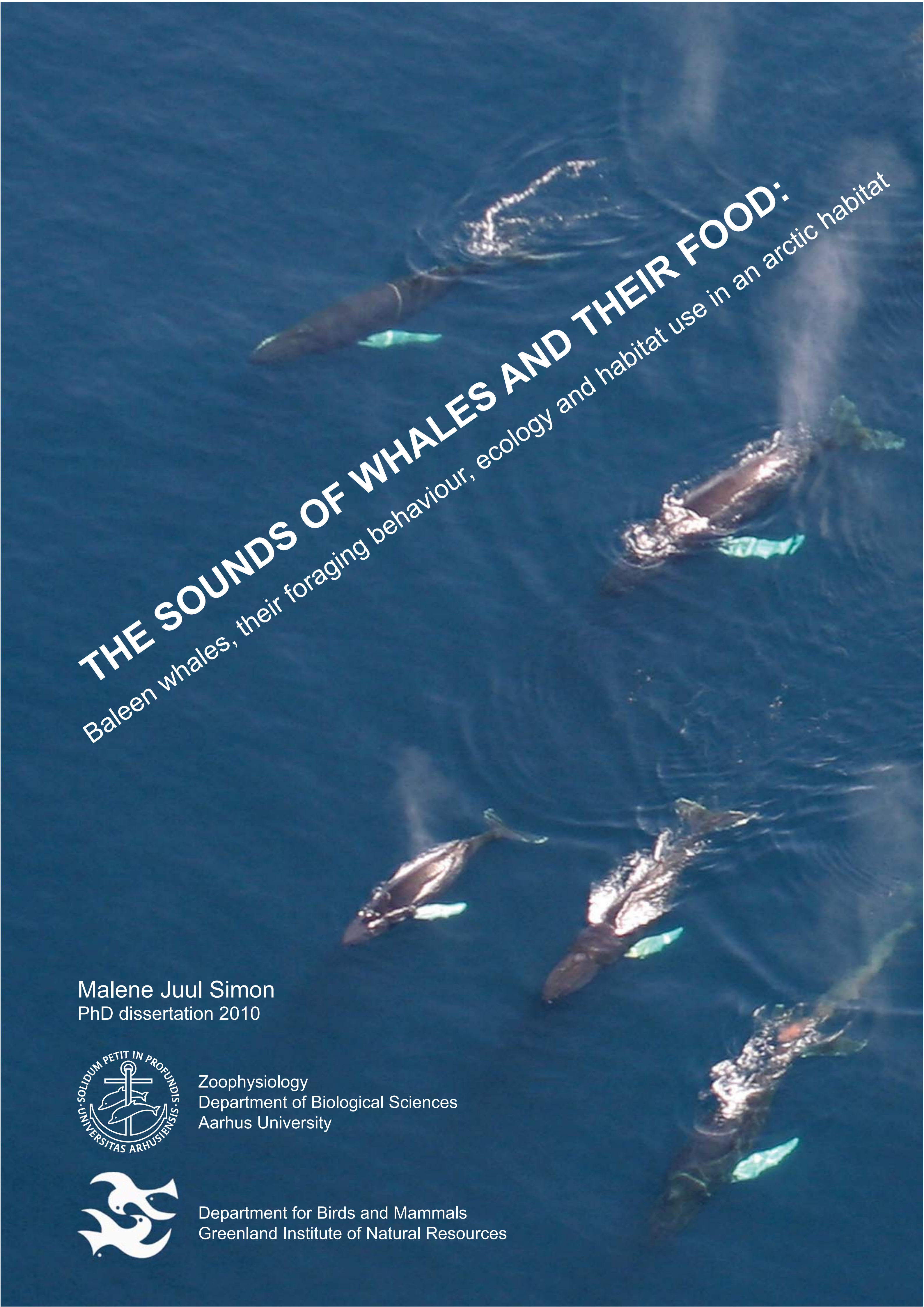


THE SOUNDS OF WHALES AND THEIR FOOD:

Baleen whales, their foraging behaviour, ecology and habitat use in an arctic habitat

Malene Juul Simon
PhD dissertation 2010

Zoophysiology
Department of Biological Sciences
Aarhus University

Department for Birds and Mammals
Greenland Institute of Natural Resources

THE SOUNDS OF WHALES AND THEIR FOOD:

Baleen whales, their foraging behaviour, ecology and habitat use in an arctic habitat

Malene Juul Simon

PhD dissertation, 2010

AGSOS

AARHUS GRADUATE SCHOOL OF SCIENCE

AARHUS UNIVERSITET

GREENLAND INSTITUTE OF
NATURAL RESOURCES

Data sheet

Title:	The sounds of whales and their food: Baleen whales, their foraging behaviour, ecology and habitat use in an arctic habitat
Subtitle:	PhD Thesis
Author:	Malene Juul Simon
Affilitations:	Zoophysiology, Department of Biological Sciences, Aarhus University. Greenland Institute of Natural Resources, Nuuk, Greenland.
URL:	http://www.marinebioacoustics.com http://www.natur.gl
Supervisor:	Professor Peter T. Madsen, Department of Biological Sciences, Aarhus University, Denmark
Cite as:	Simon, M. 2010. The sounds of whales and their food: Baleen whales, their foraging behaviour, ecology and habitat use in an arctic habitat. PhD Thesis.Department of Biological Sciences, Aarhus Univeristy, Denmark. Pp. 176.
Key words:	Baleen whales, Bioacoustics, Passive acoustic monitoring, Feeding ecology, Biomechanics, Distribution, Migration, Habitat use, DTAG, Photo-id, Prey-predator interactions, Greenland, Arctic.
Layout:	Malene Juul Simon
Frontpage and chapter title photos:	Lars Witting
Printed by:	Vester Kopi, Aarhus
Number of pages:	191
Circulation:	70
Internet version:	Available in electronic format (pdf) at the GINR website: www.natur.gl

Content

Preface **5**

Acknowledgements **7**

Summary **8**

Dansk resumé (summary in Danish) **10**

Eqikkaaneq (summary in Greenlandic) **12**

Extended summaries of chapter 2-8 **15**

Chapter 1. Introduction **21**

1.1 Background and objectives 23

1.2 Dive and feeding behavior of baleen whales 28

1.3 Prey localization 38

1.4 Spatial distribution and ecological studies of baleen whales and their prey 44

1.5 Tracking the seasonality of baleen whale song in the Davis Strait with PAM 47

1.6 Future research 55

1.7 Cited litterature 58

Chaper 2. Filter feeding bowhead whales **65**

Paper I: Simon M, Johnson M, Tyack P & Madsen PT 2009. Behaviour and kinematics of continuous ram filtration in Bowhead whales (*Balaena mysticetus*). *Proc R Soc B* 276: 3819-3828

Chapter 3. Kinematics of humpback whale lunges **79**

Paper II: Simon M, Johnson M & Madsen PT. Keeping momentum with a large mouthful of water: Behavior and kinematics of humpback whale lunge feeding. *Manuscript prepared for submission to J Exp Biol*

Chapter 4. Humpback whale habitat use **117**

Paper III: Boye TK, Simon MJ and Madsen PT 2010. Habitat use of humpback whales in Godthaabsfjord, West Greenland, with implications for commercial exploitation. *J Mar Biol Assoc UK.* 90(8): 1529-1538

Chapter 5. Large whale ship based survey **131**

Paper IV: Heide-Jørgensen MP, Simon MJ and Laidre KL 2007. Estimates of large whale abundance in Greenland waters from a ship-based survey in 2005. *J Cetacean Res Manage* 9(2):95–104

Chapter 6. Large whale aerial survey **145**

Paper V: Heide-Jørgensen MP, Borchers DL, Witting L, Laidre KL, Simon MJ, Rosing-Asvid A and Pike DG 2008. Estimates of large whale abundance in West Greenland waters from an aerial survey in 2005. *J Cetacean Res Manage* 10(2):119–129.

Chapter 7. Spatial distribution of large whales and their prey **159**

Paper VI: Laidre KL, Heide-Jørgensen MP, Heagerty P, Cossio A, Bergström B & Simon M 2010. Spatial associations between large baleen whales and their prey in West Greenland. *Mar Ecol Prog Ser* 402:269-284

Chapter 8. Acoustic monitoring of fin whales in Davis Strait **179**

Paper VII: Simon M, Stafford KM, Beedholm K, Lee CM & Madsen PT. 2010. Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging. *J Acoust Soc Am* 128(5): 3200-3210

Preface

This dissertation represents the partial fulfillment of the requirements for the degree of Doctor of Philosophy (PhD) at the Faculty of Science, Aarhus University. It is written in accordance with regulations outlined by the Faculty of Science in May 2002. My thesis work has focused on the acoustics, ecology, behaviour and distribution of baleen whales in West Greenland, and was carried out at the Department of Biological Sciences, University of Aarhus under the supervision of Dr. Peter T. Madsen. During my PhD I have been based at the Greenland Institute of Natural Resources.

When I started this PhD, my objectives were to: I. Elucidate the means by which baleen whales use sound to locate and capture prey. II. Understand the details of how baleen whales engulf and filter prey-laden water, III. Assess possible negative effects of man-made noise on foraging and communication in baleen whales and IV. Acoustically monitor baleen whales in Davis Strait with implications for habitat use and behaviour.

Field work in the Arctic is challenging, and during the first field trials it became clear that it was difficult to locate and record sounds from baleen whale prey aggregations, and that the whales were seemingly quiet while foraging. Therefore, I focused most of my research time on the kinematics of baleen whale feeding behavior after the first field season showing that we could deploy and retrieve the needed technology reliably. To do this I used multi-sensor acoustic tags (DTAGs) to quantify the acoustic behavior, the underwater feeding behavior and biomechanics of humpback and bowhead whales (Chapter 2 and 3).

Fig. 1. Map of the study area.

To pursue the question of possible effects of anthropogenic noise, I recorded ambient noise in different habitats and seasons in West Greenland and found that there was a very large variation in the ambient noise levels and frequency structure between arctic habitats and seasons (Chapter 1, section 1.5). The levels and dynamics of these noise profiles emphasized that it requires a dedicated, long term effort to address large scale questions about the consequences of natural and anthropogenic noise levels in arctic waters with respect to baleen whales and their prey. I therefore turned to the simpler question of whether the increasing whale watching in the Nuuk fjord system caused disturbance to humpbacks (Chapter 4). To address objective IV, to monitor baleen whales in Davis Strait, I used several techniques: air and ship based visual surveys (Chapters 5 and 6), combined with a hydro-acoustic survey to investigate the large-scale distribution of baleen whales in relation to their prey in West Greenland (Chapter 7). Furthermore, together with colleagues, I used passive acoustic monitoring (PAM) and data from satellite images to investigate the seasonality and behavioral ecology of offshore fin whales in the Davis Strait in relation to sea ice (Chapter 8). Fieldwork was carried out from Cape Farewell (60˚N) to Upernavik (72˚ 5'N) in West Greenland and to 68˚N in East Greenland (Fig. 1). The sighting and hydroacoustic surveys combined covered these stretches of the coastline and offshore up to 100km or to the 200m depth contour. Humpback whales were recorded (2006-2007) and D-tagged (2007-2008) in Nuuk Fjord. Bowhead whales were D-tagged in Disko Bay in 2008. Ambient noise recordings were made in Disko Bay and Nuuk Fjord between 2006 and 2009. Photo id and theodolite surveys were carried out in Nuuk Fjord in 2006-2009. Finally, moorings with passive acoustic recorders were deployed and retrieved in the Davis Strait between Greenland and Canada in 2006 – 2008 (Fig. 1).

During my PhD, I was external supervisor for three MSc students: Tenna Boye (Aarhus University), studying humpback whales in Nuuk Fjord (Chapter 4); Ida Eskesen (University of Southern Denmark), who studied the echolocation of long-finned pilot whales and Norwegian killer whales and Helen Bates (University of Exeter, Cornwall), who studied the habitat use of Icelandic killer whales.

My PhD started in May 2006. The deadline was subsequently postponed 1.5 years due to two maternity leaves, and a 6 months work leave where I was hired by the Greenland Institute of Natural Resources to coordinate the logistics of the Greenland contribution to a large scale Trans-North Atlantic Sighting Survey (T-NASS). The results of this work leave contributed directly to management advice for baleen whales by the North Atlantic Marine Mammal Commission and the International Whaling Commission, as well as four peer reviewed papers on baleen whales in West Greenland that are not included in this PhD[1]

The dissertation consists of an introduction (Chapter 1) structured as a review where I discuss my results by putting them into a broader perspective followed by 7 chapters in the form of published papers and a manuscript prepared for submission to a peer reviewed journal.

