gradually resulting in a maximum velocity of about 1462 ms^{-1}. Depending on the depth of the receiver and the depth of the source, such a sound velocity profile can form a surface duct and may no longer be predictable from a geometric spreading model. However for the localization ranges of the whales of around 5 km, such ducting is unlikely to render transmission loss that deviates much from spherical spreading providing reliable estimates of source level (Medwin and Clay, 1998). However, it may be a different issue for estimation of a much bigger active space, a problem we will return to in the discussion.

IV DISCUSSION

Bowhead whale song recorded in this study had an estimated source level of 178 dB re 1µPa (RMS) (Table 1). The source level estimates of 158 – 189 dB re 1µPa of song recorded from Bering Sea bowhead whales are presumably peak to peak values (Cummings and Holliday, 1987) whereas the

corresponding mean value found in this study is 10 dB higher (197 dB re 1μPa (PP)). The source levels of calls from fin and blue whales have been reported to range between 180 to 193 dB re 1uPa (RMS) (Cummings and Thompson, 1971; Watkins *et al.,* 1987; Širović *et al.,* 2007), and thus slightly higher, but overlapping with the range of our source level measurements made here between 178 and 187 dB re 1uPa (RMS). The major difference in singing between the similar sized bowhead whales and fin whales is thus not the level, but the frequencies at which the songs are produced. Fin whales produce a 1 sec powerful pulse, where essentially all the acoustic energy is placed in a narrow frequency band around 20 Hz (Watkins *et al.,* 1987), while bowhead whales produce 1-2 sec long song notes that are high pitched and heavily frequency modulated. The sound energy of a bowhead whale song is distributed over a frequency band several decades broader than that of fin whale song (Fig. 3). Outcomes of using the passive sonar equation to estimate active space critically hinge on the quality and reliability of the input parameters that for this study in some cases are well known and for others less so. The estimates derived below should therefore be treated with caution, but are nevertheless instructive for evaluating the active space consequences of the powerful, but high-pitched singing in bowhead whales compared to similar sized balaenopterids.

During the time of the study, the ambient noise level in Disko Bay was very low (Fig. 5) compared to normal open water Wentz curves (Wentz, 1961). This can be explained by the extensive ice coverage essentially eliminating wave noise as well as effectively preventing the movements of icebergs and ship traffic in the area. Consequently, the masking noise is likely as low as it can get in this habitat. For these circumstances, the detection threshold of a bowhead whale song note was conservatively estimated to be 71 dB re 1μPa (RMS). Frequency dependent absorption (α) for a song note with a centroid frequency of 571 Hz is around 2.7 dB/100km (Fig. 1). If we apply a spherical spreading loss model of $20 \log (R) + \alpha R$ (where R is range in meters) the bowhead whale song with a source level of 178 dB re 1uPa (RMS) in question here will reach the estimated detection threshold of 71 dB re 1μPa (RMS) at an estimated distance of 140 km. The weaker and higher harmonics of bowhead whale song notes (Fig. 3) will have much smaller active space than the fundamental. By sharp filtering we find that frequency content in bowhead whale song notes above 1 kHz is at least 20 dB lower than that below 1 kHz, so the active space of the higher part of the fundamental and the harmonics will be the order of magnitude smaller than that of the fundamental below 1 kHz.

However, while sound propagation over the short distances in question for the acoustic localization made here is likely very close to 20log(R), such a model is too simplistic for the ranges

over which we evaluate the active space (Medwin and Clay, 1998). The sound velocity profile measured in the recording habitat is a typical arctic upwards refracting propagation situation that will create a near surface sound duct, reducing the transmission loss compared to a 20log(R) + αR model, except for very low frequencies below about 20 Hz whose modes are not supported in the duct (Medwin and Clay, 1998). However, the presence of a near complete ice cover will add downward reflection to the upwards refracting propagation situation to form a low-pass filter that at long ranges will provide a much higher attenuation of high frequencies than what can be predicted from 20log(R) + αR model.

Urick (1983) compiled measurements from several studies in the arctic for ice covered situations to show that frequencies between 20 and 40 Hz propagate very well under such circumstances whereas higher frequencies at first propagate better than 20log(R) + αR, and then at longer ranges much worse. For 400 to 800 Hz that cover the centroid frequencies of the bowhead whale calls, Urick (1983) show that they break even with a 20log(R) + αR model at some 60 km, and reach a transmission loss of 107 dB re 1m at about 90 km distance from the source. For frequencies above 1 kHz (where the estimated SL is 20 dB lower than for the frequencies below 1 kHz), the estimated detection threshold will be reached at ranges no further than 10 to 20 km.

Thus, when employing a more realistic propagation model for the arctic, it becomes clear that the active space for bowhead whale song is likely no more than about 90 km under low noise conditions, and considerably smaller for more noisy conditions without ice cover. The 90 km estimate here is therefore likely the longest range that a bowhead whale can possibly expect to detect a singing conspecific; actual decoding of higher frequencies of the song can only happen at short ranges on the order of 10 km. That situation is akin to the situation for some bird species (Brenowitz, 1982b) where the low frequency part of the birds call serves as a homing signal at longer ranges, and where higher frequency components can be used at shorter ranges to extract information about the singer. Approximately 1200 bowhead whales congregate in the Disko Bay area in late spring (Heide-Jørgensen *et al.,* 2007) to feed (Laidre *et al.,* 2007; Simon *et al.,* 2009), and from the active space estimates here it seems that a whale that reside in Disko Bay (having a radius of some 50 km) will be able to detect and home in on all singing conspecifics no matter where they are in the bay area (Fig. 6). The singing whales are likely the biggest source of interference for decoding the song of one particular whale as is the case for many lekking or chorusing animals (e.g. Gerhardt and Klump, 1988). This phenomenon is also known as the cocktail party effect.

In contrast to bowhead whales, fin whales vocalize around 20 Hz where the spectral noise measured in our study in Disko Bay was 57 dB re 1uPa^2/Hz which is about 10 dB higher than at the centroid frequency of bowhead whale song (Fig. 5). However, due to the narrow BW_{RMS} of 4 Hz of a fin whale call the estimated detection threshold for fin whales under these low noise conditions is only about 63 dB re 1uPa (RMS). Therefore despite lower spectral noise levels at higher frequencies, for the same power output, bowhead whales will have comparable or most likely higher detection thresholds than fin whales due to their large song bandwidth. Using a very simplified spherical spreading model, a detection threshold of 63 dB re 1uPa (RMS) and an identical source level as bowhead whale song of 178 dB re 1uPa (RMS) for a fin whale 20 Hz pulse, the estimated range over which this fin whale signal could be detected is around 500 km. The active space will be much larger if the SL value of 189 dB re 1uPa (RMS) of Širović et al (2007) is used. Whether the animals can in fact hear each other over such distances critically hinges on the validity of the input parameters, but it is clear that the active space of bowhead whales is much smaller than that of fin whales for the same source level, because of the much higher song frequencies and much broader bandwidth.

The low frequency songs of blue and fin whales are simple, narrowband low frequency displays (Croll *et al.,* 2004). These balaenopterids do not have known small scale breeding grounds (Connor *et al.,* 2000), likely because they can hear each other at very long ranges. Bowhead whales, like humpback whales, have evolved elaborate songs most likely in a selective mating scheme, and to increase complexity of song the bandwidth and centroid frequencies are much higher than can be expected for animals of this size. These species produce source levels comparable to balaenopterids, but have a much shorter active space (both in terms of detection and decoding) than balaenopterids because of greater absorption at higher frequencies and same energy distributed over larger bandwidth. The solution for the high frequency singers is to aggregate in a small area where high pitched singing can reach enough receivers while allowing for a dynamic song repertoire. The similarity of the display strategies of these two species belonging to different families, bowhead whale to balaenid whales and humpback whale to balaenopterid whales, can be regarded as an example of convergent behavioural evolution. High pitched complex song in bowhead and humpback whales has most likely coevolved with small scale breeding grounds due to limited active space.

ACKNOWLEDGEMENTS

We thank S. Markager for CTD data calculation. The Arctic Station of Qeqertarsuaq, University of Copenhagen provided an excellent working platform for our project. Nukissiorfiit, Greenland, is thanked for granting a research leave for M. Christoffersen to conduct this study. This work was funded by Oticon Fonden (grant # 08-3469 to Arctic Station, O. T.). O. T. and M. C. were additionally funded by A .P. Møller og Hustru Chastine Mc-Kinney Møllers Fond til almene Formaal, M. S. by a PhD scholarship from Oticon Fonden and P.T.M by frame grants from the Danish Natural Science Research Council.

LITERATURE CITED

Au, W.W.L. (**1993).** The sonar of dolphins. Springer, New York

Au, W.W.L., Pack, A.A., Lammers, M.O., Herman, L.M., Deakos, M.H. and Andrews, K. (**2006**). Acoustic properties of humpback whale song. J. Acoust. Soc. Am. **120**,1103-1110.

Bradbury, J.W. and Vehrencamp, S.L. (**1998**). Principles of animal communication. Chapter 2: The properties of sound, pp. 15-40. Sinauer Associates.

Brenowitz, E.A. (**1982a**). The active space of red-winged blackbird song. J. Comp. Physiol. A. **147**, 511-522. doi: 10.1007/BF00612017

Brenowitz, E.A. (**1982b**). Long-range communication of species identity by song in the Red-winged Blackbird. Behav. Ecol. Sociobiol. **10**, 29-38. doi: 10.1007/BF00296393

Brownell, R.L., and Ralls, K. (**1986**). Potential for sperm competition in baleen whales. Rep. Int. Whaling Comm. **8**,110–141.

Cerchio, S., Jacobsen, J.K. and Norris, T.F. (**2001**). Temporal and geographical variation in songs of humpback whales, Megaptera novaeangliae: synchronous change in Hawaiian and Mexican breeding assemblages. Animal Behav. **62**, 313–329.

Clark, C. W. (**1995**). Matters arising out of the discussion of blue whales. Rep. Int. Whal. Comm. **45**, 210–212.

Connor, R.C., Read, A.J. and Wrangham, R. (**2000**). Male reproductive strategies and social bonds. In J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (Eds.) Cetacean societies, Field studies of Dolphins and Whales. Chicago, The University of Chicago Press, pp 247-270.

Cummings, W.C. and Thompson, D. (**1971**). Underwater sounds from the blue whale, *Balaenoptera musculus*. J. Acoust. Soc. Am. **50**, 1193-1198.

Cummings, W.C. and Holliday, D.V. (**1987**). Sounds and source levels from bowhead whales off Pt. Barrow, Alaska. J. Acoust. Soc. Am. **83**, 814-821.

Cummings, W.C. and Thompson ,D (**1994**). Characteristics and seasons of blue and finback whale sounds along the U.S. west coast as recorded at SOSUS stations. J. Acoust. Soc. Am. **95**, 2853-2853.

Croll, D.A., Clark, C.W., Acevedo, A., Tershy, B.R., Flores, S., Gedamke, J. and Urban. J. (**2002**). Only male fin whales sing loud songs. Nature **417**, 809. doi:10.1038/417809a

Eschricht, D.F. and Reinhardt, J. (**1861**). Om Nordhvalen (Balæna Mysticetus L.) navnlig med Hensyn til dens Udbredning i Fortiden og Nutiden og til dens ydre og indre Særkjender. (*The Northern Whale (Balaenoptera mysticetus L.) with especial reference to its geographical distribution in times past and present, and to its external and internal characteristics)*. Bianco Lunos Bogtrykkeri, Copenhagen.

Evans, P.G.H. (**1987**). The Natural History of Whales and Dolphins. Christopher Helm Ltd, Bromley, Kent, UK.

Fletcher, N.H. (**2004**). A simple frequency-scaling rule for animal communication. J. Acoust. Soc. Am. **115**(5), 2334-2338.

Gerhardt, H.C. and Klump, G.M. (**1988**). Masking of acoustic signals by the chorusbackground noise in the green treefrog: a limitation on mate choice. Animal Behav. **36**, 1247-1249.

Heide-Jørgensen, M.P., Laidre, K., Borchers, D., Samarra, F. and Stern, H. (**2007**). Increasing abundance of bowhead whales in West Greenland. Biol. Lett. **3**, 577-580.

Heide-Jørgensen, M.P., Laidre, K.L., Wiig, Ø., Postma, L., Dueck, L. and Bachmann, L. (**2010**) Large-scale sexual segregation of bowhead whales. Endang. Spec. Res. **13**, 73–78.

Janik, V.M. (**2000**). Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. J. Comp. Physiol. A. **186**, 673-680.