Nuuk, November 23th 2010

Malene Juul Simon

---

[1] Heide-Jørgensen MP, Laidre KL, Simon M, Rasmussen M, Burt ML & Borchers DL. Abundance estimates of fin whales in West Greenland in 2007. *J. Cetacean Res. Manage*. *In review*

Heide-Jørgensen MP & Simon MJ 2007. Cue rates for common minke, fin and humpback whales in West Greenland. *J. Cetacean Res. Manage* 9(3): 211-214

Laidre KL, Heagerty PJ, Heide-Jørgensen MP, Witting L & Simon MJ 2009. Sexual segregation of common minke whales (*Balaenoptera acutorostrata*) in Greenland, and the influence of sea temperature on the sex ratio of catches. *ICES J Mar Sci* 66:1-14

Tervo O, Christoffersen MF, Simon M, Miller LA, Parks SE, Jensen F and Madsen PT. Source level and active space of high pitched singing in bowhead whales (*Balaena mysticetus*). *In prep*

Acknowledgements

This dissertation is the result of my PhD study at the Zoophysiology research group, Department of Biological Sciences, Aarhus University, in collaboration with, and based at, the Greenland Institute of Natural Resources (GINR), Nuuk. I am thankful for the great support I have received from both institutions. My scholarship and part of the field work was funded by the Oticon Foundation. KIIIN (Department of Culture, Education, Research and Church, Government of Greenland) provided financial support for field work and training. Logistic support was given by: Greenland Institute of Natural Resources; Woodshole Oceanographic Institution; Applied Physics Lab, Washington University and the Centre of Marine Ecology and Climate Effects (GINR).

I owe tremendous thanks to my supervisor Peter T. Madsen for excellent supervision and support throughout my PhD. Despite the long distance and several time zones separating our offices, I never missed communication or supervision. Peter's incredible flexibility and optimism have made it possible to carry out this project, despite the numerous logistical challenges. I appreciate every bit of it. Thanks for always craving the best and, just as important, for good fun and friendship. I look very much forwards to go back to the field again.

Special thanks to Mark Johnson for letting us use the DTAGs, for analytical support and valuable discussions on baleen whale biomechanics. Thanks to Kristian Beedholm for analytical support, I am an absolute fan of your file names. Also many thanks to Kate Stafford and Craig M Lee for letting me onboard the Davis Strait PAM project. It has been really nice to get to know you and incredibly interesting to be part of the project. I hope you will continue visiting us in Nuuk regularly. Warm thanks also to Kristin Laidre for our interesting ecological discussions and continued support.

Thanks to the warm welcoming at GINR when I arrived in Greenland in 2005. Special thanks to director Klaus Nygaard, for supporting me logistically and financially in getting this PhD project together and former head of department, Lars Witting, for trusting me with the T-NASS surveys and helping me settle at the institute. Thanks to Mads Peter Heide-Jørgensen for inviting me to carry out exciting field work around the greenlandic coast and especially for getting me involved with the PAM project in Davis Strait by bringing me in contact with Kate Stafford and Craig Lee and for helping getting my PhD study started.

I would also like to thank all the people assisting in the field: Tenna K Boye, Fernando Ugarte, Abel Brandt, Ado Isaksen, Bjarke K. Nielsen, Karin Clausen. Observers: Nina Eriksen, Anna-Sofie Stensgaard, Marianne H. Rasmussen, Njáll Sigurdsson and Gudmundur Thordarson. Locals in Nuuk, Tupilak Travel and the crew on IVIK contributed with ID-photos.

I am greatful for the support of my family. We could bring my son Ari to fieldwork in Disko because his grandparents were willing to join as well. Thank for a really nice time.

Deep felt thanks to Fernando Ugarte, my wonderful husband, who has participated from the beginning to the end; in field work, interesting discussions and with an invaluable support and interest in my work. I love you and our Ari and Solomé who made our family complete.

Summary

Here I summarize the most important results of my PhD work. My dissertation consists of 8 chapters: an introduction formed as a review, one manuscript prepared for submission and six papers published in peer reviewed journals contributing to knowledge of the acoustics, eco-physiology and behavioral ecology of baleen whales in West Greenland.

With the limited visibility in water, sound plays an important role in the life of baleen whales. The powerful, species-specific, low-frequency sound signals of baleen whales are most likely used in long range intra-specific communication, navigation and perhaps even localization of prey. As the signals reflect the species identity, relative abundance, distribution and behavior of the vocalizing whales, acoustics is a powerful tool for studying these large pelagic cetaceans. The overall aim of my PhD thesis has been to investigate the acoustics, behavioral ecology and distribution of baleen whales in West Greenland to get a better understanding of the foraging behavior and distributional patterns of baleen whales and their prey. Archival tags (DTAG) were used to study the detailed kinematics of filter feeding bowhead and humpback whales, while acoustics and more traditional survey techniques were used in a large-scale investigation of factors influencing baleen whale distribution, seasonality and abundance in West Greenland.

Baleen whales feed on dynamic patches of schooling prey. The means by which they locate prey aggregations are not understood. Passive listening has been proposed as a possible strategy for prey localization. To test this I made sound recordings near schools of prey species. However, I could not unequivocally attribute any detectable sound signals to the prey aggregation. Thus, at present I cannot say if prey aggregations produce any sound signals useful for passive acoustic detection. I therefore turned to investigate how baleen whales acquire their prey. After locating a prey aggregation, the baleen whale filters the prey-laden water through baleen plates hanging from the roof of its mouth, but the details of that process are not understood. To overcome that lack of data, humpback and bowhead whales were tagged with archival tags (DTAG) collecting detailed measurements of the feeding whale´s movements and sounds. The DTAG data show that both species of whales perform oxygen saving swimming behaviors while feeding: bowhead whales use a very slow and consistent speed of less than 1 ms^{-1} while keeping their mouth open continuously filtering water during the bottom phase of feeding dives, performing so-called continuous ram filtration. While doing this they filter about 6000 tons of water per hour. Humpback whales, on the other hand, use a lunge feeding strategy where they fluke rapidly to accelerate to a speed of around 4 ms^{-1}. Then they open their mouth in a wide gape to rapidly engulf tons of prey-laden water in their largely expandable buccal pouch while still fluking to maintain a speed of about 1 ms^{-1} despite the increased drag caused by the acceleration of the engulfed water. When closing their mouths, humpback whales glide until they begin a new bout of fluking, initiating another lunge. In contrast to bowhead whales, humpback whales filter less than 1000 tons of water per hour. I conclude that bowhead and humpback whales not only are morphologically specialized to different prey and feeding techniques, but that they also employ very different gaits and swim speeds to maximize energy returns during discrete (humpback) and continuous (bowhead) filter feeding.

Photo identification and theodolite surveys were carried out concurrently with the DTAG study to investigate humpback whale habitat use and the possible disturbance of feeding whales by whale

watching boats in Nuuk fjord. Humpback whales show small-scale site fidelity to Nuuk fjord, demonstrating that individual migrating whales have navigational skills that allow them to find a fjord entrance that is less than 10km wide. A relatively small number of humpback whales feed in Nuuk fjord each year. This, together with a high degree of small-scale site fidelity, has importance in relation to whaling, with the inherent risk of whales not being replaced for ecotourism if hunted. A combination of theodolite surveys and DTAG data documents that the current behavior of whale watching vessels disturb humpback whales' natural diving behavior. When followed by whale-watching boats, humpback whales increase their swimming speed, shorten foraging dives and diminish the ratio between surfacings and long dives, which in combination calls for general whale-watching guidelines in West Greenland.

To investigate the abundance and distributional patterns of baleen whales off Greenland, simultaneous ship-based and aerial surveys of large whales were conducted, showing that sei, fin, humpback and minke whales were abundant off West Greenland in August-September 2005. These surveys in combination with a concurrent hydroacoustic survey for two species of prey (krill and capelin) revealed that the highest concentrations of whales could be predicted by the integrated krill abundance at depths greater than 150m. The data support the hypothesis that in their West Greenlandic feeding grounds baleen whales switch between three main prey species: coastal capelin, sandeel on the banks and pelagic krill.

The aerial and boat-based surveys gave a snap-shot of the distributional patterns and habitat use of baleen whales off West Greenland. To broaden the temporal scale I also monitored the occurrence of baleen whales in the Davis Strait using an array of three bottom-moored passive acoustic recorders that recorded continuously, year round. Before this study, little was known about how much of the year, and with what purposes other than feeding, baleen whales use the Davis Strait and West Greenland. Acoustic signals from all six species of baleen whales that feed seasonally in the area were recorded, but only the fin whale song has been analyzed in detail for this dissertation. Fin whales are present in the Davis Strait until late December, much longer than previously thought. The patterns in the acoustic behavior indicate that fin whales feed and mate while still in the Davis Strait, until the area is covered by sea ice. These results change views on fin whale seasonality and habitat use in the Davis Strait. I conclude that there is a large unexplored potential for investigating the distributional and behavioral ecology of baleen whales and possibly other vociferous marine mammals in the Davis Strait and West Greenland with the use of passive acoustic monitoring (PAM).

Resumé (summary in Danish)

Her opsummeres de vigtigste resultater af min PhD afhandling, som består af otte kapitler: en introduktion udformet som et review, et manuskript til snarlig indsendelse til et videnskabeligt tidsskrift, samt seks artikler publiceret i videnskabelige tidsskrifter. Afhandlingen bidrager til vores viden om de vestgrønlandske bardehvalers akustiske adfærd, økofysiologi og økologi.

Eftersom sigtbarheden i vand er begrænset, spiller lyd en vigtig rolle i bardehvalernes liv. De udsender artsspecifikke, lavfrekvente akustiske signaler, som de formentlig bruger til at kommunikere over lange afstande, navigere og måske endda til at finde deres byttedyr. Akustiske analyser af undervandslydoptagelser er effektive til undersøgelser af hvaler, fordi hvalkaldene både kan bruges til artsbestemmelse, estimering af det relative antal af syngende individer og til undersøgelser af deres udbredelse og adfærd. Det overordnede formål med nærværende afhandling er at undersøge akustik, adfærdsøkologi og udbredelse af bardehvalerne i Vestgrønland for at bidrage til en bedre forståelse af hvalernes fourageringsadfærd samt udbredelse af både hvaler og deres byttedyr.

Jeg har brugt digitale målepakker (DTAG) til at studere den detaljerede biomekanik af fødeindtag hos grønlands- og pukkelhvaler, samt akustiske og mere traditionelle overvågningsmetoder til større geografiske undersøgelser af de faktorer, der kan influere på bardehvalernes udbredelse, sæsonvariation og antal i Vestgrønland.

Bardehvaler æder tætstående stimedyr, hvis samlinger er dynamiske i tid og sted. Det er endnu uvist, hvordan hvalerne lokaliserer disse byttedyrsstimer, men brug af passiv akustik er foreslået som en mulighed. For at teste om hvalerne kan lokalisere byttedyr ved at lytte efter akustiske signaler fra stimerne, optog jeg undervandslyd i nærheden af byttedyrsstimer. Jeg kunne dog ikke med sikkerhed påvise nogen akustiske signaler som kommende fra stimerne. Jeg fokuserede herefter på at undersøge, hvordan hvalerne fanger og filtrerer deres bytte.

Efter at have lokaliseret en stime af byttedyr, filtrerer bardehvalen dyrene fra vandet gennem barderne, der hænger i to rækker fra ganen, men detaljerne i denne proces er ukendte. For at bidrage til en bedre forståelse, mærkede mine medforfattere og jeg pukkel- og grønlandshvaler med DTAGs, som optog detaljerede målinger af den fouragerende hvals bevægelser og lyde. Data fra DTAG-mærkningen viste, at begge typer af hvaler udfører en iltbesparende fødesøgningsadfærd: Grønlandshvalen svømmer med en langsom og konsistent hastighed på mindre end 1 ms^{-1} mens den holder munden åben og uafbrudt filtrerer vand gennem barderne. Dette foregår under forageringsdykkenes bundtid og kaldes kontinuerlig ram-filtrering. Ved denne fourageringsadfærd filtrerer en grønlandshval omkring 6000 tons vand og byttedyr i timen. Pukkelhvaler derimod bruger en fourageringsstrategi, hvor de accelererer til omkring 4 ms^{-1}, hvorefter munden åbnes på vid gab og hurtigt, i et såkaldt *lunge*, indtager flere tons byttedyrsrigt vand i en stor elastisk mundpose, dannet fra en omdannet tunge og mundbund gående fra underkæben og til navlen. Den fyldte pukkelhval fortsætter med haleslagene for at opretholde en hastighed på 1 ms^{-1} til trods for den øgede vandmodstand fra de store indtagene vandmængder, der skal accelereres. Når hvalen lukker munden, filtrerer den byttedyrene fra vandet imens den glider fremad, indtil den igen påbegynder et nyt lunge ved at accelerere med store kraftige haleslag. I modsætning til grønlandshvalen filtrerer pukkelhvalen mindre end 1000 tons vand i timen. Min konklusion er, at grønlandshvalen og

pukkelhvalen ikke kun er morfologisk specialiserede til forskellige typer byttedyr og filtreringsteknikker, men også benytter meget forskellige haleslagsrytmer og svømmehastigheder for at maksimere udbyttet under henholdsvis diskret (pukkelhval) og kontinuerlig (grønlandshval) filtrering.