Laidre, K., Heide-Jørgensen, M.P. and Nielsen, T.G. (**2007**). Role of the bowhead whale as a predator in West Greenland. Mar. Ecol. Prog. Ser. **346**, 285-297.

Ljungblad, D., Thompson, P. and Moore, S. (**1982**). Underwater sounds recorded from migrating bowhead whales, *Balaena mysticetus*, in 1979. J. Acoust. Soc. Am. **71**, 477-482.

Kinsler, L.E., Frey, A.R., Coppens, A.B. and Sanders ,J.V. (**2000**). Fundamentals of Acoustics. John Wiley and Sons, Inc.

Madsen, P.T. and Wahlberg, M. (**2007**). Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales. Deep-Sea Res. **54**, 1421-1444. doi:10.1016/j.dsr.2007.04.020

Medwin, H. and Clay, C.S. (**1998**). Fundamentals of Acoustical Oceanography. Academic Press, New York, pp. 712.

Møhl, B. and Andersen, S. (**1973**). Echolocation: high-frequency component in the click of the Harbour Porpoise (*Phocoena ph. L.*). J. Acoust. Soc. Am. **54,** 1368-1372.

Møhl, B., Wahlberg, M. and Heerfordt, A. (**2001**). A large-aperture array of non-linked receivers for acoustic positioning of biological sound sources. J. Acoust. Soc. Am. **109**, 434 – 437.

Payne, R.S. and Webb, D. (**1971**). Orientation by means of long range acoustic signalling in baleen whales. Ann. NY. Acad. Sci. **188**, 110-141. doi: 10.1111/j.1749-6632.1971.tb13093.x

Payne, K. and Payne, R. (**1985**) Large scale changes over 19 years in songs of humpback whales in Bermuda. Z. Tierpsychol. **68**, 89-114.

Poole, J.H., Payne, K., Langbauer, W.R. Jr. and Moss, C.J. (**1988**). The social contexts of some very low frequency calls of African elephants. Behav. Ecol. Sociobiol. **22**, 385–392.

Simon, M., Johnson, M., Tyack, P. and Madsen, P.T. (**2009**). Behaviour and kinematics of continuous ram filtration in bowhead whales (Balaena mysticetus). Proc. R. Soc. B **276**, 3819–3828.

Širović, A., Hildebrand, J.A. and Wiggins, S.M. (**2007**). Blue and fin whale call source levels and propagation range in the Southern Ocean. J. Acoust. Soc. Am. **122**, 1208-1215.

Spiesberger, J.L. and Fristrup, K.M. (**1990**). Passive localization of calling animals and sensing of their acoustic environment using acoustic tomography. Am. Nat. **135**, 107-153.

Tyack, P.L. and Clark, C.W. (**2000**). Communication and Acoustic Behavior of Dolphins and Whales. In W. Au, A. Popper and R. Fay (Eds.) Hearing by Whales and Dolphins. Springer Handbook for Auditory Research.

Urick, R.J. **(1983**). Principles of underwater sound. 3rd edition, New York: McGraw- Hill.

Wahlberg, M., Mohl, B. and Madsen, P. T. (**2001**). Estimating source position accuracy of a large-aperture hydrophone array for bioacoustics. J. Acoust. Soc. Am. **109**, 397-406.

Watkins, W.A., Tyack, P., Moore, K.E. and Bird, J.E. (**1987**). The 20-Hz signals of finback whales (*Balaenoptera physalus*). J. Acoust. Soc. Am. **82**, 1901-1912.

Wenz, G.M. (**1961**). Some periodic variations in low-frequency acoustic ambient noise levels in the ocean. J. Acoust. Soc. Amer. **33**, 64-74.

Figures

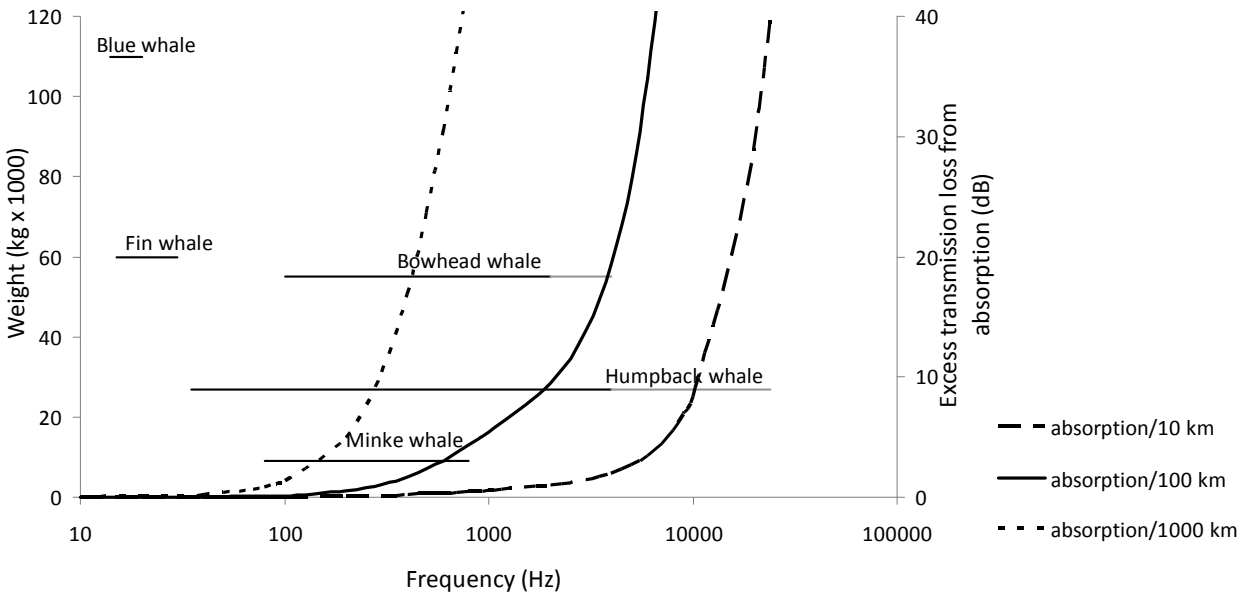

Figure 1. Fundamental frequency of songs and body weights for the singing baleen whale species together with the excess transmission loss due to absorption at 10 km, 100 km and 1000 km (Kinsler et al. 2000). The grey lines for bowhead whale and humpback whale mark the frequency range of harmonics. Note that the active spaces of the bowhead and humpback whales will be limited for the high frequencies of their songs. For blue whale (Cummings and Thompson 1971); fin whale (Watkins et al. 1987); bowhead whale (Ljungblad et al. 1982; Cummings and Holliday 1987); humpback whale (Payne and Payne 1985; Cerchio et al. 2001; Au et al. 2006); and minke whale (Mellinger et al. 2000).

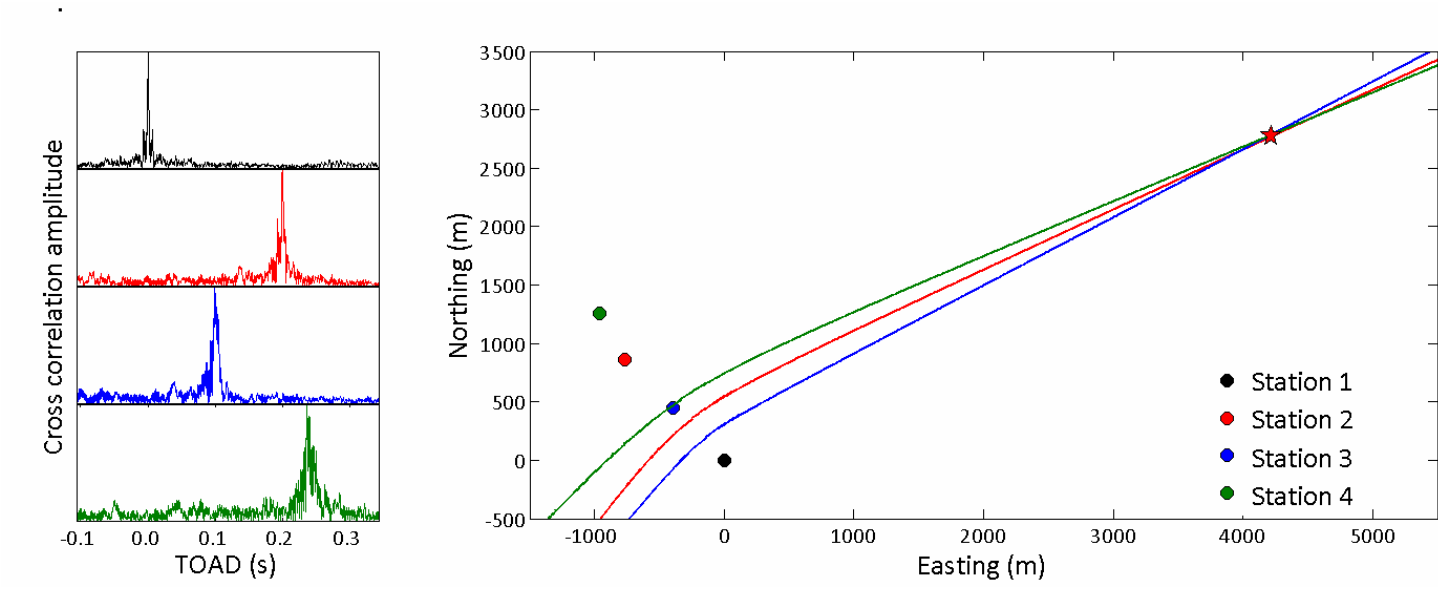

Figure 2. Acoustic localisation using our four-channel hydrophone array. Left: Cross correlation functions for three channels relative to channel 1 (an autocorrelation). The peak of each channel (stations 2 to 4) indicates the time-of-arrival difference (TOAD) relative to channel 1. Right: 2D localization plot in a coordinate system (m) referenced to channel 1. Each hyperbola indicates all source positions that would result in the time-of-arrival difference measured between station 1 and the station with corresponding colour. The red star indicates the most likely position of the source as calculated with the method of least squares.

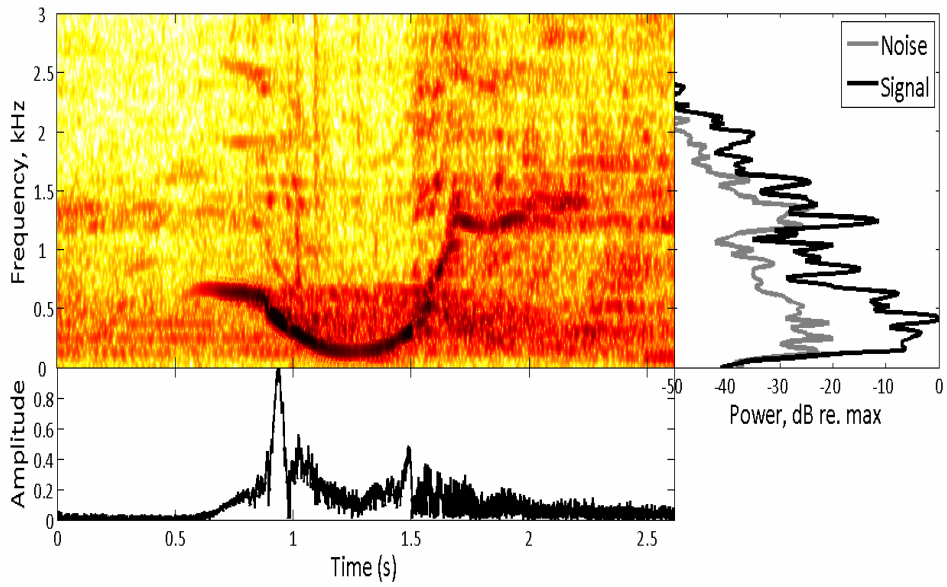

Figure 3. Spectrogram, oscillogram and power spectrum of a note from the song of the bowhead whale at the position determined in Figure 2. The song was composed of repetitions of this single

song note. The frequency of the fundamental ranged in average from 105 Hz ± 12 Hz to 1380 Hz ± 97 Hz (Table 1). Harmonics are seen up to about 4 kHz.

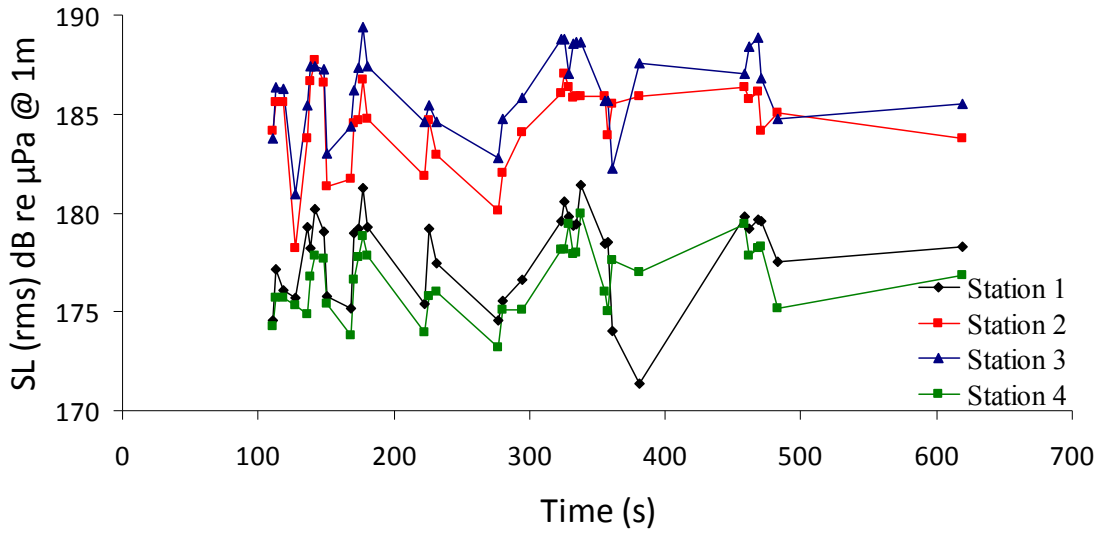

Figure 4. Source level (RMS) of 35 song notes from each of four recording stations during a song session presumably produced by one individual at 5041± 295 m from the centre of the array.

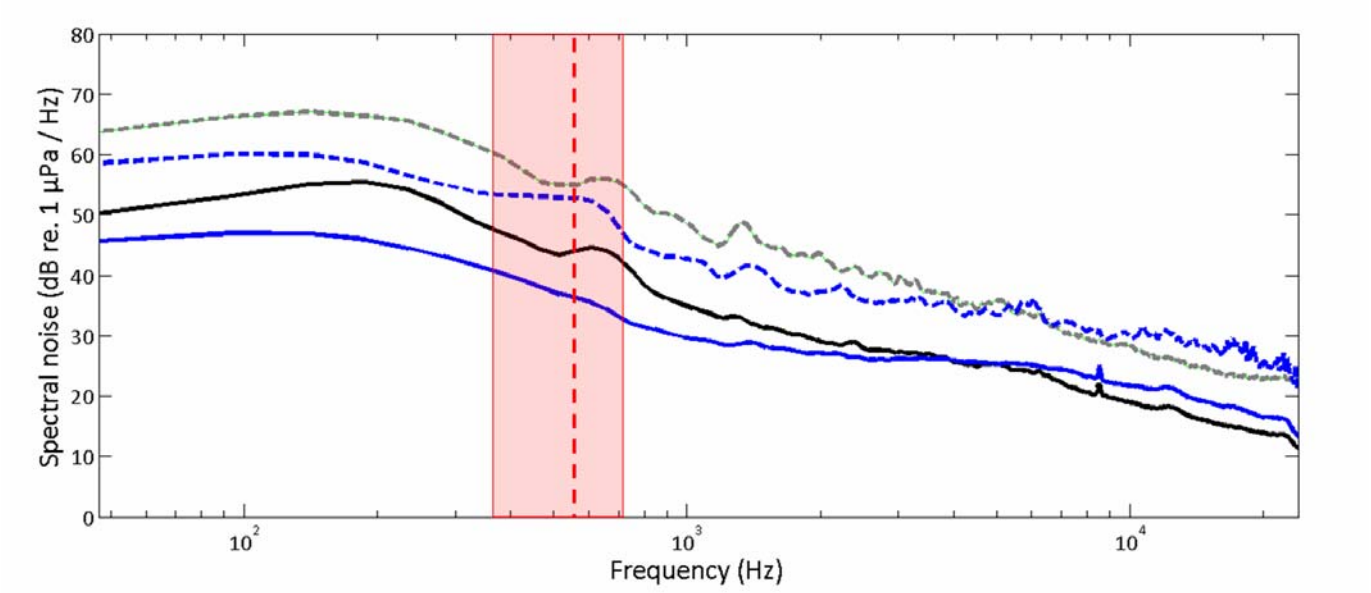

Figure 5. Ambient spectral noise level in Disko Bay at 10 m depth. The solid blue line shows the ambient noise level and the dashed blue line shows the positive standard deviation for these values. The solid black line shows the ambient noise including faint bowhead whales singing and the dashed grey line shows the positive standard deviation for those values. The vertical dashed red line marks the centroid frequency of 571 Hz of bowhead whale song notes and the red area indicates the

365 Hz RMS bandwidth of these signals. The spectrum level of the masking noise is about 71 dB in the bandwidth of a bowhead whale call.

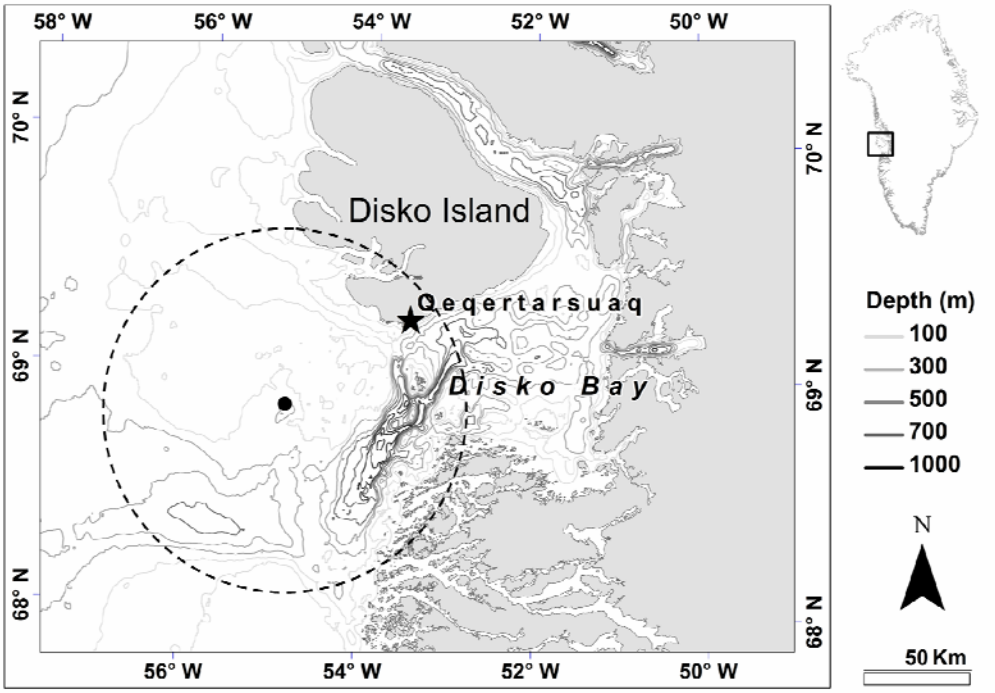

Figure 6. The estimated active space of the bowhead whale song in Disko Bay. The dashed circle illustrates the estimated active space of the bowhead whale song (105 Hz to 1380 Hz) with an imaginary whale at the centre of it marked with a black dot. The radius for the active space of the bowhead whale song is 90 km. Qeqertarsuaq, where Arctic Station is situated is marked with a black star.

Table 1. Measured parameters for 35 song notes from the localised bowhead whale and for the remaining song notes (n=107). *T* = duration, *CF* = centroid frequency, *BW* = centralized root mean square (RMS) bandwidth, *R* = distance, *TL* = transmission loss, *RL* = received level (efd=energy flux density, pp=peak to peak), *ASL* = apparent source level, NA = not applicable).

Station 2		T (s)	Min freq (Hz)	Max freq (Hz)	CF (Hz)	BW (Hz)	R (m)	TL (dB)	RL pp (dB re µPa)	RL rms (dB re µPa)	RL efd (dB re µPa^{2}s	ASL pp (dB re µPa)	ASL rms (dB re µPa)	ASL efd (dB re µPa^{2}s)
SL n=35	Mean	1.6	105	1380	571	365	5041	74	130	110	112	197	178	180
	St Dev	0.2	12	97	83	77	295	1	3	3	2	3	2	2
Other n=107	Mean	1.5	120	1267	464	361	NA	NA	125	106	108	NA	NA	NA
	St Dev	0.2	26	236	90	114	NA	NA	5	5	5	NA	NA	NA

Paper IV

Tervo, O. M., Christoffersen, M.F., Parks, S. E., Kristensen, R. M. and Madsen, P. T. Simultaneous sound production in the bowhead whale (*Balaena mysticetus). Journal of the Acoustical Society of America,* (in review).

Evidence for simultaneous sound production in the bowhead whale (*Balaena mysticetus)*

Outi M. Tervo[a)]

Arctic Station, University of Copenhagen, P.O. Box 504, 3953 Qeqertarsuaq, Greenland

Mads Fage Christoffersen

Arctic Station, University of Copenhagen, P.O. Box 504, 3953 Qeqertarsuaq, Greenland

Susan E. Parks

Applied Research Laboratory, Pennsylvania State University, P.O. Box 30, State College, PA 16804-0030, USA

Reinhardt Møbjerg Kristensen

Natural History Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen OE, Denmark

Peter Teglberg Madsen

Zoophysiology, Department of Biological Sciences, Building 113,1C. F. Møllers Allé 3, 8000 Århus C, Denmark

(Received:

Running title: Evidence for two-voice singing in bowhead whale

[a)]Electronic mail: ote@science.ku.dk

Simultaneous production of two harmonically independent sounds, the two-voice phenomenon, is a well-known feature in bird song. Some toothed whales can click and whistle simultaneously, and a few studies have also reported simultaneous sound production by baleen whales. The mechanism for sound production in toothed whales has been largely uncovered within the last three decades, whereas mechanism for sound production in baleen whales remains poorly understood. This study provides three lines of evidence from recordings made in 2008 and 2009 in Disko Bay, Western Greenland, strongly indicating that bowhead whales are capable of simultaneous dual frequency sound production. This capability may function to enable more complex singing in an acoustically mediated reproductive advertisement display, as has been suggested for songbirds, and/or have significance in individual recognition.

[DOI:]

PACS number(s): 43.80.Ka, 43.30.Sf

I. INTRODUCTION

Songbirds are able to produce two sounds independently using two separate sound generators located in the syrinx (Suthers, 1990; Fee *et al.*, 1998). This production of two independent signals results in the remarkable structural and temporal complexity of bird song that is used by females to select a mate, by males in territorial displays (Borror and Reese, 1956; Greenewalt, 1968; Searcy and Andersson, 1986), and for individual recognition in colonial breeding species (Aubin *et al*., 2000). Song of baleen whales is, like to bird song, also considered to be a reproductive advertisement signal, (Payne and McVay, 1971) likely playing a significant role in mate choice in a polygamous mating system (Tyack and Clark, 2000). Most species of baleen whales sing including the bowhead whale *Balaena mysticetus* (Clark, 1990). The song of bowhead whales is composed of repeated series of highly stereotyped song notes, and the song notes change completely between years, resulting in distinctive songs in each year (Würsig and Clark, 1993; Tervo *et al*., 2011). Multiple songs are produced within a season (Stafford *et al*., 2008; Delarue *et al*., 2009; Tervo *et al*., 2011) with one dominant song of the season that is most common, and one or two other songs, which are heard less frequently (Stafford *et al*., 2008; Tervo *et al*., 2011).

Like songbirds, all toothed whales except for the sperm whales (*Physeteridae*) have a bilateral configuration for sound production (Cranford *et al*., 1996). In non-physeterid toothed whales two sound generating structures, the paired phonic lips, are located in each of the nasal passages providing the toothed whales the possibility of simultaneous sound production (Cranford, 2000). So far biphonation has been suggested for bottlenose dolphins *Tursiops truncatus* (Cranford, 2000) and killer whales *Orcinus orca* (Tyson *et al.*, 2007). Anatomical studies of baleen whales suggest that sounds are produced in the larynx (Reidenberg and Laitman, 2007). The arytenoid cartilages in the larynx support a U-shaped fold, which may function to regulate airflow through the larynx much in

the manner of true vocal folds (Reidenberg and Laitman, 2007). Despite there being only a single candidate organ for sound production in baleen whales, e.i. the larynx, the sounds produced by some species, including the minke whale *Balaenoptera acutorostrata* (Gedamke *et al.*, 2001) and North Atlantic right whale *Eubalaena glacialis* (Tyson *et al.*, 2007), suggest that biphonation occurs. These biphonate vocalizations included the production of two harmonically unrelated sounds by the minke whale (Gedamke *et al.*, 2001) and the presence of sidebands and unrelated nonparallel bands in the northern right whale (Tyson *et al.*, 2007). Two simultaneously occurring song notes have also been reported for bowhead whales (Würsig and Clark, 1993), but in remains unclear whether these observations were due to a duet of two individuals or due to simultaneous sound production by a single individual.