Fotoidentifikation og teodolitopmålinger af pukkelhvaler blev udført samtidig med DTAG-studierne for at undersøge pukkelhvalernes habitatbrug samt om hvalsafaribådene i Nuuk fjord forstyrrer de fouragerende pukkelhvaler. Fotoidentificeringen viste, at de samme hvaler kommer til Nuuk fjord for at fouragere år efter år, hvilket betyder, at de individuelle migrerende hvaler har navigationsfærdigheder, der tillader dem hvert år at finde en fjordmunding på mindre end 10 km bredde langs den grønlandske vestkyst. Relativt få hvaler fouragerer i Nuuk fjord hvert år, og mange af dem er gengangere. Det kan betyde at der er risiko for at individer, der bliver skudt i Nuuk fjord, ikke bliver erstattet, hvilket kan have følger for øko-turismen. En kombination af teodolitopmålinger og DTAG data dokumenterede, at den nuværende adfærd af hvalsafaribåde forstyrrer pukkelhvalernes naturlige dykkeadfærd. Pukkelhvaler med følge af hvalturisme både øger deres svømmehastighed, forkorter fourageringsdyk og formindsker forholdet mellem overfladeophold og lange dyk. Denne kombination af adfærdsændringer bør medføre udarbejdelse af generelle retningslinjer for hvalsafari i Vestgrønland.

For at undersøge antallet af bardehvaler og deres udbredelse blev to samtidige hvaltællinger udført i august-september 2005, fra henholdsvis skib og fly langs den grønlandske vestkyst. Tællingerne viste at sejhval, finhval, pukkelhval og vågehval er talrige i Vestgrønland i sensommeren. Samtidig med hvaltællingerne blev tilstedeværelsen og mængden af kril og lodde undersøgt ved brug af hydroakustik fra skibet. En analyse af de tre datasæt viste, at høje koncentrationer af kril på mere end 150 m dybde er, at den af de undersøgte parametre der bedst forudsiger høje koncentrationer af hvaler udfor Grønlands vestkyst. Data er således konsistente med hypotesen om, at vestgrønlandske bardehvaler (med undtagelse af grønlandshvalen) skifter mellem tre arter af byttedyr: kystnære lodder, tobis på bankerne og pelagisk kril.

Fly- og skibstællingerne gav et øjebliksbillede af udbredelsesmønstre og habitatbrug af bardehvaler ud for Vestgrønland. For at udvide tidshorisonten til at undersøge hvilke perioder hvalerne er der over hele året, moniterede jeg også bardehvaler i Davis Strædet ved brug af bund-fastgjort passive akustiske optagere, som optog kontinuerligt året rundt. Inden dette studie vidste man næsten intet om hvor stor del af året og med hvilke andre formål end fødesøgning, bardehvaler var i Davis Strædet og ved Vestgrønland. Seks forskellige arter af bardehvaler fouragerer i Vestgrønland, og de fastgjorte akustiske instrumenter optog kald fra alle seks arter. I nærværende PhD har jeg koncentreret mig om at udføre en detaljeret analyse af finhvalernes sang. Analysen viste, at der er finhvaler i Davis Strædet indtil slutningen af december. Dette er meget senere på året end hidtil antaget. Variationerne i den akustiske adfærd indikerer, at finhvalerne fouragerer og parrer sig i Davis Strædet, indtil området dækkes af havis. Disse resultater ændrer den generelle opfattelse af finhvalernes sæsonvariation og habitatbrug i Davis Strædet. Jeg konkluderer, at der er store perspektiver i at benytte akustik til at undersøge udbredelse af og adfærdsøkologi for bardehvaler, og formentlig også andre vokaliserende havpattedyr i Davis Strædet og Vestgrønland.

Eqikkaaneq (summary in greenlandic)

PhD-iutigalugu allaaserisanni paasisat pingaarnerpaat matumani eqikkarpakka. Ilisimatusaatigalugu allaaserisara arfineq-pingasunik kapitaleqarpoq; aallaqqaasiut takussutissiatut suliaq, allaaserisaq ataaseq tunniussassatut suliaq aammalu allaaserisat arfinillit atuagassiani ilisimatuunit allanit naliliiffiusartuni saqqummersitat Kalaallit Nunaata kitaani arferit soqqallit nipiliortarneri, uummaffimminni timimikkut qanoq issusii uummaffimminnilu pissusilersuutaat pillugit ilisimasanut amerlisaataasussat.

Immap isiginiarfiusinnaassusia killeqarmat arferit soqqallit inuuneranni nipi pingaaruteqarluarpoq. Nipit qatituut sakkortuut, arferni assigiinngitsuni immikkuullarilluartut, ungasilluni attaveqatigiinnermut, sumiissusersiornermut immaqalu allaat neriniakkanik sumiissusersiiniutitut atorneqartarput. Mattallit itisuumiittartut angisuut taakku misissuiffigineqarnerini nipit arfernit aalajangersimasunit pisarnerat tusaaneqarsinnaasarmat, arferit nilliasartut amerlassusii, siammarsimassusii pissusilersornerilu paasiniarlugit nipit sakkusaapput pitsaviit. PhD-inngorniutigalugu allaaserisanni anguniagaq pingaarneq tassaavoq arferit soqqallit neriniartarneri aammalu taakku namminneq aammalu neriniartagaasa siammarsimassusii paasilluarnerujumallugit Kalaallit Nunaata kitaani arferit soqqallit nipaat, uummaffimminni pissusilersuutaat aammalu siammarsimassusii paasiniassallugit. Arfiviit qipoqqaallu qaloornerminni aalaasii sukumiisumik misissorniarlugit atortorissaarutit nalunaarsuutitallit atorneqarput kiisalu nipit misissueriaatsillu qangatoornerusut atorlugit Kalaallit Nunaata kitaani arferit soqqallit siammarsimassusiinut, ukiut qanoq ilinerani tamaaniittarnerinut amerlassusiinullu tunngasut sunit sunnerneqartarneri annertuumik misissuiffigineqarlutik.

Arferit soqqallit sunik attarmoorlutik ingerlaartunik neriniartartuupput. Neriniakkatik attarmoortut qanoq sumiissusersisarneraat ilisimaneqanngilaq. Nipaqaratik naalarnillutik neriniakkaminnik sumiissusersiiniartarsimasutut ilaannit oqaatiginiarneqartarput. Tamanna paasiumallugu neriniagaat attarmoortut qanittuini nipinik immiussisarpunga. Taamaattorli nipit tusaaneqarsinnaasut neriniagaasa ataatsimoornerinut qularnaatsumik nalunaaqqutaasutut oqaatigisinnaanngilakka. Taamaammat massakkut oqaatigisinnaanngilara neriniagaat nipaqarani naalarninnikkut sumiissusersiiniarnermi atorsinnaasunik ilumut nipiliortarnersut. Neriniakkatik sumiissusereeraangamikkik arferit soqqallit imeq neriniakkaminnik akulik soqqatik qilaaminniittut atorlugit akuiartarpaat, tamatumali qanoq pisarnera paasilluarneqarsimanngilaq. Paasissutissat taakku amigaatigineqartut pissarsiariniarlugit qipoqqaat arfiviillu uuttortaatinik immiussisartunik, tassa arferit neriniartillutik aalaasiinik nipaannillu immiussisartunik ikkussiffigineqarput. Atortorissaarutit taakku takutippaat arferit assigiinngitsut taakku marluk immap iluaniitsillutik silaannarmik atuivallaarnaveersaartartut; Arfiviit issariarnermut 1 meterinit kigaannerullutik kigaatsuararsuusarput immallu naqqani neriniarnerminni qanertik ammatiinnartarlugu. Arfiviit akunnermut imeq 6000 tons qanermikkut ingerlaartittarpaat. Qipoqqaat paarlattuanik tassanngaannaq oqummerseriartarput, tassa tassanngaannaq aatsarujussuartarput imerlu neriniakkaminnik ulikkaartoq oqummersarlugu. Tassanngaannaq oqummerseriartarnerminni qipoqqaat sukkatseriasaartarput issariarnermut 4 meterit missaanni ingerlasarlutik, oqummerseriarnerminilu imeq oqummigartik kinaqutigigaluarlugu issariarnermut 1 meterit missaat ingerlasarlutik. Qipoqqaat ipummeraangamik kajusigallartarput aatsarujussuarlutik

oqummerseriaqqinnissamik tungaannut. Arfivittut innatik qipoqqaat akunnermut imermik 1000 tonsinit minnerusumik qanermikkut ingerlaartitsisarput. Inerniliussara tassaavoq arfivik qipoqqarlu neriniakkanut assigiinngitsunut timimikkut assigiinngitsumik naleqqussarsimaannaratik aammattaaq ingerlaariaatsit sukkassutsillu assigiinngilluinnartut atortaraat tassanngaannaq oqummerseriertarnerminni (qipoqqaat) ingerlaavartumillu qanermikkut immikkoortiterisarnerminni (arfiviit).

Atortorissaarutit nalunaarsuutitallit atornerinut ilanngullugu assiliissut atorlugu arferit sorliunerinik nalunaarsuineq, immap iluatigoornerminni sammivissiut aammalu atortorissaarutit nalunaarsuutitallit atorlugit uumaffimminnik qanoq atuisarnerat, aalaakaassusiat aammalu Nuup Kangerluani qipoqqarnik neriniartunik takornariartitsisarnerup sunniutai misissuiffigineqarput. Qipoqqaat Nuup Kangerluani najugannaaqartut paasineqarpoq, tamatumuunakkullu qipoqqaat ingerlaartut ataasiakkaat sumiissusersiullaqqissusiat takuneqarsinnaavoq tassami kangerluup paava 10 kilometerinit ikikinnerusoq nassaarisinnaasarpaat. Qipoqqaat amerlagisassaanngitsut ukiut tamaasa neriniarlutik Nuup Kangerluanut uteqqiattuupput. Taamaannerat, aammalu najugannaaqartarnerat arfanniarnermut pingaaruteqarpoq, tassami piniarneqarunik allanik taarteqanngitsooratarsinnaapput taamalu pinngortitamut takornariartunik takuneqarsinnaajunnaassallutik. Immap iluani sammiviinik misissuinerit aammalu atortorissaarutit nalunaarsuutitallit atorlugit uppernarsarneqarpoq ilumut arfernik takornariartitsinermi pissusilersuutaasartut arferit aqqartarnerminni pissusilersuutaasut akornutaasarmata. Qipoqqaat arfernik takornariartitsisunit malinneqartillutik sukkanerulersarput, neriniarlutik aqqaamasarnerat sivikinnerusarluni aammalu immami qatsinnerusumiittarnerat sivisuumillu aqqaamasarnerat sivisoqatigiikannernerulersarlutik, taakkulu tamarmik Kalaallit Nunaata kitaani arfernik takornariartitsinermi malittarisassiortoqartariaqavinneranik ersersitsisuupput.

Kalaallit Nunaata avataani arferit soqqallit amerlassusii siammarsimaffiilu misissorniarlugit arferit angisuut umiarsuarmiit timmisartumiillu annertuunik misissuiffigineqarput, paasineqarporlu sejhvalit, tikaagulliusaat, qipoqqaat tikaagulliillu Kalaallit Nunaata kitaani 2005-imi august-septemberimi amerlasimaqisut. Misissuinerit taakku aammalu neriniartagaannik (krillit ammassaallu) nipit atorlugit misissuinerit takutippaat 150 meterinik itinerusumi krillit amerlassusii tunngavigalugit arferit sumi amerlanerpaajunissaat eqqoriarneqarsinnaasoq. Paasissutissat atorlugit Kalaallit Nunaata kitaani arferit neriartarfiinik eqqoriaanerit taperserneqarput, neriniartagaallu pingaarnerit pingasut paarlakaanneqartartut tassaapput: sinerissami ammassaat, ikkannersuarni putooruttut aammalu immap ikerani krillit.