To test the hypothesis that individual bowhead whales can produce two sounds simultaneously, we analyzed bowhead whale songs recorded with hydrophone arrays during the spring of 2008 and 2009 in Disko Bay, Greenland. Our results strongly indicate that singing bowhead whales include simultaneous dual frequency sound production as part of their singing behavior.

II. MATERIAL AND METHODS

A. Data collection

The data were collected in Disko Bay, Western Greenland, 69ºN and 54ºW, from March 12 to April 14, 2008, and from March 5 - 9, 2009. In 2008 recordings were made using two HTI-94-SSQ hydrophones (High Tech, Inc., Gulfport, USA) (-198 dBV/1µPa) with a flat (±2 dB) frequency response from 2 Hz to 30 kHz. The hydrophones were connected to a custom built amplifier (highpass filter at 30 Hz, 20 dB gain), and deployed through holes in fixed/stable sea ice 20 m apart at a depth of 10 m. The signals were recorded using a SONY DAT TCD-D8 tape recorder with a

sampling frequency of 44.1 kHz and with 16-bit resolution. The data were digitized into standard wave files in *Raven Pro 1.3* (Cornell Laboratory of Ornithology, Ithaca, NY).

In 2009 we used a non-linked array of three independent receivers that were synchronized with 50 µsec timing from GPS satellite signals using a frequency shift keying device (FSK) (see Møhl *et al.*, 2001 for details). Each recording station consisted of a B&K 8101 hydrophone (-184 dBV/1µPa) connected to a low noise amplifier (40 dB gain) with 10 Hz highpass and a 25 kHz lowpass filters, a FSK device and a stereo M-Audio Microtrack II 24/96 digital recorder. The FSK signal and acoustic signals were recorded on the two channels on the M-Audio Microtrack II 24/96 digital recorder sampling at 96 kHz with 16-bit resolution. The recordings from the three receivers were then time-aligned using the FSK signals. Hydrophones at each recording station were deployed at 25 m depth through holes in the fixed stationary coastal sea ice. The stations formed a linear array of 1 km where the spacing between stations was 700 m and 300 m (Fig. 1A).

B. Data analysis

Three analyses were conducted: 1) localization of the source with a three hydrophone array, 2) comparison of time of arrival differences on a two hydrophone array and 3) spectral analysis of spectrograms of the recorded signals.

In 2009, the sources of the two simultaneously occurring sounds recorded with three hydrophone array were localized using the hyperbolic method in *Ishmael 1.0* (D. Mellinger, Oregon State University, Newport, OR) with time of arrival difference (TOAD) of the song components time aligned via FSK recordings with an accuracy of 50 µs (Møhl *et al.*, 2001). The localization of each song component was repeated 10 times in order to account for differences in the localization accuracy caused by the size of the measuring window in *Ishmael 1.0*. The localization error for this type of array was estimated by assuming a 100 µs error in time measurements, 10 m/s variation in

sound velocity and 1 m in receiver locations. For each location, 1000 iterations were computed and new locations were calculated accordingly. The low and high bounds of the new locations were used in estimating the localization error (sensu Wahlberg *et al*., 2001).

In 2008, we measured the TOAD between the two hydrophone receivers for the two simultaneously occurring song components. If the two song components originated from two different, independently moving, sources the differences in the time of arrival between the two song components should change. If the different components are produced by a single source or by two sources with fixed distance to each other the time of arrival differences between the two song components should always be the same on both channels at any point of time. The onset time of signals was determined visually from the spectrogram with a time resolution of 11.6 ms and each measurement was repeated three times (Hamming window with 512-point FFT size, 50% overlap). The significance of the time of arrival differences between the two components was tested with a T-test in *S-PLUS 6.2* (TIBCO Software Inc, Palo Alto, CA).

For the spectral analysis of the data from 2008 and 2009 a Hamming window with a FFT size of 1024 was chosen yielding a frequency resolution of 43 Hz at 44.1 kHz sampling. The minimum amplitude of the first song note HI was measured from three sequential 300 ms analysis windows. The measurement windows were labeled 1, 2, and 3 (Fig. 2A). Window 1 started 600 ms before the onset of the second song note BS, window 2 started 300 ms before the onset of the second song note BS and the last window 3 started at the onset of the second song note BS. These measurements were made using the cursor tool in *Adobe Audition 3.0* (Adobe Systems Inc., San Jose, CA, USA).

III. RESULTS

For the duration of the recording periods in 2008 and 2009 bowhead whales were the only baleen whale species heard and observed in Disko Bay. One other vocally active species, the bearded seal *Erignathus barbatus*, was recorded in 2009. Due to the extensive ice coverage during the time of the recordings in both 2008 and 2009 it was not possible to obtain direct visual observations of the bowhead whales producing the recorded vocalizations.

In 2009, 4 h of data were analyzed and two simultaneously occurring song notes were recorded on March 6, 2009 as part of the second song type of that year (Fig. 1B). The two song notes, high and low, were localized on average 59 m apart at a distance of about 1.6 km from the centre of the array (Fig. 1A). The 10 repeated localizations of the same high and low song notes resulted in an elongated location cluster with a width of 37 m and length of 317 m (Fig. 1A). The minimum distance between a localized high and low song note was 6 m and the equivalent maximum distance was 317 m. Thus the expected localization error for this array based on the error analysis ranged between 20 m and 400 m.

In 2008, 7.75 h of data were analyzed and 3 h contained a song type where two song notes, called HI and BS (Tervo *et al*., 2011), occurred simultaneously (Fig. 3). Each song was composed of one HI song note together with three to 18 repetitions of song note BS. Song note HI was a continuous, highly frequency modulated signal with a mean duration of 15.2 (± 0.4) s (n=11) and song note BS was a low frequency upsweep with a short mean duration of 0.2 (± 0.0) s (n=19) (Fig. 3A, Table I). The harmonics of the fundamental frequencies of HI and BS extended to 3500 kHz and to 700 Hz, respectively (Fig. 3). The mean duration of a song was 15.2 (± 0.4) s (n=11) and was the same duration as song note HI which continued throughout the song. We extracted 11 songs from a 20 min song session recorded on March 19, 2008 for the analysis on the basis that no other songs were heard during this song session and all the songs had a signal-to-noise ratio of > 20 dB. The two song components HI (n=11) and BS (n=19) were significantly different in their minimum

and maximum frequencies. The lowest frequency of HI was higher than the highest frequency of BS by more than an octave at any given time and the two components were not harmonically related (Table I). The measurements of the time of arrival differences between components HI and BS (n=11) showed no significant difference (T-test: t= 0.0029, p = 0.997, df = 36). The time of arrival measurements from the 20 min song session were temporally spaced with an average time interval between consecutive measurements of 1.1 (± 2.4) min. This indicates that the source or sources producing the two song components HI and BS were always on the same hyperbola, even though the time of arrival difference between hydrophone 1 and hydrophone 2 (ranging from -20 ms to 40 ms) showed that the source or sources were moving.

The sound intensity measurements of the data from 2008 showed that the minimum amplitude of song note HI was lowest in measurement window 2 starting 300 ms before the onset of the song component BS (n=19) (Fig. 2B). The minimum amplitude of song note HI in the measurement window 2, right before the onset of BS was on average 10 (± 6) dB lower than the minimum intensity in the measurement window 1. Similarly, the minimum amplitude in window 2 was 13 (± 6) dB lower than the minimum amplitude in the window number 3 after the onset of BS (Fig. 2B). Only on one occasion, (measurement number 19 Fig. 2B), the minimum sound amplitude of song note HI was not lowest in window 2. In this case, the minimum sound amplitude was lowest in window 1, 600 to 300 ms before the onset of song note BS.

The data from 2009 (n=1) showed a different phenomenon. The window of lowest amplitude was in window 3, 300 ms after the onset of the low song component (measurement 20, Fig. 2B). However, the ca. 60 ms long area of lowest amplitude in window 3 in the high song component coincides with an area of high amplitude in the low song component (Fig. 1C). Furthermore, this is immediately followed by a 140 ms long area of high amplitude in the high song component which

coincides with an area of low amplitude in the low song component indicating that the sources of these two sounds are connected (Fig. 1C).

IV. DISCUSSION

In this study we analyzed two different bowhead whale songs from 2008 and 2009 composed of simultaneously occurring song notes to test whether bowhead whales are capable of two-voice singing. In 2009, when localizing with a three-hydrophone array, we found that the two simultaneously produced sound sources were located to the same position well within the estimated localization error of the array. In 2008, when obtaining bearings with a two-hydrophone array, the two simultaneously occurring song notes in the song were always co-located on the same hyperbola during a 20 minute long continuous song session. Finally, we found that the two simultaneously occurring sounds had an influence on the production of each other indicating that they are produced by the same sound producing structures or that they are driven by the same pneumatic pressurization events.

For the 2009 data (three hydrophone array), the potential error in absolute positions at the localized range was calculated based on random iterations to vary between 20 m and 400 m. Since the focus of this study is in the relative positions of the two song notes occurring at the same time, , differences in the positions between the 10 repetitions of each song note caused by variation in the size of the measurement window and in the performance of the localization method when applied to different frequency contours in *Ishmael 1.0* can be regarded as the relevant error of the system. In figure 1A, the 10 repetitions of localizations of both song notes show a strong tendency to form an elongated cluster perpendicular to the array. This suggests that the differences in localization between repetitions are most likely due to bearing lines crossing at low angles resulting in minor

error in the direction of the source but major error in the distance between the source and the array. We therefore argue that it is plausible that the two sounds were produced by a single source and that the relatively large maximum distance of 317 m between localizations of low and high song notes is an artifact of the localization method.

The behavior of bowhead whales during winter at the time of the data collection is not well documented. The most commonly observed surface behaviors in March in Disko Bay include resting and traveling where animals are typically solitary spaced > 300 m from each other. Co-operative skim feeding at the surface and pairs of whales swimming next to each other is most commonly seen later in the season in April and May, lending weight to the contention that the co-located sound sources are from a single whale and not two close by conspecifics.

For the 2008 data (two hydrophone array) the time resolution of the analysis was 11.6 ms, which corresponds to an error in distance of about 17 m. In this case as well, two bowhead whales could have been located right next to each other, each producing one song note in a duet, and our coarse resolution would have been unable to discriminate the two sources. Another explanation for the result that the two sounds from 2008 were co-located during a 20 minute long song session is that two bowhead whales could have been located in different positions on the same hyperbola line with fixed distance to one another while performing a duet. In fact, the time interval between subsequent TOAD measurements ranged from 2 seconds to 10 minutes indicating that if the two sounds were produced by two animals, the two individuals must have maintained precise orientation and distance to one another with respect to the array throughout the entire song session. Duets have been described for many song bird species (Hall 2009), a few terrestrial mammals (Janik and Slater 1997) but never for marine mammals. Coordinated movements during the duet are rarer and described for some bird species (Hall 2009), but again never for marine mammals. Instead

of a duet with coordinated movements, it therefore seems more parsimonious that our results are due to simultaneous sound production by a single individual.

This interpretation is also supported by spectral and intensity analyses of the sounds. The spectral analysis of the 2008 data (two hydrophone array) showed that the intensity of the first song note HI dropped before the onset of the second song note BS in average 10 (± 6) dB. The spectral analysis of the 2009 data (three hydrophone array) showed that the intensity of the first song note dropped after the onset of the second song note, but it also revealed areas of high and low amplitude shifting between the two sounds when high amplitude events in the one sound coincided in time with an area of low amplitude in the other, and vice versa. We propose that the intensity from one sound source within the animal is affected by the onset of activity in another source within the same animal, implying that the same whale simultaneously produced the two sounds. This phenomenon, where activity in the one sound producing organ has an impact on the performance of the other, has also been described for song birds that employ two-voice singing (Zollinger, 2007).