Timmisartumiit angallammiillu misissuinikkut Kalaallit Nunaata kitaata avataani 2005-imi august-septemberimi arferit soqqallit siammarsimaffii najukkaminillu qanoq atuisarnerat piffissami tassanerpiaq qanoq innersoq paasineqarpoq. Piffissami sivisunerusumi qanoq issusiat paasilluarnerujumallugu aammattaaq nipinik immiussissutit immap naqqanut kisakkat pingasut ukioq kaajallallugu Davis Strædimi immiussitillugit arferit naammattuugassaassusiinik paasiniutigaakka. Misissuinerup taassuma siornagut arferit soqqallit neriniartarnermik saniatigut Davis Strædimik ukiup ingerlanerani qanoq sivisutigisumik sunalu siunertaralugu atuisarnersut ilisimaneqarluarsimanngilaq. Arferit soqqallit assigiinngitsut arfinillit ukiup ilaani neriniartartut tamarmik nipaat immiunneqarput, allaaserisamili uani tikaagulliusaat nipaat kisimik sukumiisumik misissuiffigineqarlutik. Tikaagulliusaat Davis Strædimiittarput decemberip naanissaata tungaanut, siusinnerusukkut ilimagineqaraluartumiit sivisuneroqisumik. Nipaat naapertorlugit takuneqarsinnaavoq decemberip naajartornerani sikunialernissaa tikillugu Davis Strædimi neriniarlutillu nuliusartut. Tikaagulliusaat ukiup ingerlaneranni Davis Strædimiittarnerat piffimmillu atuisarnerat pillugu isumaliutaasimagaluartut misissuinikkut allanngortinneqarput. Inerniliussaralu tassaavoq nipinik immiussisutit atorlugit Davis Strædimi Kalaallillu Nunaata kitaani arferit soqqallit miluumasullu imarmiut allat nilliasartut siammarsimassusii uumaffimminnilu pissusilersuutaat suli maannamut misissuiffigineqarsimasut misissuiffigilluarneqarsinnaasut.

Summary of chapter 2: Kinematics of filter feeding bowhead whales

Simon M, Johnson M, Tyack P & Madsen PT 2009. Behaviour and kinematics of continuous ram filtration in Bowhead whales (*Balaena mysticetus*). *Proc R Soc B* 276: 3819-3828

Here I found that bowhead whales:

1. Feed by employing a continuous fluking gait and swim slowly at less than 0.07 body lengths s^{-1}, allowing them to ram filter feed continuously at depth during long breath-hold dives.
2. Feed in all parts of the water column and not just at the bottom or surface as proposed in earlier studies.
3. Must feed in high density copepod patches, likely 10-fold larger than was previously estimated.
4. Filter 2000 tons of water and prey per feeding dive, totaling some 6000 tons per hour of foraging.

Air-breathing aquatic animals display a number of adaptations to access two spatially separated, but vital resources: oxygen at the surface and food at depth. To get a sufficient net uptake of energy, they must balance the metabolic costs of locomotion and prey acquisition against their oxygen reserves while foraging. Balaenid whales perform long breath-hold foraging dives despite a high drag from their ram filtration of zooplankton. To maximize the volume of prey acquired in a dive with limited oxygen supplies, balaenids must either filter feed only occasionally when prey density is particularly high, or they must swim at slow speeds while filtering to reduce drag and hence oxygen consumption. Using archival tags with three-axis accelerometers, my co-authors and I studied bowhead whales feeding off West Greenland and present here the first detailed data on the kinematics and swimming behavior of a balaenid whale filter feeding at depth. Swim speed was estimated from the low-frequency flow noise, calibrated to the pitch-corrected depth rate of the descent. The tagged whales performed two types of dives: V-shaped and U-shaped dives. Whales adopted a stroke-and-glide gait, resulting in overall mean (over the dive phase) fluking rates of 0.08Hz (s.d.=0.03) during descent and 0.06Hz (s.d.=0.02) during ascent. In comparison, whales fluked almost continuously during the bottom phases of U-dives, with a mean fluking rate of 0.12 Hz (s.d.=0.08). Despite the significantly higher mean fluking rate in the bottom phase compared to the overall mean descent and ascent fluking rates, the estimated swim speeds were 0.75ms^{-1} (s.d.=0.08) (noise-based estimates), about one-half of the speeds of descent (1.4ms^{-1}) and ascent (1.2ms^{-1}). The most parsimonious explanation for this reduction in speed is that their drag coefficient has increased significantly through opening of their mouth for filter feeding. Distinct rattle-like sounds were detected and mainly occurred during the bottom phase of U-dives. These sounds were likely to be rattling from the baleen during filter feeding. Based on these data the U-dives are considered to be foraging dives. The maximum depths of foraging dives varied across whales from 17 to 127m and had a mean duration of 15.2min.

Swimming with an open mouth to force water past a dense curtain of baleen changes the hydrodynamic shape of the animal and increases the drag with a factor 6. Despite this increased drag, balaenid whales perform long foraging dives lasting between 10 and 40min. Despite the slow speeds, the large mouth aperture provides a water filtration rate of approximately 3m^3s^{-1}, amounting to some 2000 tones of water and prey filtered per dive. We conclude that a food niche of dense, slow-moving zooplankton prey has led balaenids to evolve locomotor and filtering systems adapted to work against a high drag at swimming speeds of less than 0.07 body length s^{-1} using a continuous fluking gait very different from that of nekton-feeding, aquatic predators.

Summary of chapter 3: Kinematics of lunge feeding humpback whales

Simon M, Johnson M & Madsen PT. Keeping momentum with a large mouthful of water: Behavior and kinematics of humpback whale lunge feeding. *Manuscript prepared for submission to J Exp Biol*

Here I found that feeding humpback whales:

1. do not come to a stop during a lunge, but rather fluke to keep momentum after and in between lunges, maximizing energy returns.
2. keep a strict consistency in the relative timing and choreography of lunge events and a stereotypic depth profile, in all likelihood representing an optimum in the kinematics of the lunge behavior

Rorqual baleen whales lunge feed by rapid engulfment of many tons of prey-laden water in their large expandable buccal pouch. This process is energetically costly and probably accounts for the strikingly short dive times of rorquals given their size. According to the currently held view on lunge feeding, the whale accelerates prior to mouth opening to attain a high speed to expand and fill the buccal pouch with water. The increased drag from the open mouth then decelerates the whale to a near halt, after which the engulfed water is filtered through the baleens as the whale reaccelerates for the next lunge. We used digital archival tags (DTAGs) sampling three-axis accelerometers and magnetometers, pressure sensors and sound. This fast-sampling sensor-array provided fine-scale information about the kinematics and swimming behavior of tagged lunge feeding humpback whales. Here we investigate the apparent paradox that such large animals, which attain high Reynolds numbers when moving, should develop a feeding strategy that involves a costly near-stop hundreds of times a day. During the bottom phase of most dives deeper than 40 m, tagged whales (n=6) performed several vertical excursions of 10 to 40m amplitude. These depth dynamics coincided with signatures of lunges in the form of high peak excess acceleration. The number of lunges per foraging dive ranged from 1 to 9 with a mean of 3.0 (±0.77 sd, n=357). The analysis revealed a high degree of stereotypy and consistent timing in the choreography of lunging and inter-lunge-interval (ILI) (53.4 ±5.79 s, n=551). The ILI was consistent with those reported from two other species of rorquals: fin whales (45 ±19 s, n=121) and blue whales (71 ±9 s, n=9). The consistencies in the sequence and timing of lunging events, within and across rorqual species, indicate that lunging behavior at depth is controlled by biomechanical limitations rather than by food density or prey behavior.

We conclude that a lunge starts with the whale accelerating using a bout of 3-4 fluke strokes while generally pitching upwards. When reaching a speed of 3-4 ms^{-1} the whale opens its jaws and fills the buccal cavity with prey-laden water. We propose that the whale is not slowed down when opening its mouth, but rather that it continues to accelerate or maintain its speed until the end of the pouch filling. The deceleration of the whale happens when the pouch is full and it starts to move the engulfed water forward. It avoids coming to a stop by producing a strong fluke stroke at the moment the pouch is full, and moves forward after the lunge in a bloated tadpole shape at a speed of 1 ms^{-1} without fluking while filtering. The whale changes the pitch towards the end of the lunge and starts to glide downwards. When the whale has used some 36 seconds to filter out the engulfed water, it initiates a new bout of fluking while pitching towards the surface initiating execution of the next lunge. Hence, lunge-feeding humpback whales do not come to a complete or near halt from increased drag from the open mouth, as previously proposed. Instead they fluke through the lunge to overcome counter-directional forces from drag and acceleration of engulfed water masses, keeping a speed of minimum 1 ms^{-1} throughout the lunge. After the lunge, these large filter-feeders can keep momentum with a mouthful of water without fluking because of their high Reynolds numbers. By avoiding a stop while lunging at depth, they in all likelihood save oxygen for use in the next lunge, maximizing the number of lunges per unit of time.

Summary of chapter 4: Habitat use of humpback whales in Godthaabsfjord

Boye TK, Simon M & Madsen PT 2010. Habitat use of humpback whales in Godthaabsfjord, West Greenland, with implications for commercial exploitation. *J Mar Biol Assoc UK.* 90(8): 1529-1538.

Here we find that humpback whales:

1. show high navigation skills by displaying small-scale site fidelity to the Godthaabsfjord (Nuuk fjord) feeding area.
2. have variable residence time that is probably timed with food blooms.
3. diving and feeding behavior is disturbed by current whale watching, calling for official guidelines.
4. might not be replaced if hunted, due to small-scale site fidelity to Godthaabsfjord, calling for collaboration between the management and tourist industry regarding hunting quotas.

North Atlantic humpback whales migrate from low latitude breeding grounds to high latitude feeding areas, to which individuals display large scale site fidelity. They mate and give birth during winter in less productive areas close to the equator with little or no food availability. The whales therefore rely on their fat reserves during winter. As spring approaches, the humpback whales migrate to highly productive areas at high latitudes, and through the summer they restore their fat reserves for use in the breeding grounds in winter. In West Greenland, humpback whales are affected directly by anthropogenic activities such as hunting and whale watching. They constitute a key species for the whale watching industry in West Greenland, where commercial and private whale watching is quickly growing. Godthaabsfjord Nuuk fjord, Greenland, is one of the central areas for these activities. In addition, Denmark requested an IWC-quota of ten humpback whales in 2007. After a quota of zero since 1986, West Greenland was granted a quota of nine humpback whales in 2010, one of these was caught in the Godthaabsfjord (*after the publication of this paper*).

In Godthaabsfjord humpback whales are present from late spring to late autumn. Little is known about small-scale site fidelity within the feeding ground, where the same individuals may return annually to the same area within a few kilometers. We used photo-ID to investigate how many whales use Godthaabsfjord as a feeding area and how long individuals spend in the fjord during the feeding season. Additionally, we set out to investigate possible effects of whale tourism on feeding humpback whales using theodolite surveys. Furthermore, we used D-TAG data to compare the dive time of a whale before, during and after it was exposed to intensive whale watching.

Identification photographs were collected from May to September 2007 and 2008 and compared with an older catalogue (YONAH, West Greenland). We found a high level of small-scale site fidelity, in which 40% of the whales present in 2007 were resighted in 2008. The average resight rate from 1992 to 2008 was 30.2%. Individuals did not remain in the fjord the entire season and the time spent in the fjord was highly variable amongst individuals varying between 7–60% of the time from May to September. Individual humpback whales in the presence and absence of boats were tracked with a land-based theodolite to test for the effects of whale watching on whale behavior. Whale watch vessels were shown to significantly increase whale swimming speed, to shorten long dives and diminish the ratio between surfacings and long dives.

The first sightings of humpback whales are temporarily linked to the arrival of spawning capelin in Godthaabsfjord. Some humpback whales showed small-scale site fidelity to this feeding area, revisiting Godthaabsfjord between and within years, indicating good navigation skills. The fact that whale watching boats disturb the natural dive behavior of humpback whales calls for regulation of whale watching.

Summary of chapters 5 & 6: Abundance of large baleen whales in West Greenland

Heide-Jørgensen MP, Simon M, and Laidre KL 2007. Estimates of large whale abundance in Greenland waters from a ship-based survey in 2005. *J Cetacean Res Manage* 9(2): 95-104

Heide-Jørgensen MP, Borchers DL, Witting L, Laidre KL, Simon MJ, Rosing-Asvid A and Pike DG 2008. Estimates of large whale abundance in West Greenland waters from an aerial survey in 2005. *J Cetacean Res Manage* 10(2):119–129.

Here we find that:

1. The high abundance of balaenopterid apex predators, is likely to constitute an important top-down regulation of the ecosystem
2. With sightings of 13 different species, the East and West Greenlandic ecosystem supports a high diversity of cetaceans
3. The high occurrence of sei whales is likely to be linked to the influx of warm Irminger water

Abundance estimates of large baleen whales in the arctic are of ecological interest and quantitative measures of the energy transfer between these apex predators and lower trophic levels are lacking. Besides this, estimates of baleen whale abundance in West Greenland are of management importance due to the aboriginal subsistence quotas from the IWC. Despite large efforts to obtain abundance estimates, the weather conditions of the Arctic with fog, wind, sea ice etc. make sighting surveys challenging. The scarce and outdated abundance estimates of baleen whales in West Greenland have raised management concerns.