Simultaneous sound production enables individuals to produce complex acoustic signals in frequency and in time (e.g. Suthers, 1990; Gedamke *et al.*, 2001). Acoustic complexity of the song is an indication of high vocal motor control in songbirds (Nowicki *et al*., 1986), which may be used as an honest signal of the singer's quality in a mate choice context (Vallet *et al.*, 1998; Ballentine *et al.*, 2004). In canaries, *Serinus canaria*, a certain phrase of the song, composed of two simultaneously produced syllables, is more difficult to produce than other phrases and females prefer the males that master the production of this section (Vallet *et al.*, 1998). Bowhead whales are known to have a have a high degree of seasonal and annual variation in their song repertoire (Würsig and Clark, 1993; Tervo *et al*., 2009; Tervo *et al*., 2011). The simultaneous production of two independent sounds enhances the potential for creating complex acoustic signals and this complexity could play a role in mate choice. Simultaneous sound production has also been documented to function for communicating identity (Aubin *et al*., 2000; Miller *et al*., 2007) and orientation of the signaler in

relation to the receiver in some species (Miller *et al*., 2007), which could be a function of dual sound production in bowhead whales as well.

In conclusion, the three lines of evidence presented in this study all point to simultaneous dual frequency sound production by bowhead whales. With the sound source localization results, we demonstrate the co-location of the sound sources, though it is not possible to definitely determine whether a single whale or two whales closely associated, produced the sounds. The analysis of the amplitude modification of one signal by the onset of the second signal provides additional evidence of a direct linkage between the sound production mechanisms for the two sounds. In combination these observations strongly suggest that individual bowhead whales are capable of dual sound production. We propose that two-voice singing may have evolved through acoustically mediated sexual selection for individuals that demonstrate their ability to perform complex signals with a finely controlled vocal apparatus in a polygamous mating system. This result, together with the other reports on baleen whale simultaneous sound production emphasize the need for further investigations on the sound production of mysticetes which appears to be more complex than previously suggested.

ACKNOWLEDGMENTS

We thank M. Simon and L. Miller for their help in the data collection, F. Jensen for his help with acoustic localization and M. Wahlberg for calculating the localization error estimates. P. Tyack, A. Foote and two anonymous reviewers provided helpful critique to previous versions of this manuscript. Arctic Station, University of Copenhagen, Qeqertarsuaq, is thanked for the logistical support out in the field. Nukissiorfiit, Greenland, is thanked for granting a research leave for MFC. This study was funded by A.P. Møller og Hustru Chastine Mc-Kinney Møllers Fond til almene Formaal (grant to RMK and OT) and Oticon Fonden (grant # 08-3469 to Arctic Station, OT).

LITERATURE CITED

Aubin, T., Jouventin, P., and Hildebrand, C. (**2000**). Penguins use the two-voice system to recognize each other. Proceedings of the Royal Society of London B. **267**, 1081-1087.

Ballentine, B., Hyman, J. and Nowicki, S. (**2004**). Vocal performance influences female response to male bird song: an experimental test. Behavioral Ecology. **15**, 163-168.

Borror, D.J. and Reese, C.R. (**1956**) Vocal gymnastics in wood thrush songs. The Ohio Journal of Science. **56**, 177-182.

Clark, C.W. (**1990**). Acoustic behavior of mysticete whales. In J. Thomas and R. Kastelein (Eds.), Sensory Abilities of Cetaceans (pp. 571-583). New York: Plenum Press. 710 pp.

Cranford, T.W., Amundin, M. and Norris, K.S. (**1996**). Functional morphology and homology in the Odontocete nasal complex: Implication for sound generation. Journal of Morphology. **282**, 223-285.

Cranford, T.W. (**2000**). In search of impulse sound sources in odontocetes. In A. Whitlow, A. Popper and R. Fay (Eds.), Hearing by Whales and Dolphins (pp. 156-224). New York: Springer Handbook for Auditory Research. 485 pp.

Delarue, J., Laurinolli, M., and Mate, B. (**2009**). Bowhead whale (*Balaena mysticetus*) songs in the Chukchi Sea between October 2007 and May 2008. Journal of the Acoustical Society of America **126**, 3319-3328.

Fee, M. S., Shraiman, B., Pesaran, B., and Mitra, P.P. (**1998**). The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. Nature. **395**, 67-71.

Gedamke, J., Costa, D.P. and Dustan, A. (**2001**). Localization and visual verification of a complex minke whale vocalization. Journal of the Acoustical Society of America. **109**, 3038-3047.

Greenewalt, C.H. (**1968**). Bird Song: Acoustics and physiology. Washington D.C, Smithsonian Institution Press. 194 pp.

Hall, M. (**2009**). A review of vocal duetting in birds. Advances in the Study of Behavior. **40**, 67-121.

Janik, V.M., and Slater, P.J.B. (**1997**). Vocal Learning in Mammals. Advances in the Study of Behavior. **26**, 59-99.

Miller, P. J. O., Samarra, F. I. P., and Perthuison, A. (**2007).** Caller sex and orientation influence spectra of two-voice' stereotyped calls produced by free-ranging killer whales *Orcinus orca*. Journal of the Acoustical Society of America. **121**(6), 3932–3937.

Møhl, B., Wahlberg, M. and Heerfordt, A. (**2001**). A large-aperture array of nonlinked receivers for acoustic positioning of biological sound sources. Journal of the Acoustical Society of America. **109**(1), 434-437.

Nowicki, S., Westneat, M. and Hoese, W. (**1986**). Birdsong: motor function and the evolution of communication. Seminars in Neuroscience. **4**, 385-390.

Payne, R.S. and McVay, S. (**1971**). Songs of Humpback Whales. Science **173**, 585-597.

Reidenberg, J.S., and Laitman, J.T. (**2007**). Discovery of a low frequency sound source in Mysticeti (baleen whales): Anatomical establishment of a vocal fold homolog. The Anatomical Record. **290**, 745-759.

Searcy, W.A. and Andersson, M. (**1986**). Sexual selection and the evolution of song. Annual Review of Ecology and Systematics. **17**, 507-533.

Stafford, K.M., Moore, S.E., Laidre, K.L.,and Heide-Jørgensen, M.P. (**2008**). Bowhead whale springtime song off West Greenland. Journal of the Acoustical Society of America **124**, 3315-3323.

Suthers, R.A. (**1990**). Contributions to birdsong from the left and right sides of the intact syrinx. Nature. **347**, 473-477.

Tervo, O.M., Parks, S.E. and Miller, L.A. (**2009**). Seasonal changes in the vocal behavior of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland. Journal of the Acoustical Society of America **126**, 1570-1580.

Tervo, O.M., Parks, S.E., Christoffersen, M.F., Miller, L.A. and Kristensen, R.M. (**2011**). Annual changes in the winter song of bowhead whales *Balaena mysticetus* in Disko Bay, Western-Greenland. Marine Mammal Science doi: 10.1111/j.1748-7692.2010.00451.x

Tyack, P.L. and Clark, C.W. (**2000**). Communication and Acoustic Behavior of Dolphins and Whales. In A. Whitlow, A. Popper and R. Fay (Eds.), Hearing by Whales and Dolphins (pp. 156-224). New York: Springer Handbook for Auditory Research. 485 pp.

Tyson, R.B., Nowacek, D.P. and Miller, P.J.O. (**2007**). Nonlinear phenomena in the vocalizations of North Atlantic right whales (*Eubalaena glacialis*) and killer whales (*Orcinus orca*). Journal of the Acoustical Society of America. **122**, 1367-1373.

Vallet, E., Beme, I. and Kreutzer, M. (**1998**). Two-note syllables in canary songs elicit high levels of sexual display. Animal Behaviour. **55**, 291-297.

Wahlberg, M, Møhl, B. and Madsen, P.T. (**2001**). Estimating source position accuracy of a large-aperture hydrophone array for bioacoustics. Journal of the Acoustical Society of America **109**, 397-406.

Würsig, B. and Clark, C. (**1993**). Behavior. In J.J. Burns, J.J. Montague and C.J. Cowles (Eds.) The bowhead whale (pp. 157-200). Special publication Number 2: The society of marine mammalogy. 787 pp.

Zollinger, S.A. (**2007**). Performance constraints and vocal complexity in birdsong: Evidence from a vocal mimic. (Ph.D. dissertation, Indiana University, Bloomington, IN, USA). 135 pp.

Table legends

Table I. Measured parameters for the two simultaneously occurring song notes BS and HI from 2008. Notice the large difference between the maximum frequency of BS and the minimum frequency of HI.

song component		duration (s)	minimum frequency (Hz)	maximum frequency (Hz)
BS	mean	0.2	149.1	241.2
	SD	0.0	43.5	62.1
HI	mean	15.2	819.5	2465.8
	SD	0.4	86.8	145.7

Figure legends

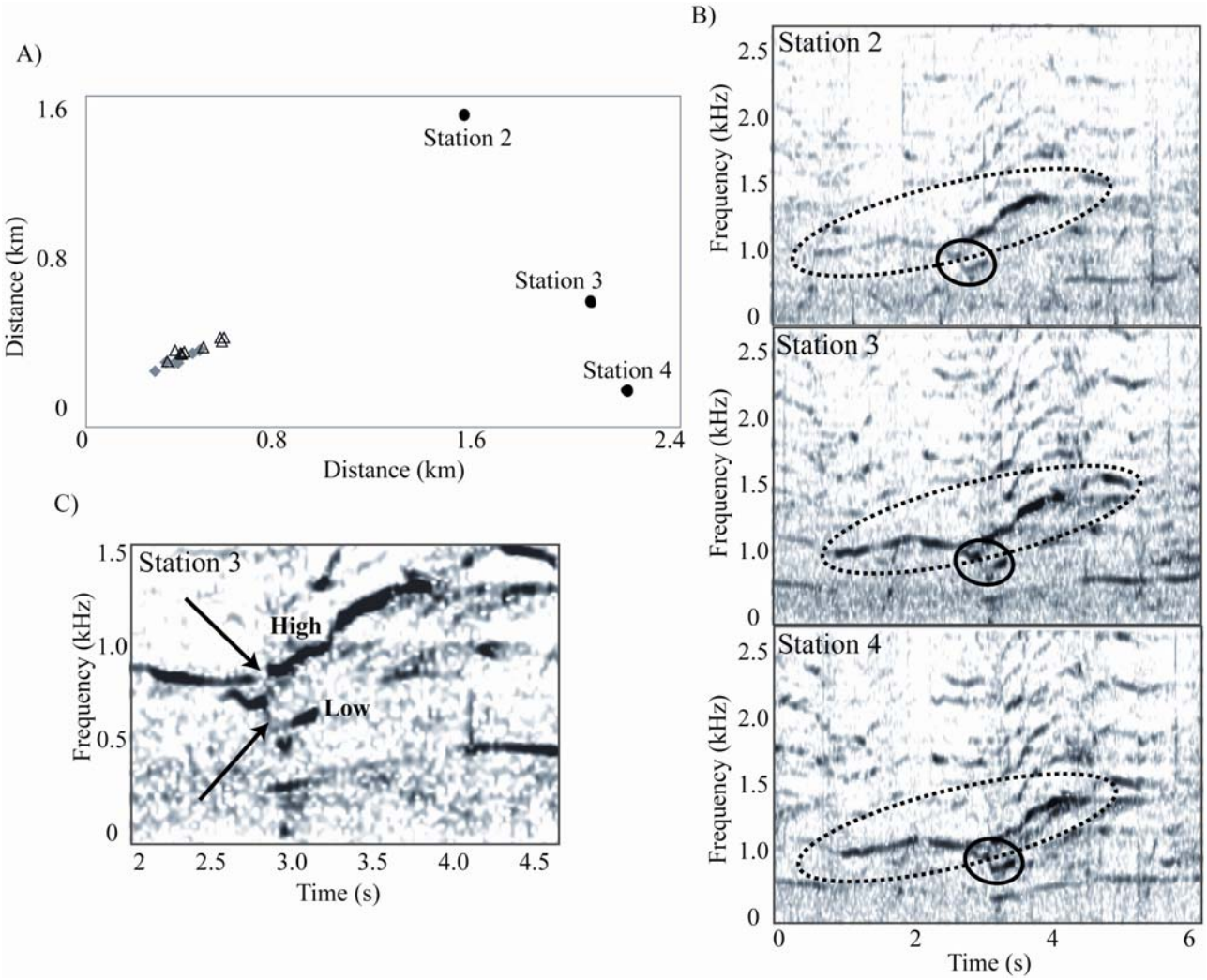

Figure 1. A) 10 repetitions of localization of the two simultaneously occurring song components with a three hydrophone array in 2009. The high song notes are marked with black triangles and the low song notes with grey diamonds. The localizations form an elongated cluster perpendicular to the array. B) Spectrograms of the simultaneous sound production event time aligned from the three recording stations. The high song component is marked with a dotted circle and the low component with a solid circle (Hamming window, FFT size 1024, 50% overlap, sampling rate 44 kHz). C) A zoomed in section of the two song notes, high and low, from Station 3. The black arrows mark the areas of low intensity on the two song notes which coincide with areas of high intensity in the other song note.

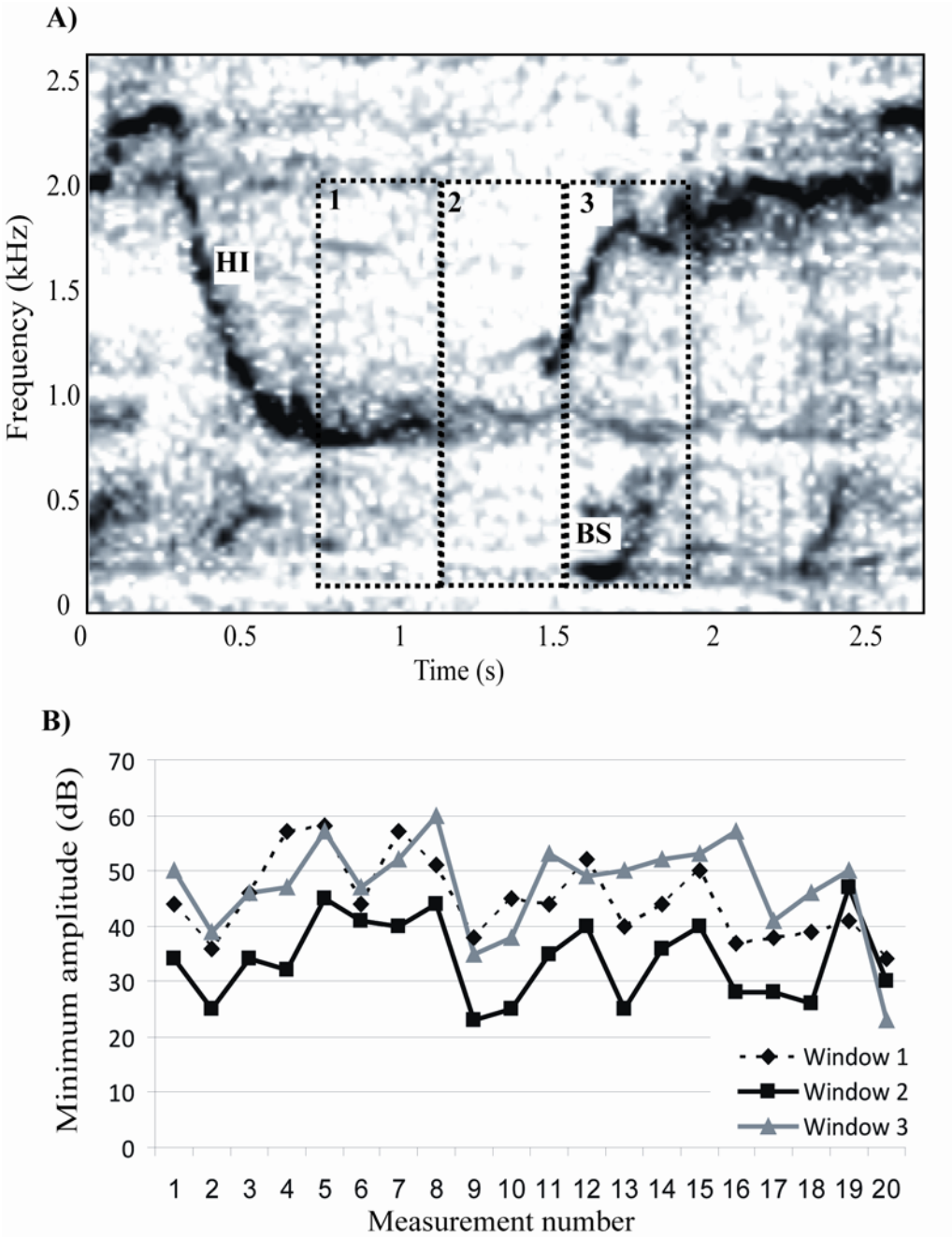

Figure 2. A) Spectrogram with song notes HI and BS (Hamming window, FFT size 1024, 50% overlap, sampling rate 44 kHz). The dotted squares illustrate the positioning of the three measurement windows 1, 2 and 3. Each window was 300 ms long. This particular spectrogram is from measurement number 3 (Fig. 2B). Notice the decline in amplitude of song note HI in window 2. B) Line chart of the minimum amplitude (dB) within the three windows 1, 2 and 3 for the different measurements from 2008 (n=19) and 2009 (n=1). On 96 % of the measurements from

2008 (18/19) the lowest amplitude of HI was found in the centre window number 2 illustrated with the solid black line. Notice the differing curve for the last measurement number 20 from 2009, which is presented in Figure 1 in detail.

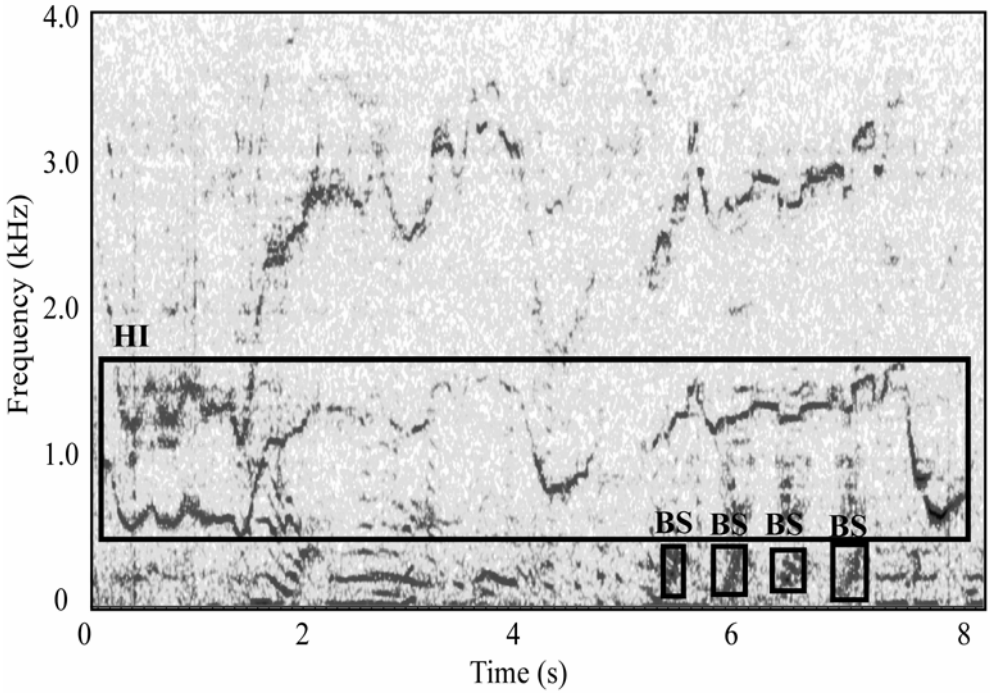

Figure 3. Spectrogram showing a song with the two song components HI and BS marked with solid squares recorded in 2008. Notice the very different frequency contours of HI and BS, where the first is fluctuating with multiple inflection points and the latter is a frequency upsweep. There is a frequency modulated call of another bowhead whale in the background.

Paper V

Tervo, O.M., Christoffersen, M.F., Frasier, T.R., Ilmoni, C.E., Parks, S.E., Miller, L.A. and Kristensen, R.M. Female bowhead whales sing songs. *Science* (in review).

Female bowhead whales sing songs

Outi M. Tervo[1], Mads F. Christoffersen[1], Timothy R. Frasier[2], Camilla E. Ilmoni[1], Susan E. Parks[3], Lee A. Miller[4] and Reinhardt M. Kristensen[1,5]

[1] *Arctic Station, University of Copenhagen, 3953 Qeqertarsuaq, Greenland*

[2]*Department of Biology, Saint Mary's University, Halifax, NS B3H 3C3, Canada*

[3] *Applied Research Laboratory, Pennsylvania State University, P.O. Box 30, State College, PA 16804-0030, USA*

[4]*Institute of Biology, University of Southern Denmark, 5230 Odense M, Denmark*

[5]*Natural History Museum, University of Copenhagen, 2100 Copenhagen OE, Denmark*

To whom correspondence should be addressed. E-mail: ote@science.ku.dk

Song is one of the most conspicuous acoustic displays in the animal world and is comprised of a series of stereotyped notes repeated in a pattern (*1*; *2*). Singing is found across animal taxa, from small invertebrates to the largest whales. Song is associated with breeding behavior since singing primarily occurs during the breeding season and in most species the singers are males (*3*).

The bowhead whale is an Arctic baleen species with an extensive acoustic repertoire (*4*). The singing activity of bowhead whales in Disko Bay, Western Greenland, is highest during winter (*5*) when bowhead whales are presumed to mate (*6*). Although this habitat is primarily utilized by females, it has previously been assumed that only males do the singing (e.g. *7*).

We determined the sex of singing bowhead whales in Disko Bay by localizing singers with a stereo-hydrophone system (Fig. 1A) and by collecting biopsy samples from these individuals for sex determination (Fig. 1B) (8). In this study, all of the sampled singers (N=3) were female (Fig. 1C). From our total of 22 biopsies in March 2010 the sex ratio was skewed towards females (95% females (n=21): 5% males (n=1)). These data unequivocally show that females sing, however a

more extensive sampling is necessary to assess whether male bowheads also sing. Previous bowhead whale song studies have assumed that all singers are male, thus our results indicate that a reassessment of earlier results is needed.

Female singing is most common in song birds (*9*) and rare in mammals (*10*). The suggested functions of female song include territorial defense, mate guarding, coordination of breeding activities (*10*), and more seldom mate attraction and advertising (*11*). Complete courtship role reversal is only expected to occur when parental investment by males exceeds that of females, limiting the number of males available for mating (*12*). This has been described in some frog, fish, crustacean, and insect species, and more than 30 bird species, but never for mammals where females have the highest parental investment (*13*).

Partial courtship role reversal, where both sexes engage in intra-sexual competition for access to high quality mates, can occur even when females are the limiting sex in reproduction (*13*). In the North Atlantic right whale, *Eubalaena glacialis,* a closely related species to the bowhead whale, the female produces simple calls, not song, during sexual interactions (*14*) that function for mate attraction (*15*). Consequently, we suggest that the elaborate songs of female bowhead whales may function for mate attraction and represent a novel example of partial courtship role reversal in mammals.

References and notes

1. R. S. Payne, S. McVay. *Science* **173**: 585-597 (1971).

2 .C.K. Catchpole, P.J.B. Slater. *Bird song: Biological themes and variations* (Cambridge University Press, Cambridge 1995).

3. W.A. Searcy, M. Andersson. *Ann. Rev. Ecol. Syst*. **17**: 507-33533 (1986).

4. D.K. Ljungblad, P.O. Thompson, S.E. Moore. *J. Acoust. Soc. Am.* **71**: 477-482 (1982).

5. O.M. Tervo, S.E. Parks, L.A. Miller. *J. Acoust. Soc. Am.* **126**: 1570-1580 (2009).

6. M.D. Nerini, H.W.Barham, W.M. Marquette, D.J. Rugh. *J. Zool.* **204**: 443-468 (1984).

7. M.P. Heide-Jørgensen *et al*. *Endang. Species Res.* **13**: 73-78 (2010).

8. Materials and methods are available as supplemental material on *Science* Online.

9. N.E. Langmore. *Trends Ecol. Evol.* **13**: 136-140 (1998).

10. V. Janik, P.J.B. Slater. Vocal Learning in Mammals. *Adv. Stud. Behav*. **26**: 59-99 (1997).

11. N.E. Langmore, N.B. Davies, B.J. Hatchwell, I.R. Hartley. *Proc. R. Soc. B* **263**:141-146 (1996).

12. S.T. Emlen, L.W. Oring. *Science* **19**: 215-223 (1977).

13. D.T. Gwynne. *Trends Ecol. Evol.* **6**: 118-121 (1991).

14. S.D. Kraus, J.J. Hatch. *J. Cetacean Res. Manage.* **2**: 237-244 (2001).

15. S.E. Parks. *Mar. Mamm. Sci.* 19(3): 563-580 (2003)

16. We wish to acknowledge A. Dahl, Arctic Station, Nukissiorfiit of Greenland, Ministry of Fisheries, Hunting and Agriculture, Greenland and A.P. Møller og Hustru Chastine Mc-Kinney Møllers Fond til almene Formaal.