The aims of the present studies were to obtain reliable abundance estimates of large whales off West Greenland. Simultaneous ship-based and aerial line-transect surveys of large whales in Greenland were conducted in August-September 2005.

The ship-based survey platform primarily targeted capelin, *Mallotus villosus*, using acoustic methods and systematically covered the east and west coasts of Greenland from the coast to the shelf break (approximately 200m). The surveyed area comprised 81,000k m^2 in East Greenland and 225,000 km^2 in West Greenland. 13 cetacean species were observed and standard line transect methods were used to derive abundance estimates of the four most commonly encountered large cetaceans: fin whales, *Balaenoptera physalus* (n=54 sightings), humpback whales, *Megaptera novaeangliae* (n=30 sightings), sei whales, *B.borealis* (n=21 sightings) and minke whales, *B. acutorostrata* (n=14 sightings).

Concurrent with the ship-based survey, an aerial line-transect and cue counting survey of large whales was conducted from a *Partenavia Observer P-68*. The survey covered the area of 163,574km^2 between Cape Farewell and Disko Island on the West Greenland coast out to the 200m depth contour. Nine cetacean species were observed and abundance estimates were derived for the three most commonly encountered large cetaceans: fin whales (n=78 sightings), humpback whales (n=21 sightings), and minke whales (n=42 sightings).

We showed that the East and West Greenlandic ecosystems support a rich diversity of cetacean top-predators (13 species observed). The similar abundance estimates of fin, humpback and minke whales derived from the two sets of independent simultaneous surveys showed that these balaenopterids were abundant in West Greenland, August-September 2005. Sei whales are not commonly seen in West Greenland in high numbers. The sudden occurrence may be related to the generally increasing sea surface temperature and influx of warm Irminger water to the southern part of the Davis Strait.

Summary of chapter 7: Spatial distribution of large whales and their prey

Laidre KL, Heide-Jørgensen MP, Heagerty P, Cossio A, Bergström B & Simon M 2010. Spatial associations between large baleen whales and their prey in West Greenland. Mar Ecol Prog Ser 402:269-284

Here we show that:

1. Integrated krill abundance is an important parameter in predicting baleen whale presence
2. Krill biomass was most predictive of whale presence at depths >150m
3. A high degree of spatio-temporal synchrony in visual and hydroacoustic observations is necessary for quantifying predator–prey relationships

Finding high density prey patches in a highly variable environment, such as West Greenland, requires that foraging baleen whales exploit diverse prey resources and adopt multiple foraging strategies to succeed. Balaenopterids on their West Greenlandic feeding ground are believed to switch between three main prey species: coastal capelin (*Mallotus villosus*), sandeel (*Ammodytes sp.*) on the banks and pelagic krill *(e.g.: Meganyctiphanes norvegica* and *Thysanoessa sp)*. However, this hypothesis is mainly based on stomach samples of catches and is highly speculative. Here we investigated relationships between the spatial distribution of balaenopterids and their prey.

We combined data on sightings of fin whales, humpback whales, minke whales and sei whales from large-scale visual ship-based (chapter 5) and aerial (chapter 6) surveys with synoptic acoustic sampling of krill and capelin abundance in September 2005. Krill densities were obtained from backscattering strengths of krill. Krill data were vertically integrated in 25 m depth bins between 0 and 300 m to obtain water column biomass (gm^{-2}). Standard regression models were developed to identify possible important explanatory variables relating the presence, absence, and density of large whales to the physical (depth, slope, temperature, latitude and longitude) and biological (krill water column biomass) environment and different survey platforms.

Large baleen whales were concentrated in three focal areas. There was a bimodal pattern of mean krill density between depths, with one peak between 50 and 75 m (mean 0.75 gm^{-2}, s.d. 2.74) and another between 225 and 275 m (mean 1.2-1.3 gm^{-2}, s.d. 23-19). Total depth-integrated krill biomass was 1.3×10^9 kg (CV 0.11). In contrast to the off-shore krill, capelin were virtually absent on the banks but present in large numbers inside the fjords with a total biomass of about 2.0×10^8 kg[1]. The coastal and discontinuous nature of capelin distribution made correlations impossible.

Models indicated that the most important parameter in predicting large baleen whale presence was integrated krill abundance, although this relationship was only significant for sightings obtained by the ship survey, suggesting that a high degree of spatio-temporal synchrony in observations is necessary for quantifying predator–prey relationships. Krill biomass was most predictive of whale presence at depths >150m, suggesting a threshold depth below which it is energetically optimal for baleen whales to forage on krill in West Greenland.

A high correlation does not necessary mean that there is a causal link. However, supported by stomach contents from past whaling, it is very likely that balaenopterids feed on the high densities of krill on the offshore banks. Unfortunately, abundance estimates of West Greenland sandeel are not available, but experimental fisheries indicate a high biomass. Our data indicates that krill is a key prey for balaenopterids in West Greenland, and support the hypothesis that these whales shift between inshore capelin and off-shore sandeel and krill over the season.

---

[1] Bergström and Vilhjalmarsson (2007) Cruise report and preliminary results of the acoustic/pelagic trawl survey off West Greenland for capelin and polar cod 2005. Technical report no. 66, Pinngortitaleriffik, Greenland Institute of Natural Resources.

Summary of chapter 8: Acoustic monitoring of fin whales in the Davis Strait

Simon M, Stafford KM, Beedholm K, Lee CM & Madsen PT. Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging. 128(5): *J Acoust Soc Am, In press.*

Here we show that:

1. Fin whales stay in the Davis Strait at least until the end of December, much longer than previously thought.
2. The seasonal peak in fin whale song coincides with the estimated conception time of fin whales, suggesting that fins whales start mating while still in the Arctic Davis Strait.
3. Clear diel pattern in fin whale song in November-December suggests that fin whales feed in the Davis Strait until late December.

Most baleen whales undertake migrations between low-latitude breeding grounds and high-latitude feeding grounds. Though little is known about the timing of their migration from the Arctic, fin whales are assumed to undertake a similar migratory pattern. Fin whales produce a characteristic song consisting of a low frequency (LF) 20-Hz, 1 second long downsweep centered at 20Hz and a simultaneous high frequency (HF) pulse with a variable frequency, presumably linked to population identity. The acoustic characteristics of the song make it suitable for passive acoustic monitoring of fin whales. To address questions of habitat use and migration, the acoustic activity of fin whales in the Davis Strait, between Greenland and Canada, was monitored continuously for two years. Three calibrated bottom-moored autonomous acoustic recorders (HARU-Phone III) sampling continuously at 2,000Hz with band pass filtering between 0.1 and 970Hz were deployed with a distance of 45–85km between the instrument moorings. Some months of the year the fin whale's "20-Hz" call was so abundant that it formed a continuous band around 20Hz in spectrogram displays, rendering automatic kernel detections futile. We therefore quantified fin whale calls as the power in the frequency band around the fin whale calls (F_{fin} 19–28Hz) relative to the summed powers in the surrounding noise bands (F_{noise} 13–17Hz and 33–37Hz).

Fin whales were acoustically active and hence present in the Davis Strait from June to December. The acoustic power of the fin whale call frequencies peaked in November–December, showing that fin whales are present in the Davis Strait much later in the year than previously thought. A clear annual peak in the fin whale singing activity, lasting for about four months, has been reported from the northern and southern hemisphere. This seasonal peak in fin whale song coincides with the estimated conception time of fin whales, suggesting that the song is part of a mating display, possibly to attract mates. This is further supported by the fact that only males have been reported to sing. The contemporaneous peaks in song activity and conception time in the Davis Strait suggest that not all fin whales migrate south to mate, but rather that some stay at high latitudes perhaps to exploit food niches that are not available at lower latitudes while mating. The latter notion is supported by the fact that the singing activity of fin whales in the Davis Strait is strongly linked to daylight hours, and could be controlled possibly by the vertical migratory behavior of their prey. This suggests that fin whales might feed during the few daylight hours of the late fall and early arctic winter.

The difference in magnitude of fin whale signal detections among the three recorders shows that the distribution of fin whales in the Davis Strait may in part be controlled by the advance of the sea ice edge during winter. Further, we observed a negative correlation between fin whale song and sea ice whereby the song stopped when the sea ice covered the mooring. Consequently, changing sea ice conditions may change the winter distribution of singing fin whales in the future and such changes may be monitored successfully by using passive acoustic monitoring (PAM).

Introduction

Chapter 1

1.1 Background and objectives

Most baleen whales undertake long migrations between high latitude, productive feeding grounds during summer and warmer oligotrophic mating/breeding grounds at low latitudes during winter (Kellogg 1929; Norris 1967; Corkeron and Connor 1999; Mizroch et al. 2009). Migratory routes have been mapped for humpback whales, right whales (*Eubalaena australis and E. glacialis*) and gray whales (*Eschrichtius robustus*) with identified high latitude feeding and low latitude breeding grounds (e.g. Bannister et al. 1999; Clapham 1996; Kraus et al. 1986; Perryman et al. 2002). Discovery tag returns from commercial whaling and passive acoustic monitoring (PAM) suggest that fin whales (*Balaenoptera physalus*) and blue whales (*B. musculus*) may undertake similar migrations: feeding at high latitudes during summer and moving to lower latitudes for mating during winter (Fig. 2; Kellogg 1929; Norris 1967; Stafford et al. 1999; Sirovic et al. 2009; Mizroch et al. 2009; Chapter 8). While most baleen whales migrate north-south, the Eastern Canada-West Greenland bowhead whales stay in the Arctic year round, performing seasonal east-west migrations between West Greenland in spring and the High Arctic in the summer (Heide-Jørgensen et al. 2006). Though the main part of a baleen whale population migrates from the feeding grounds, there are multiple reports of individual whales wintering at the feeding grounds, including humpback, fin, right and minke whales (see Corkeron and Connor 1999 for a review; Christensen et al. 1992; Ingebrigtesen 1929; GINR, Unpubl. data).

Fig. 2. Aggregation of fin whales off West Greenland taken during an aerial survey. Photo: L. Witting

Many ecological factors such as resources, predation, habitat and competition influence migratory behavior, but seasonal variation in resources is often a major driving force for long distance migrations (Alerstam *et al.* 2003). Migrating baleen whales perform the longest known seasonal movements of any mammal and the driving forces for this behavior remain poorly understood (Corkeron and Connor 1999). However, four main explanations have been proposed for these migrations:

1. Optimization of energy budget: Brodie (1975) suggested that there is no extra cost of transport for migrating baleen whales and that migration to warmer waters when prey might be scarce in high latitude winters would optimize their energy budget overall.

2. Resource tracking: This hypothesis involves food being the driving factor in migration, with baleen whales leaving the high latitudes in winter when productivity decreases to feed on planktonic prey in warmer areas (Payne 1995).

3. Evolutionary history: Migration to equatorial breeding grounds has been explained as being a vestigial behavioral left-over from times when high plankton productivity may have been distributed differently (Evans 1987).

4. Predatory pressure on calves: In a review on the migratory behavior in baleen whales, Corkeron and Connor (1999) hypothesized that predatory pressure from killer whales (*Orcinus orca*) on newborn calves presented a likely explanation for baleen whales migrating to lower latitudes to breed, despite the low availability of food in these areas.

Fig. 3. Fluke of humpback whale in West Greenland with toothe rakes. ID-catalogue, GINR.

These four hypotheses on why baleen whales migrate are still heavily debated and no data have so far conclusively supported any one of them, but several suffer from one or more problems. Hypothesis *1, Optimization of energy budget* has been weakened by modelling studies indicating that baleen whales do not improve their energy budget by moving to higher temperatures. In fact, the lower critical temperature is below any temperature realized in salt water (Watts *et al.* 1993). Hypothesis *2, Resource tracking* assumes that there is no available prey for balaenopterid whales in polar habitats during winter. However, the fact that individuals of minke, humpback and fin whales have been reported to over-winter in polar areas (Ingebrigtsen 1929; Christensen et al. 1992; Gill and Thiele 1997) and that 1-3 humpback whales stay in Nuuk Fjord to feed most winters (GINR Unpubl.) suggests that the whales may also migrate south for other reasons than a decrease in accessible prey (Corkeron and Connor 1999). This is also supported by the fact that gray and humpback whales seldom feed during winter while at the breeding grounds (Nerini 1984; Clapham 1996). Hypothesis *3, Evolutionary history* is hard to test especially as we do not know the behavior of earlier baleen whales. However, one could argue that if it was a purely vestigial behavior and that there was at present an energetic advantage in staying at high latitudes to breed, then natural selection should have acted on the migratory behavior. Finally, hypothesis *4, Predation*, suggests that the predation by killer whales has shaped the migratory behavior of many species of baleen whales. This hypothesis is the subject of debate (review Mehta et al. 2007). The fact that 22 % (n=163 ID-photos) of identified West Greenlandic whales (North Atlantic Humpback Whale Catalogue, College of Atlantic) have tooth rakes (Fig. 3) strongly suggests that killer whales do present a threat to humpback whales, even though violent interactions are not always lethal. This, together with the supposition that most whales with scars were attacked as calves (Dolphin 1987, Mehta et al. 2007), lends support in favor of the hypothesis that killer whale predation on balaenopterid calves is a driving force for the migratory behavior to low-latitude breeding grounds. However, analyses of killer whale attacks and fresh wounds on southern hemisphere balaenopterid whales suggest that most attacks occur on the migration (Shevchenko 1975, in Metha et al. 2009). This is also the case with gray whales, where calf mortality is highest during migration (Goley and Straley 1994). Polar regions are less populated and the chance of seeing a killer whale in West Greenland, and, even less a killer whale attack on a large whale, is scarce. Nevertheless, reports of costal killer whale attacks on humpback whales in Greenland are regular (Unpublished data, GINR). Thus, this hypothesis is still open to debate.