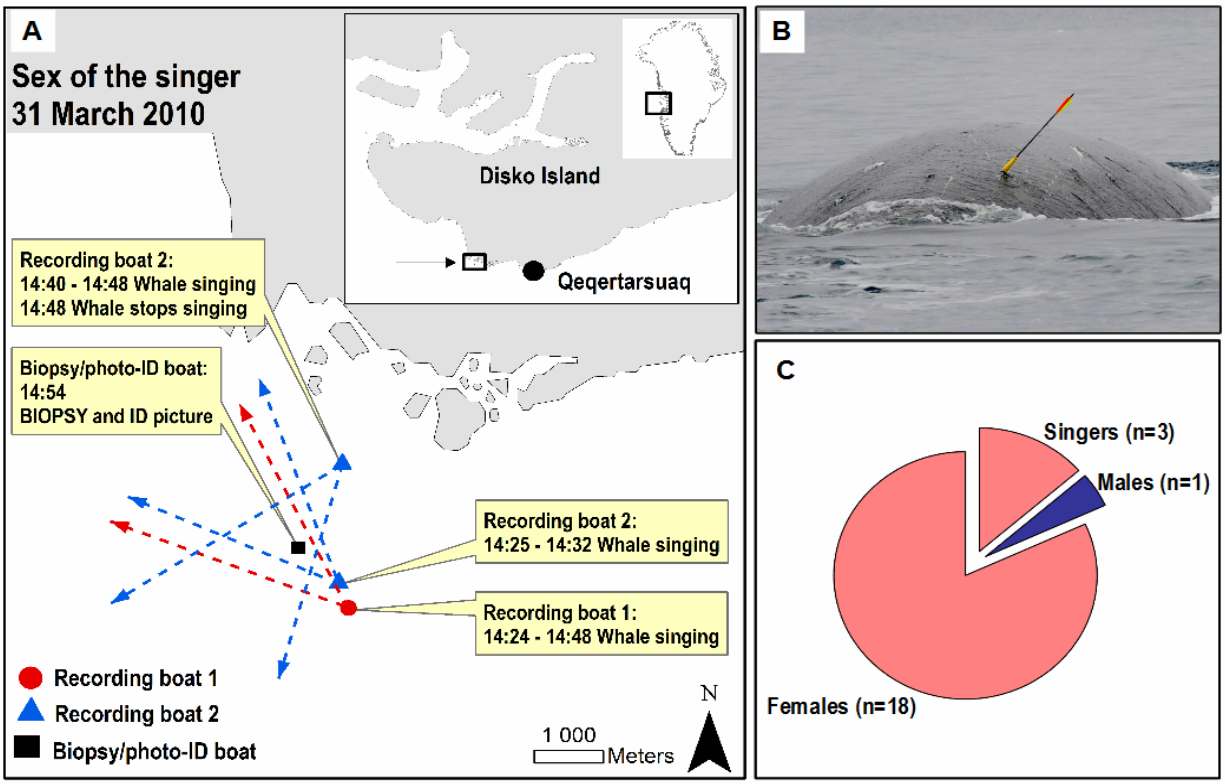

Figure 1. A) An example of an acoustically localized singing whale using two stereo hydrophone setups simultaneously on two recording boats. B) Biopsy dart on a bowhead whale. C) The division of the biopsied whales in March 2010 into females (pink) and males (blue). All the singers (n=3) were females.

Female bowhead whales sing songs – supporting online material

Outi M. Tervo[1], Mads F. Christoffersen[1], Timothy R. Frasier[2], Camilla E. Ilmoni[1], Susan E. Parks[3], Lee A. Miller[4] and Reinhardt M. Kristensen[1,5]

[1] *Arctic Station, University of Copenhagen, 3953 Qeqertarsuaq, Greenland*

[2]*Department of Biology, Saint Mary's University, Halifax, NS B3H 3C3, Canada*

[3] *Applied Research Laboratory, Pennsylvania State University, P.O. Box 30, State College, PA 16804-0030, USA*

[4]*Institute of Biology, University of Southern Denmark, DK-5230 Odense M, Denmark*

[5]*Natural History Museum, University of Copenhagen, 2100 Copenhagen OE, Denmark*

Material and methods

A. Localisation of the singing individual

A stereo hydrophone listening post (70 cm hydrophone spacing) was used to estimate a bearing to a singing whale (*1*). The bearing accuracy was tested using two sound sources (an iron pipe 1 m long placed through holes in the sea ice and hit with a hammer) placed 100 m from a listener and using a double blind procedure. The 70 % correct level occurred at 10° for two listeners (Fig. S1). The stringent criteria used to confidently locate a singing whale included a bearing to one singing whale, increasing song level when approaching the individual, singing stopped when the target whale surfaced (*2*) and no other whales were visually detected within 1000 m over a 30 min period.

B. Biopsy collection

Biopsy arrows launched from a crossbow at 10-30 m range were used to collect small skin samples from three localized singing whales. All encounters followed a fixed scheme: when within 500 m of the whale, the whale was approached in a 5 m boat with constant slow speed and bearing. Samples

were stored in a 20% DMSO solution (*4*). The biopsies were collected under a permit from the Ministry of Fisheries, Hunting and Agriculture, Greenland.

C. Genetic Analysis

For each skin sample, approximately 40 mg of tissue was prepared for extraction using previously described protocols for extracting DNA from whale skin (*5*). DNA was extracted from each sample using phenol:chloroform protocols (e.g. *6*). DNA concentration was estimated based on spectrophotometry using a NanoDrop 2000 (ThermoFisher Scientific), and DNA quality was assessed by running 20 ng of DNA through a 1.5% agarose gel stained with SYBR Green I (Invitrogen).

The sex of each sample was determined using a multiplex reaction combining one pair of primers that amplifies a 224 bp region of the *sry* gene and another pair that amplifies a 445 bp fragment of the *ZFX/ZFY* gene (*7*). This protocol has proven to provide reliable sex determination across a range of mammalian species, including whales (*7; 8*). PCR amplifications included 10 ng of template DNA, 1X PCR buffer [20 mM Tris-HCL (pH 8.4), 50 mM KCl], 0.2 mM of each dNTP, 1.5 mM $MgCl_2$, 0.3 μM of each primer, and 0.05 U/μl of *Taq* DNA polymerase (Invitrogen). Cycling conditions consisted of an initial denaturing step of 94 °C for 5 minutes; 30 cycles of 94°C for 30 seconds, 60°C for 1 minute, and 72°C for 1 minute; followed by a final extension step of 64°C for 45 minutes. PCR products were size-separated and visualized on 1.5% agarose gels stained with ethidium bromide at a concentration of 0.5 μg/ml, with a Low Mass DNA Ladder (Invitrogen) as a size and quantity standard.

References:

1. K.M Dudzinsky, C.W. Clark, B. Würsig. *Aquat. Mamm*. **21**: 187-193 (1995).
2. P. Tyack. *Behav. Ecol. Sociobiol.* **8**: 105-116 (1981).
3. M.P. Heide-Jørgensen *et al*. *Endang. Species Res.* **13**: 73-78 (2010)
4. G. Seutin, B.N. White, P.T. Boag. *Can. J. Zool.* **69**: 82-90 (1991).
5. J.Y. Wang, T.R. Frasier, S.C. Yang, B.N. White. *Heredity* **101**: 145-155 (2008).
6. J. Sambrook, D.W. Russell *Molecular Cloning: A Laboratory Manual* (Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, 2001).
7. A. Gilson, M. Syvanen, K. Levine, J. Banks. *Calif. Fish Game* **84**: 159-169 (1998).

8. R.M. Gillett, T.R. Frasier, R.M. Rolland, B.N. White. *Mar. Mamm. Sci.* **26**: 917-936 (2010).

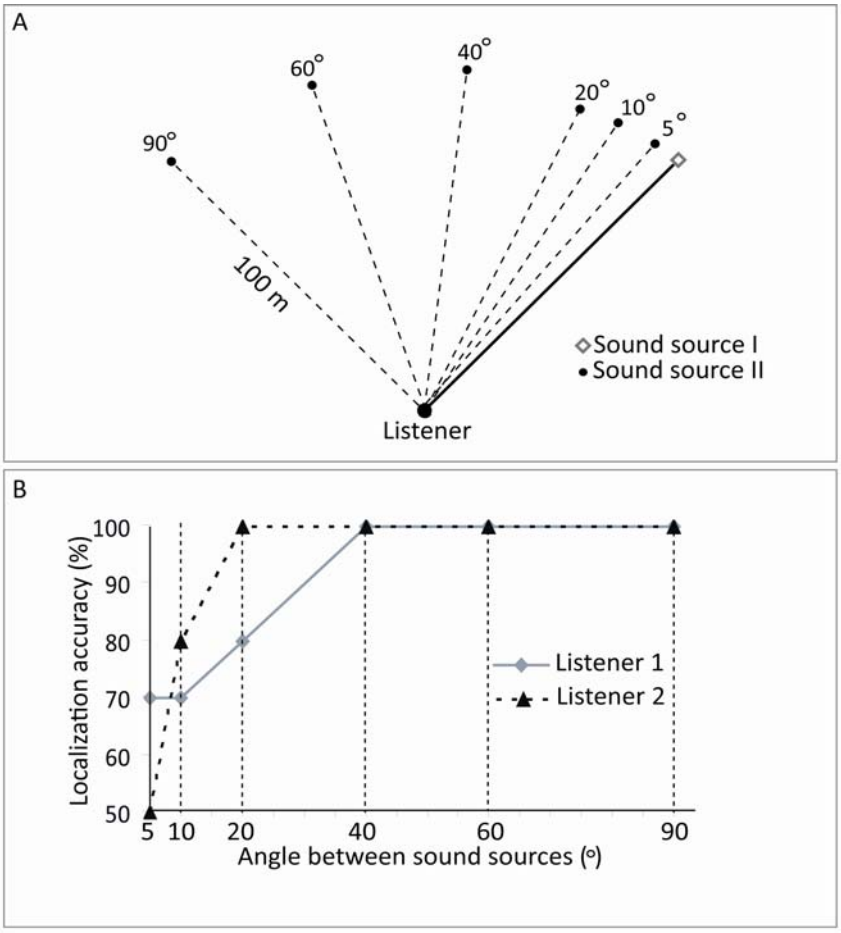

Figure S1. A) Calibration tests of the stereo hydrophone setup where the angle between the two sound sources ranged from 90° to 5°. B) Average localization accuracy of two listeners (n=10 per listener per angle).

Appendix

Tervo, O.M., Christoffersen, M.F., Ilmoni, C.I. and Kristensen R.M.Rare sighting of a bowhead whale calf (*Balaena mysticetus*) in Disko Bay, Western Greenland. (manuscript in prep.)

Rare sighting of a bowhead whale calf (*Balaena mysticetus*) in Disko Bay, Western Greenland

OUTI M. TERVO

ote@science.ku.dk

MADS FAGE CHRISTOFFERSEN

CAMILLA E. ILMONI

Arctic Station, University of Copenhagen, P.O. Box 504, 3953 Qeqertarsuaq, Greenland

REINHARDT MØBJERG KRISTENSEN

Zoological Museum, Natural History Museum of Denmark, University of Copenhagen,

Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

On April 5 2010 a bowhead whale calf *Balaena mysticetus* was observed in Disko Bay, Western Greenland (69° 15’ 12,05 N; 54° 41’ 34,98 W) (Figure 1). This is only the fourth documentation of a bowhead whale calf from Disko Bay spread out over one and half centuries (Eschricht and Reinhardt 1861, Knudsen 1983). This single observation of a calf presented in this paper is a result of intensive field work extending from late January to early June, covering the time period when bowhead whales frequent the area (Eschricht and Reinhardt 1861), over five consecutive years from 2005 to 2010.