While researchers argue about which factors may drive baleen whales to seasonally migrate to areas of poorer feeding opportunities (the mating grounds), it is well established that baleen whales use high latitudes to feed and restore fat reserves during spring and summer (Ingebrigtsen 1929; Norris 1967; Laws 1985; Tynan 1998). Large numbers of at least six species of baleen whales feed seasonally in the productive waters of West Greenland: blue whale, fin whale, humpback whale (Megaptera novaeangliae), sei whale (B. borealis), minke whale (B. acutostrata) and bowhead whale (Balaena mysticetus). As abundant top predators with a large biomass (see chapter 5 and 6 for estimates of abundance), baleen whales most likely constitute important top-down regulators of the marine ecosystem on their West Greenlandic feeding grounds.

Changes in temperature and decreasing sea ice coverage (Fig. 4; Parkinson 1999) are expected to cause changes in the productivity and energy cascades through the ecosystem (Heide-Jørgensen et al. 2007a). In addition, anthropogenic activities in West Greenland are increasing, with the inherent risks of disturbing the whales in the area. These activities include increased shipping, oil, gas and mineral exploration, tourism and whaling.

Sea ice has previously been the main limiting factor in shipping and oil and gas exploration in the Arctic. However, with the decreasing sea ice cover (Fig 4) these activities are increasing and the seismic investigations of the West Greenlandic underground are extensive (Fig. 5). In September 2010, Cairn Energy started the first drilling activities on the Greenlandic shelf and soon after announced the finding of hydrocarbon deposits of unspecified quality (http://www.cairnenergy.com/NewsDetail.aspx?id=1363). Given these positive preliminary results, drilling and seismic activities will continue over the coming years. The increased traffic and exploration in the Arctic will probably raise the

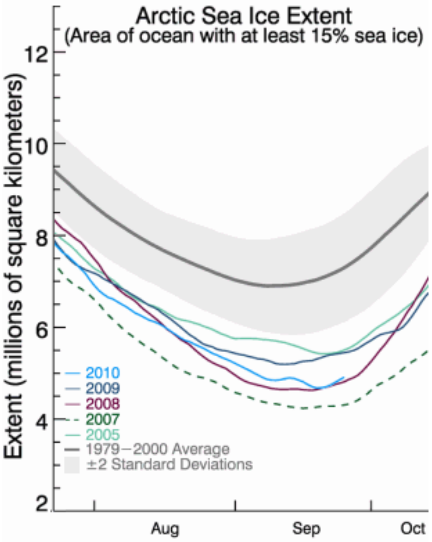


Fig. 4. The yearly minimum of the Arctic sea ice extent in 2005, 2007-2010 in relation to the average sea ice extent in 1979-2000. Source: The National Snow and Ice Data Center, US.

average noise level of the sea off West Greenland with possible negative effects on the marine mammals in the area (Richardson et al. 1995).

Besides hydrocarbon exploration, eco-tourism has exploded over the past decade with 18 cruise ships (1632 persons) visiting West Greenland in 2003 and 41 (7969 persons) in 2008 (GTE, selvstyret). Inshore whale watching companies have also flourished calling for more general codes of conduct regarding whale watching in West Greenland (Chapter 4).

Finally, another anthropogenic pressure upon baleen whales off West Greenland are the quotas under the IWC aboriginal subsistence whaling scheme for fin whales (9 per year), minke whales (175 per year), bowhead whales (2 per year) and humpback whales (9 per year).

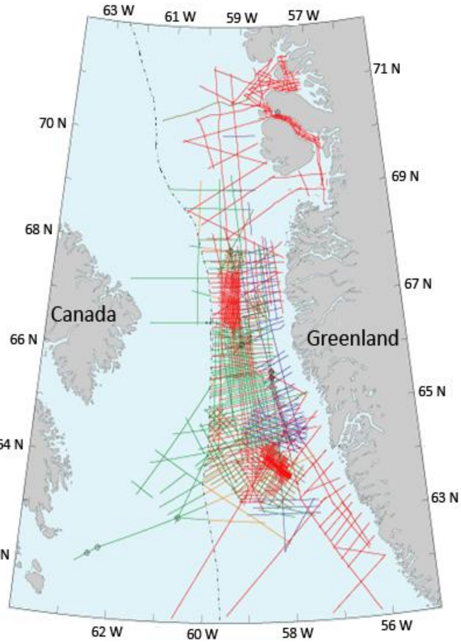


Fig 5. Map of seismic surveys in 1990-2001. The seismic surveys have continued at a higher rate since 2001. Modified from www.GEUS.dk.

Without doubt, baleen whales play an important cultural and economic role in the Greenlandic society. Increasing human activities in the sea and climate change might have severe effects on the West Greenlandic ecosystem upon which baleen whales rely. However, at present very little is known about their behavioral ecology, interactions with lower levels in the food chain and how future changes in the ecosystem might affect the distribution and abundance of these large predators in the Arctic. There is a mutual dependence between trophic levels where fluctuations in population size and distribution at one level can affect those of another level or skew the trophic energy cascades in the food chain. Because of this, the International Whaling Commission (IWC) and the North Atlantic Marine Mammal Commission (NAMMCO) have repeatedly recommended a more ecosystem-based approach for the management of marine mammals (NAMMCO 2009; IWC 2009). However, with a limited quantitative knowledge on the link between marine mammal apex predators and lower trophic levels, it is not yet possible to carry out ecosystem-based management in practice. Motivated by this lack of knowledge, I started my PhD with the aim of expanding knowledge of the acoustics, ecology and behavior of baleen whales in West Greenland.

With the limited visibility in water, especially at depth, sound plays an important role in the life of baleen whales (Au 2000). The powerful, species-specific, low-frequency sound signals of baleen whales are most likely used in long range intraspecific communication, navigation and localization of prey (Payne and McVay 1971; Payne and Webb 1971). As the signals reflect the species identity, relative abundance and behavior of the vocalizing whales, acoustics is a useful and widely used tool to study these large pelagic species (Mellinger et al. 2007). The overall aim of my PhD thesis was to investigate the acoustics, behavioral ecology and distribution of baleen whales in West Greenland to get a better understanding of the foraging behavior and distributional patterns of baleen whales and their prey. The aims were bi-focal; I) A detailed small-scale quantification of the feeding behavior and II) a large-scale investigation of factors influencing the baleen whale distribution, seasonality and abundance in West Greenland.

With this introduction (Chapter 1), I intend to put the main findings of my PhD work as presented in Chapters 2-8 into a broader context. In accordance with the requirements for a PhD dissertation at the Faculty of Science, Aarhus University, I have structured chapter 1 as a review where I begin with a detailed outline of the kinematics of foraging Balaenids and Balaenopterids followed by a comparison of their different techniques to filter out aggregated prey (section 1.2). This is followed by a discussion on how the baleen whales locate prey patches based on previous hypotheses and in the light of data I obtained during my PhD (section 1.3). Broadening the view even more, I proceed to discuss the distributional patterns of baleen whales in West Greenland in relation to the distribution of their prey based on sighting and hydroacoustic surveys (section 1.4). As this survey technique provides a good spatial resolution, but a very poor temporal resolution, I then turn to evaluation of the potential for using passive acoustic monitoring as an alternative or complementary method to study the occurrence and behavior of vociferous marine mammals in West Greenland (section 1.5). Finally, I end this introduction with an outline and discussion of the future studies that I believe can contribute to a better understanding of the West Greenlandic ecosystem and of baleen whales as apex predators in the Arctic (section 1.6).

1.2 Dive and feeding behavior of baleen whales

To get a sufficient net uptake of energy during breath-hold dives, marine mammals must balance the metabolic costs of locomotion and prey acquisition against their oxygen reserves while foraging (Kramer 1988; Williams 1999). Larger animals have a higher ratio between the carrying capacity of oxygen and the mass-specific metabolism compared to smaller animals (Hochachka and Somero 1984; Kooyman 1989, Croll et al. 2001). The theoretical aerobic dive limit (TADL) in general scales with body mass by the power of 0.25 (Kooyman 1989). As the overall TADL limits breath-hold dives, the dive times of marine mammal dives generally increase with body size (Kooyman et al. 1980; Kooyman 1989). The large balaenopterid whales constitute an exception to the general rule, as they perform much shorter dives than would be expected given their large body mass (Fig. 6; Croll et al. 2001; Acevedo-Gutiérrez et al. 2002). Their relatively short dive times have been explained by the costs of negotiating large drag forces encountered when the whales open their mouths to filter feed (Croll et al. 2001; Acevedo-Gutiérrez et al. 2002).

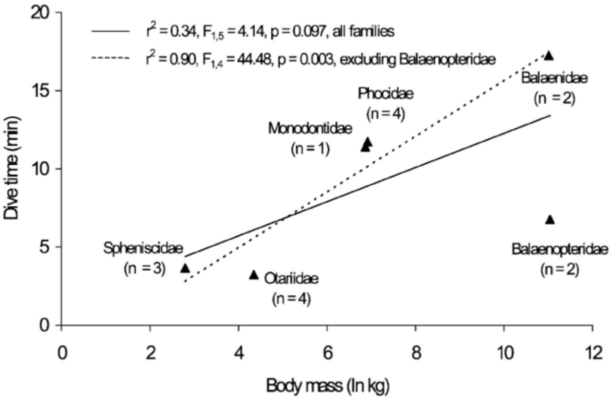


Fig. 6. Marine mammal dive time generally increases with body mass. Balaenoptera constitute an exception, performing very short dives despite the large body mass. Modified from Croll et al. 2001.

Though baleen whales perform a wide range of feeding strategies to meet the behavior and ecology of their prey, they all use keratinous baleen plates hanging from the top of the mouth to filter small prey items from high density patches of zooplankton and schooling fish (Croll and Tershy, 2002). Three general filter feeding behaviors have been identified in baleen whales:

1) *Skimming / continuous ram filtration* where the whale slowly swims with open mouth filtering prey from the passing water: this is mainly performed by the right whales, such as bowhead whales (Watkins and Schevill 1979; Würsig et al. 1985, 1989).

2) Gray whales (*Eschrichtius robustus*) feed by *sediment-straining,* placing one side of the mouth on the bottom and sucking in water, which is then expelled from the other side of the mouth, filtering the prey through the baleen (Ray and Schevill, 1974).

3) *Lunge feeding / intermittent ram filtration,* where whales repeatedly engulf many tons of prey-laden water in their buccal pouch before filtering the prey through the baleen: this is

the main feeding strategy for rorquals, such as fin whales and humpback whales (Pivorunas 1979; Lambertsen 1995).

Baleen whale filter feeding strategies have evolved in two overall directions, reflected in the swimming and prey capture behavior, morphology and prey choice: Discrete filtration events aimed at capturing larger, elusive nekton capable of evading a vertebrate predator, and continuous filtration targeting small zooplanktonic organisms (Pivorunas 1979; Lambertsen 1995; Watkins and Schevill 1979; Würsig et al. 1985, 1989). Most baleen whales are discrete filter feeders, where the whale engulfs a mouthful of water either by suction created with the tongue as in sediment straining or by ramming as in lunge feeding. The water is then expelled through the baleens, whereby the food is filtered from the water. These discrete feeding events create a bidirectional water flow within the mouth (Werth 2000). In contrast, balaenids perform continuous ram filtration where the filter apparatus has evolved to support a continuous unidirectional flow of water through the baleen curtain while the whale moves forward with open mouth (Werth 2000). These two filter feeding strategies have fundamentally different morphologic, behavioral, mechanical and energetic ramifications. Here I will describe and compare the detailed kinematics of continuous ram filtration of bowhead whales (Chapter 2) and the discrete lunge feeding of humpback whales (Chapter 3).

Balaenid feeding

Fig. 7. Bowhead whale at the spring feeding ground off Qeqertarsuaq, Disko Bay, Greenland. Photo M. Simon.

The large head of the bowhead whale (Fig. 7) comprises approximately one-third of its total body length and with the highly curved maxillary and premaxillary bones, supporting two rows of up to 4 m long curved baleen plates, it makes out an enormous filtering apparatus (Lambertsen et al. 2005, Werth 2004). The specialized mouth area constitutes a fascinating morphological adaptation to filter out planktonic animals from the water, with a unique morphology that optimizes water flow through the baleens (Werth 2004). The left and right row of baleen plates are divided with a central cleft; the subrostral gap (Lambertsen et al. 2005). When ram filter feeding, a balaenid open its mouth and prey-filled water flow into the buccal cavity through the subrostral gap and over the baleen (Pivorunas 1979; Lambertsen et al. 2005; Werth 2004), sifting out the prey via the forward movement of the whale through the water aided by the hydrodynamic forces created by the morphology of the mouth (Werth 2004).

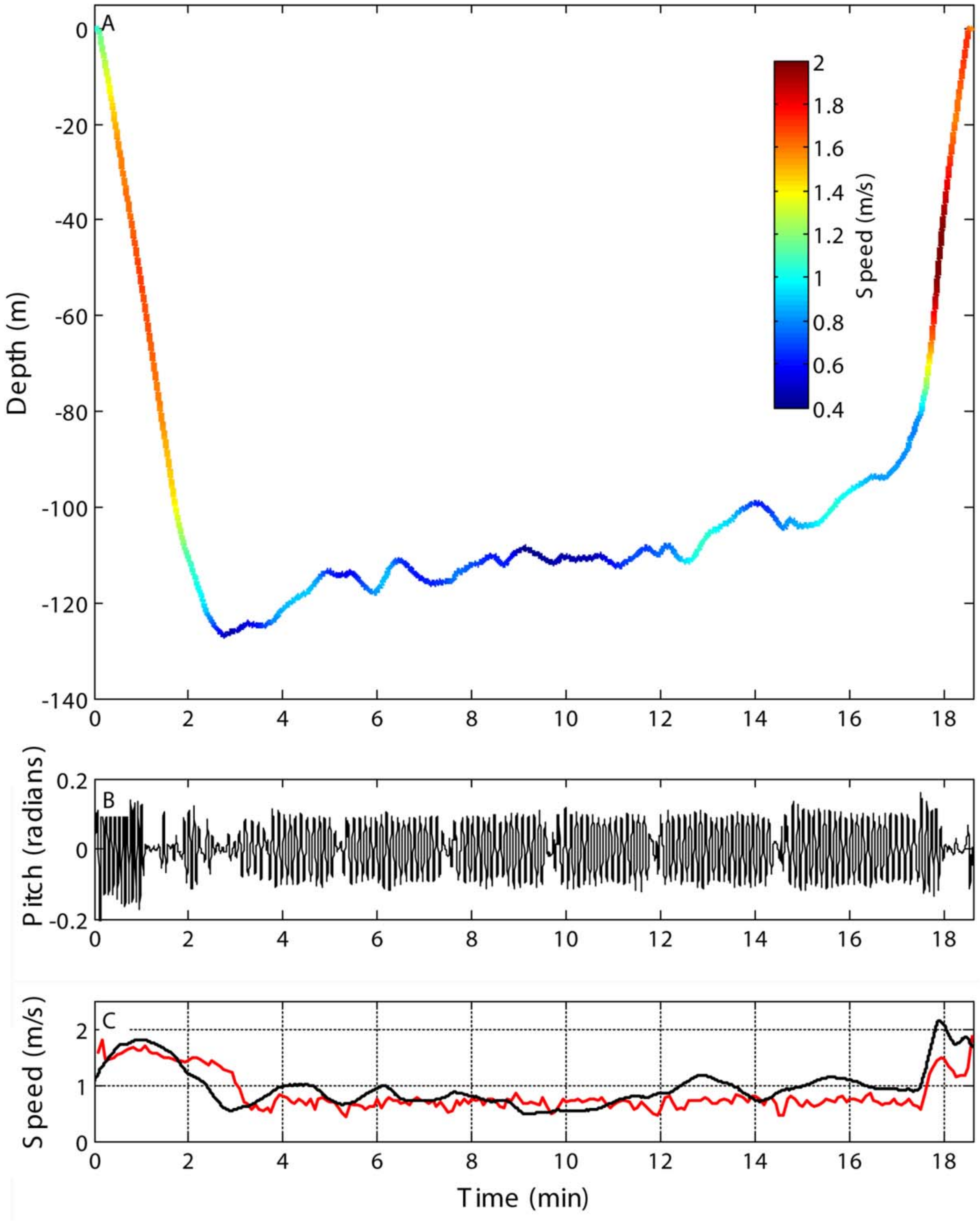


Fig. 8. A. Dive profile of a continuously ram filtrating bowhead whale tagged with DTAG. B. Fluking illustrating fluke-and-glide gait at descent and ascent and continuous fluking at bottom phase. C. Speed estimated from orientation corrected depth rate, filtered with a Kalman filter (black) and speed estimated from the low-frequency flow noise (red).

Opening of the mouth for filter feeding changes the hydrodynamic shape and increases the drag (Sanderson & Wassersug 1990; Werth 2004). To optimize foraging energetics, bowhead whales face a trade-off between keeping up the speed to increase filtration rates and the energetic consumption from drag that goes up with the cube of speed (Hind and Gurney 1997; Fish 2002). Despite an expected high drag and hence oxygen consumption from the open mouth with an estimated effective cross-sectional area of 4.23 m^2 (Werth 2004), bowhead whales perform long foraging dives of 10 to 40 minute duration (Laidre et al. 2007). How these whales can perform long breath hold foraging dives while operating against a large drag from the open mouth represents a conundrum in balaenid feeding behavior. For the present thesis I hypothesized that the long dive times with an expected high drag from the open mouth are only possible if the whales either perform intermittent filtration by only opening the mouth intermittently during foraging dives e.g. when prey are especially dense, or if the whales perform continuous ram filtration at very low speeds to keep the drag and hence oxygen consumption low. Together with my co-authors, I tested these two alternative hypotheses using archival DTAGs (Chapter 2). We show that bowhead whales use continuous ram filtration propelled forward with a continuous fluking gait (Fig. 8) with a rate of 0.12 Hz. This enables a slow but steady speed of less than 1 ms^{-1} despite the drag from the large filter apparatus. The filtered water volume increases no more than linearly with speed while drag increases with the square of speed. Thus such slow swimming in all likelyhood represents an optimum point in the effort-gain trade-off for feeding bowhead whales. This means that one of the largest predators on earth captures its prey at extremely slow speed when expressed in body lengths per second

The question then is: How can one of the largest predators on earth successfully catch prey with a hunting speed of 0.07 bodylength per second? The bowhead whales seem to feed almost exclusively on copepods (*Calanus hyperboreus*) while in Disko Bay (Fig. 9; Heide-Jørgensen et al. 2010). These large copepods are, on a relative scale, among the strongest and fastest animals on earth, whose evolutionary success is explained by their ability to escape predators (Kiørboe et al. 2010; http://www.sciencecentric.com/news/10051306-the-strongest-animal-the-world.html). However, their relative size (0.0007 of the length of a bowhead whale) makes them easy bowhead prey and any evasive behavior from the copepods will not escape the 4.23 m^2 (Werth 2004) aperture of the bowhead mouth capturing them.

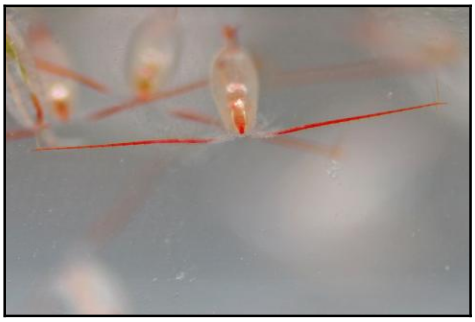


Fig. 9. *Calanus borealis* caught off Qeqertarsuaq in Disko Bay. Photo F. Ugarte

Our results thus explain how bowhead whales can successfully feed on small planktonic prey using continuous ram filtration (Chapter 2). However, we are still left with a conundrum regarding bowhead whale feeding behavior. The stomach contents of bowhead whales caught in other areas, such as the Western Beaufort Sea, showed that *Euphausiids* make up an important part of the prey (Lowry 1993; Lowry et al. 2004). Euphausiids are fast swimming animals that balaenopterid whales have developed a specialized set of morphological and behavioral adaptations to catch (Goldbogen et al. 2006; Chapter 3), so how can bowhead whales catch these fast swimming species with a feeding apparatus apparently adapted to slow steady speeds (Chapter 2)? Can they switch foraging behaviors according to the prey type and if so, how? These interesting questions could be pursued by tagging krill-eating bowhead whales with DTAGs.

Now let us turn to the balenopterids that have developed a very different functional morphology and swimming behavior to catch and filter out faster swimming evasive prey.

Balaenopterid feeding

Balaenopterids are the most streamlined and fastest among baleen whales, behaviorally and morphologically adapted to catch and filter small elusive schooling fish and euphausiids from the water (Lambertsen 1995). The specialized tissue of the throat and the ventral thorax is pleated into elastic, longitudinal furrows that together with the flaccid poorly musculated tongue (Fig. 10) form a highly expandable cavity for engulfment of tons of preyladen water (Ingebrigtsen 1929; Pivorunas 1979; Lambertsen et al. 1983). The gape area is increased by rotation of the mandibles and the presence of the frontomandibular stay that enables balaenopterid mandibles to open almost 90 degrees to the skull (Lambertsen et al. 1983).

Fig. 10. Tongue of fin whale stranded and dissected in Denmark 2009. The throat tissue has been cut loose near the mandibles. The baleen rack is visible at the right side. The picture is taken from the rostrum of the whale and into the mouth cavity. Photo: CB Christensen.

To catch fast prey by bulk engulfment, feeding balaenopterids operate under a set of energetic, biomechanical and behavioral restrictions where three things are necessary for success: large gape aperture, fast forward speed while approaching and surrounding the prey and a large engulfment volume. These requirements are energetically costly, resulting in short dive times (Croll et al. 2001; Acevedo-Gutiérrez et al., 2002). Besides the morphological adaptations described above, balaenopterids, have developed behavioral adaptations to balance the energetic cost of lunging with the calorific gain of the catch. These include energy saving gait, consistent choreography of lunging events and transfer of momentum during lunges. Here I will describe these behavioral specializations in more detail:

Energy saving gait: Most marine mammals, including balaenopterids prolong breath hold dives by performing oxygen saving fluke-and-glide gait (Williams 2000). Balaenopterids use this strategy during all dive phases: descent, ascent and in between lunge sequences at depth, increasing time at foraging depth (Fig. 11).

Consistent choreography: A lunge consists of a sequence of events: 1. acceleration; 2. mouth opening; 3. buccal pouch filling, and acceleration of the entrained water and deceleration of the body; 4. mouth closing; 5. gliding while filtering water, and 6. harvesting of prey from baleen plates (Chapter 3; Goldbogen et al. 2006). In chapter 3, my co-authors and I show that humpback whales keep a strict choreography and consistency in the relative timing of these events that make up a lunge. Also we show that the inter-lunge interval is consistent within and between several balaenopterid species. The strict choreography is translated into a high degree of stereotypy in the depth pattern of humpback whale lunges (Chapter 3). Such choreography may represent an optimum in the kinematics of the lunge behavior and I propose that the timing and stereotypy evolved as part of optimizing the effort-gain trade-off from lunging.

Transfer of momentum: Goldbogen et al. (2006) investigated the question of why the lunging behavior apparently is so energy consuming. Tagging fin whales with a digital tag (b-probe), they came up with the acceleration-deceleration theory, suggesting that a lunging whale accelerates, opens the mouth and then decelerates from the increased drag from the open mouth bringing it to a near halt (Goldbogen et al. 2006; 2007). Thus, Goldbogen et al. explains the short dive times mainly by their apparent observation that the whale has to re-accelerate from a near halt after each lunge. Balaenopterids are the largest whales on earth which makes it relatively costly to reaccelerate from a dead halt, whereas in movement these large animals have high Reynolds numbers, favoring efficient fluke-and-glide gaits. Together with my co-authors I used multi-sensor DTAGs sampling three-axis accelerometers and magnetometers, and a pressure sensor at a high sampling rate of 50 Hz (Johnson and Tyack 2003) to investigate the behavioral ecology and detailed kinematics of lunge feeding humpback whales in Greenland (Chapter 3). We used this fast-sampling sensor-array to test the question of whether such large animals have evolved a highly specialized feeding strategy involving a drastic acceleration-deceleration after each gulp as proposed by Goldbogen et al. (2006). The DTAGs provided fine-scale information about the kinematics and swimming behavior, and we show that a lunge feeding humpback whale does not come to a stand-still. Rather, they keep a speed above 1 ms^{-1} during and after lunges overcoming drag from the open mouth and the mass acceleration of the engulfed water by intense fluking. Thus, balaenopterids seem to fluke hard in order not to lose momentum, and the costly part of a lunge is not reacceleration from a standstill as proposed by Goldbogen et al, but rather to accelerate a water volume comparable to their own body mass. By avoiding a stop while lunging at depth, they probably save oxygen to be used in the next lunge, maximizing the number of lunges per unit of time (Chapter 3).