The calf from April 5 2010 was photographed from a small vessel with an outboard engine at a distance of approximately 200 m (Figure 2 A). The resting calf was first mistaken for a hooded seal *Cystophora cristata* due to its general petite appearance. The calf was dark grayish in color, had no scars on the back nor on the tail fluke and the shape of the head (the area in front of the blow hole = upper jaw) was slender and appeared more elongated than that of an adult. These

observations are consistent with the calf identification keys used by Koski et al. 1993. The calf was resting at the surface near the shore in front of a plate of ice (Figure 2 A). The ice plate was also photographed from the same angle together with a reference of known size (a green glove) and was used in estimating the size of the bowhead whale calf (Figure 2 B). The exact distance between the whale and the ice plate is unknown but due to the fact that the whale was in front of the ice plate that we used for size reference, this will increase the chance that we underestimate the length of the whale. Given the estimate that 50% of the total body length of a resting bowhead whale is visible above the surface (W. Koski pers. comm.) the calf was approximately 7 m long. The length of a bowhead whale neonate is estimated to be 4-4.5 m and a one-year old yearling will reach a length of an average 8.2 m (Nerini et al. 1984). If we assume a linear growth rate for bowhead whale calves as for Northern right whale calves *Eubalaena glacialis*, (Moore et al. 2005) a closely related species, the calf we observed was approximately 8-9 months old.

There were three other adult bowhead whales within 500 m of the calf. Bowhead whale calf is weaned at approximately 1 year of age (Nerini et al. 1984) and we assume that one of the three adults was the mother of the offspring. We stayed with the calf for about 20 minutes before it dived into the drift ice where we did not want to pursue it.

Although bowhead whale calves have only been documented four times in the past 150 years in Disko Bay (Eschricht and Reinhardt 1861, Knudsen 1983, this study), small juvenile bowhead whales (*arfivik mikisoq*, grl.) are reported infrequently by local hunters from the town of Qeqertarsuaq. Eschricht and Reinhardt (1861) also report pregnant females being harvested in Disko Bay - on April 29 1801 a pregnant bowhead whale female was caught carrying a 4.55m long fetus. More recently, three of the five bowhead whale females landed in Disko Bay in May 2009 and 2010 were pregnant (APNM - Ministry of Fisheries, Hunting and Agriculture, Greenland). The size of the fetus found inside one of the pregnant females in Disko Bay in May 12 2009 was 4 m (M. Christoffersen, pers. obs.). The large sizes of the two fetuses from 1801 and 2009 indicate that

they were mature and due to be born within weeks, suggesting that occasionally calves may be born in Disko Bay in May before the whales depart towards Lancaster Sound across Davis Strait (Heide-Jørgensen et al. 2003). The timing of calving is consistent with the data from the Bering-Chukchi-Beaufort Sea bowhead whale population where the principal calving period is estimated to range from the beginning of April to the beginning of June (Koski et al. 1993). The calf we observed was estimated to be 8-9 months of age resulting that it was born in July - August 2009. Even if this is later than expected, bowhead whale neonates have been observed as early as March (Eschricht and Reinhardt 1861) and as late as August (Davis et al. 1983).

Disko Bay has traditionally been considered an aggregation area for adult bowhead whales (Eschricht and Reinhardt 1861, Heide-Jørgensen et al. 2003). This study indicates that although observed infrequently, calves are present in Disko Bay. In addition, pregnant females may contribute a large percentage of the adult population of bowhead whales in Disko Bay since 60% (3/5) of the bowhead whale females harvested in 2009 and 2010 were pregnant.

ACKNOWLEDGEMENTS

We wish to thank A. Dahl for his help in the field. Arctic Station, University of Copenhagen, Qeqertarsuaq, is thanked for providing working facilities. W. Koski is thanked for his help in the size determination and S. Parks for her comments to this manuscript. Nukissiorfiit, Greenland, is thanked for granting a research leave for MFC. This study was funded by A .P. Møller og Hustru Chastine Mc-Kinney Møllers Fond til almene Formaal (grant to RMK and OMT, Arctic Station).

LITERATURE CITED

Eschricht, D.F., and J. Reinhardt. 1861. Om Nordhvalen (Balæna Mysticetus L.) navnlig med Hensyn til dens Udbredning i Fortiden og Nutiden og til dens ydre og indre Særkjender. (The Northern Whale (Balaenoptera mysticetus L.) with especial reference to its geographical distribution in times past and present, and to its external and internal characteristics). Bianco Lunos Bogtrykkeri, Copenhagen, DK.

Davis, R.A., W.R. Koski and G.W. Miller. 1983. Preliminary assessment of the length-frequency distribution and gross annual reproductive rate of the western arctic bowhead whale as determined with low-level aerial photography, with comments on life history. Report from LGL Ltd., Toronto and Anchorage, to U.S. National Marine Mammal Laboratory.

Heide-Jørgensen, M.P., K.L. Laidre, Ø. Wiig, M.V. Jensen, L. Dueck, H.C. Schmidt and R.C. Hobbs. 2003. First successful satellite tracking of bowhead whales, *Balaena mysticetus*, in Baffin Bay: From Greenland to Canada in ten days. Arctic 56: 21-31.

Knudsen, E. 1983. Grønlandshvalen vrikkede med motorbåden. Pages 54-64 *in* Nørregaard, K. and J. Würtz, J. eds. Grønlandserindringer. Det grønlandske selskabs skrifter XXVI.

Koski, W.R., and R.A. Davis. 1979. Distribution of marine mammals in northwest Baffin Bay and adjacent waters, May October 1978. Report by LGL Ltd. for Petro Canada Exploration Inc., Calgary.

Koski, W.R., R.A. Davis, G.W. Miller and D.E. Withrow. 1993. Reproduction. Pages 239-274 *in* J.J. Burns, J.J. Montague and C.J. Cowles eds. The bowhead whale. Special publication Number 2: The society of Marine Mammalogy.

Moore, M.J., A.R. Knowlton, S.D. Kraus, McLellan, W.A. and R.K. Bonde. Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970-2002). Journal of Cetacean Research and Management 6(3): 199-214.

Nerini, M.D., H.W.Barham, W.M. Marquette and D.J. Rugh. 1984. Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). Journal of Zoology 204:443-468.

Reese, S.C., J.A. Calvin, J.C. George and R.J. Tarpley. 2001. Estimation of fetal growth and gestation in bowhead whales. Journal of the American Statistical Association 96: 915-938.

Figure legends

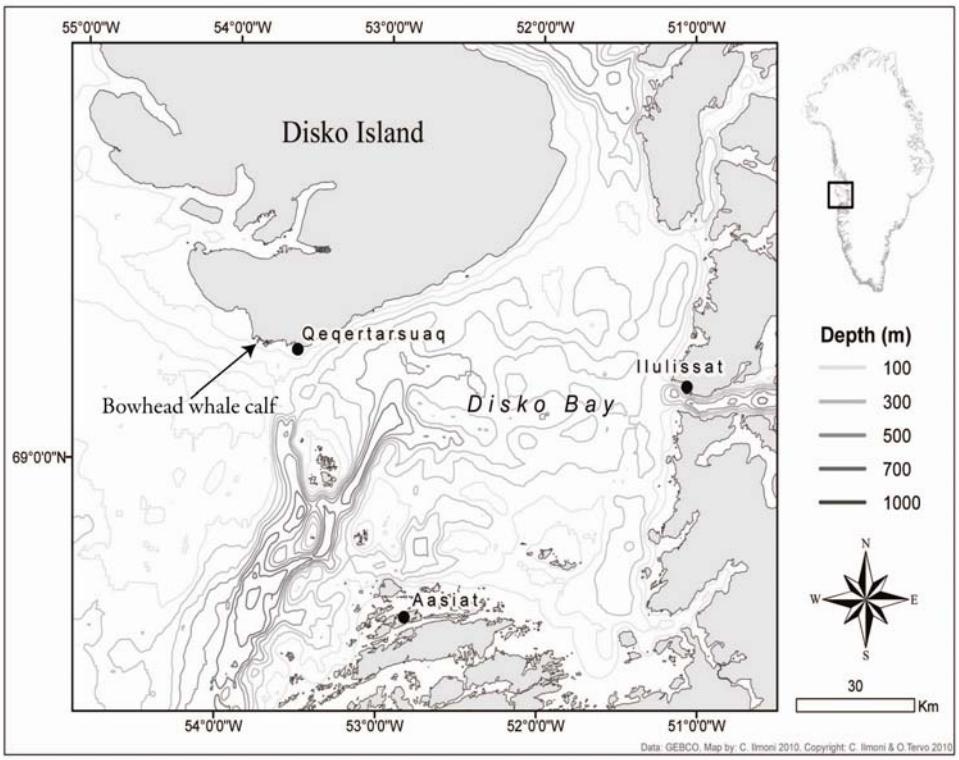

Figure 1. Map of Disko Bay with an arrow pointing to the location (69°15’12,05 N; 54°41’34,98 W) where the bowhead whale calf was observed on April 5 2010.

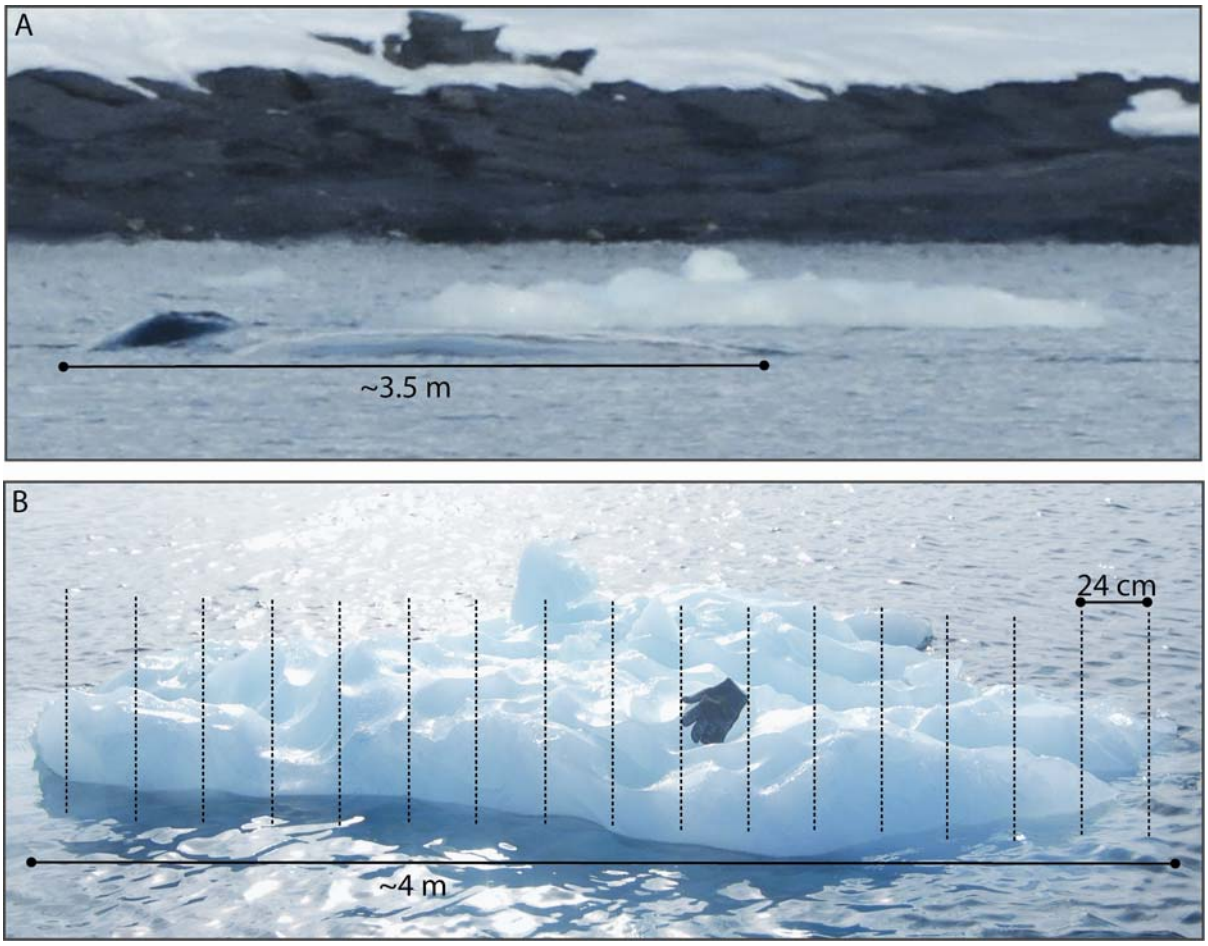

Figure 2. A) Bowhead whale calf resting at the surface in front of an ice plate. The length of the area of the whale above the surface was estimated to be 3.5 m. B) The same ice plate photographed for size reference. The distance between the dotted lines was estimated to be 24 cm resulting in an approximate length of 4 m for the entire plate of ice. (Photos by C. Ilmoni).