Here I have outlined the feeding behaviors, adaptations and energy saving strategies characterizing balaenopterid and balaenid whales. In the following, I will compare the filtering capacities of the two feeding strategies and discuss their efficiency in energy uptake, and implications for the whales overall feeding behavior.

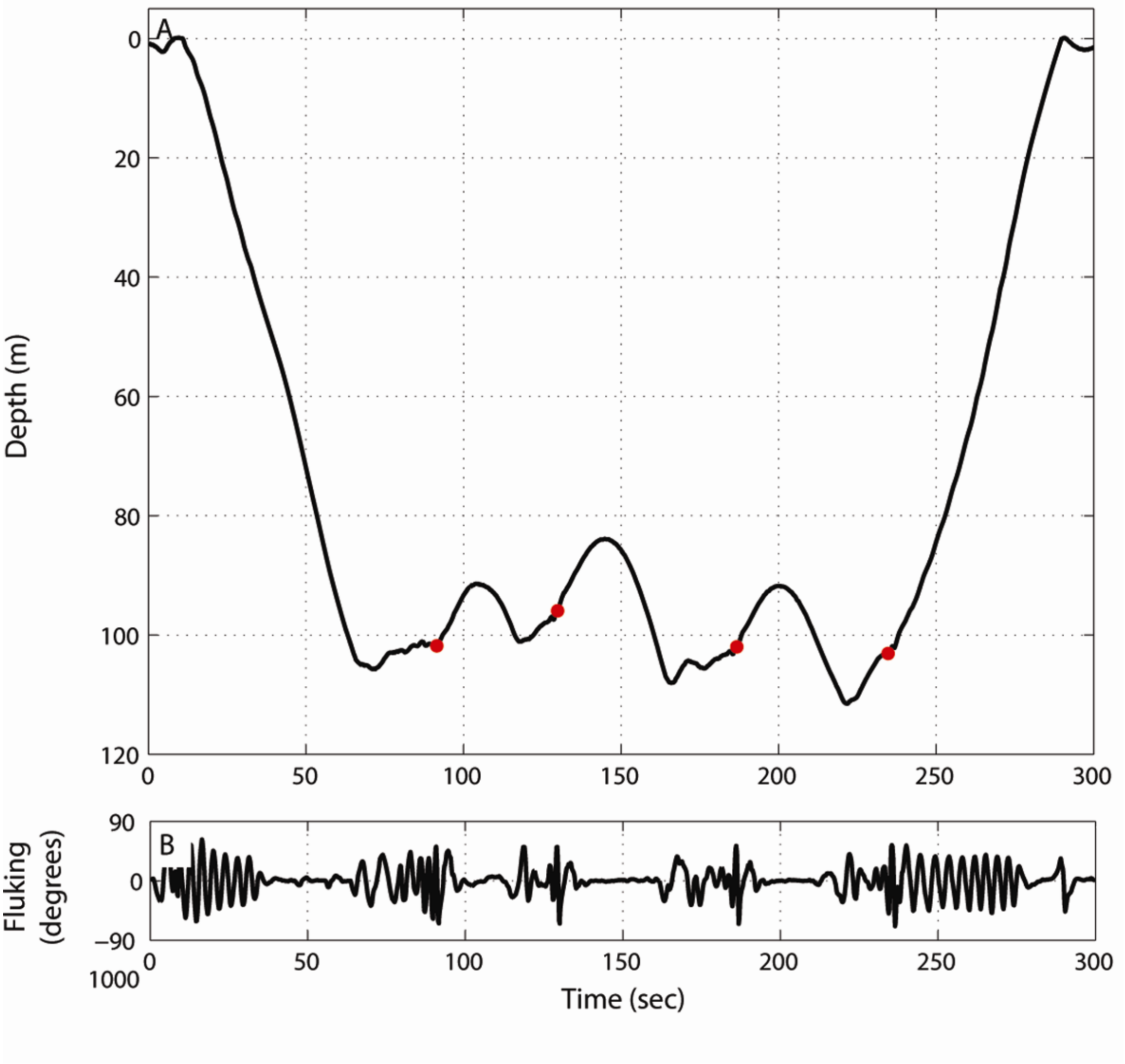


Fig. 11. A. Dive profile of a lunge feeding humpback whales tagged with a DTAG. Red dots indicate a lunge. B. Fluking pattern showing a fluke-and-glide gait

Implications of filter feeding strategies

Fig. 12. Humpback whale lunge feeding at krill. Photo M. Simon.

Balaenid and balaeniopterid whales are highly specialized in filtering out aggregations of prey from a volume of water. The differences in morphology and feeding behavior are striking and have been a point of interest since the early whaling epoch where Ingebrigtsen (1929) made a written account comparing their feeding behavior and morphology. For me, questions of energetics and ecology naturally follow from these comparisons. For example, how efficient are they? How much prey and water do they filter? In the following, I will use the data I obtained during the present thesis work to start addressing these questions.

Assuming a body weight of 30 ton in a humpback whale and a maximum engulfment volume

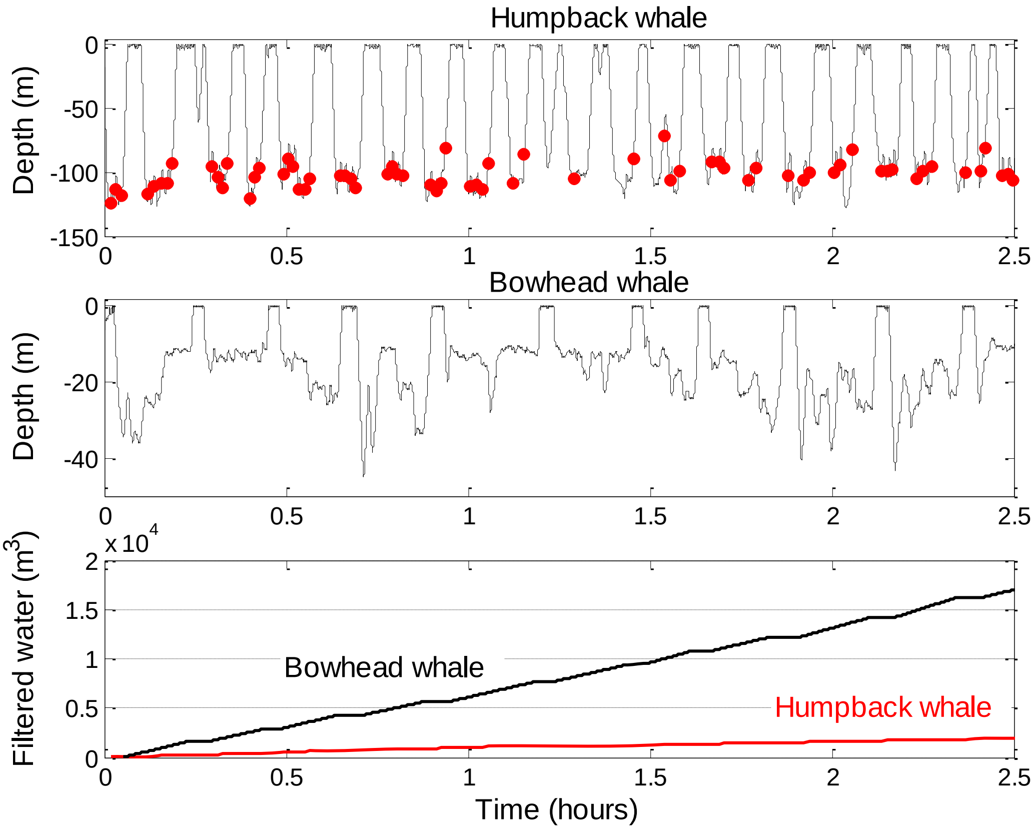


Fig. 13. A. Dive profile from humpback whale tagged with a DTAG in Nuuk fjord. The red dots indicate lunges detected from the accelerometer sensors. B. Dive profile of bowhead whale tagged with a DTAG. C. Estimated accumulated filtered water of Black: Feeding bowhead whale assuming a cross sectional gape area of 4.23 m^2 (Werth 2004) and a speed 0.75 ms^{-1} and Red: Lunge feeding humpback whale assuming engulfment volume of 30 tons per lunge.

equaling the body volume (Goldbogen et al. 2009), I estimated that a feeding humpback whale would filter an accumulated volume of prey-laden water of less than 1000 tonnes pr hour of continuous feeding dives (Fig. 13). For comparison I used the estimated foraging speed of 0.75 ms^{-1} (Chapter 2) and a cross- sectional gape area of 4.23 m^2 (Werth 2004) to reveal the filtering rate of 3.2 m^3s^{-1} when a bowhead moves forward in continuous ram filtration (Chapter 2). Using this result I estimated that a bowhead whale filters an accumulated water mass of around 6000 tonnes per hour of continuous feeding dives (Fig. 13, Chapter 2). Does this mean that the bowhead feeding strategy is more efficient than that of humpback whales?

This question is closely linked to the prey and carbon density of the feeding patches. Logistic challenges make it difficult to get the spatial and temporal resolution to reliably estimate the prey density of the engulfed water masses for feeding baleen whales. Instead prey density has been estimated from trawls and hydroacoustic surveys in areas of feeding whales (e.g. Dolphin 1987; Sameoto 1983; Laidre et al. 2007; Baumgartner et al. 2003). The prey densities near feeding balaenopterids are in the range of 0.01–0.5 kg m^{-3} (Dolphin 1987; Sameoto 1983; Piatt and Methven 1992) whereas copepod densities near feeding balaenids are in the range 0.001-0.01 kg m^{-3} (Mayo and Goldman 1992; Beardsley et al. 1996; Laidre et al. 2007; Chapter 2) more than tenfold lower than balaenopterid prey patches. Though some of these estimates are likely to be underestimates of the actual prey density in the filtered water, the relative estimates of balaenid and balaenopterid prey densities suggest that one reason for balaenids filtering much more water per hour could be that their target prey species occur in lower densities than balaenopterid prey. Moreover, when discussing the efficiency of the two strategies, the energy budget should be taken into account; how much time is spent feeding, searching for food and what is the energetic cost per ingested calorie? One way to approach questions of energetic budgets is to use DTAGs. This is further elaborated in section *1.6, Future research* of this introduction.

All filter feeding marine animals from zooplankton to the largest whales have to filter a certain volume of water for prey to maintain a viable population (Kiørboe 2010). It might seem intuitive that the clearance (volume of water cleared $ind^{-1}d^{-1}$) of relative body volume (BV) decreases with size. However, the fact is that a clearance rate of 10^6 BVd^{-1} relatively size is independent across a wide range of body sizes from $5x10^{-3}$ to 5 cm (Fig. 14B; Kiørboe 2010). Large vertebrate filter feeders, like sharks and whales, with clearance rates of only 800-10,000 BVd^{-1} do not fit this rule (Fig. 14A). Actually, for a 90 ton bowhead whale to fit the rule, it should filter $90x10^6$ ton d^{-1}. In reality, they filter a thousand times less than that (Fig 14B, chapter 2). Why do the filter-feeding vertebrates not fit the Kiørboe rule?

First of all, the size independent clearance rates are explained by the fact that prey size generally increases with body size; thus the available biomass of food as a proportion of the predator biomass will not increase (Oleson 1995). Common for all whale and shark filter feeders is that they specialize in filtering zooplankton from the water, taking advantage of the large biomass at the lower trophic levels (Werth 2000). Secondly, in contrast to the planktonic organisms described by Kiørboe (2010), the whale and shark filter feeders can actively localize and move between high density prey patches at relatively low costs due to their high Reynold’s numbers (Brodie 1978). Thus, vertebrates are most likely able to maintain their large bodies despite the low specific clearance rates, because they developed means of actively searching for and locating high density prey patches. However, how baleen whales locate these prey-patches on very large spatio-temporal scales is one of the key questions for understanding the ecological role of large marine predators. In the following I will discuss different prey localization theories in relation to my own observations in West Greenland.

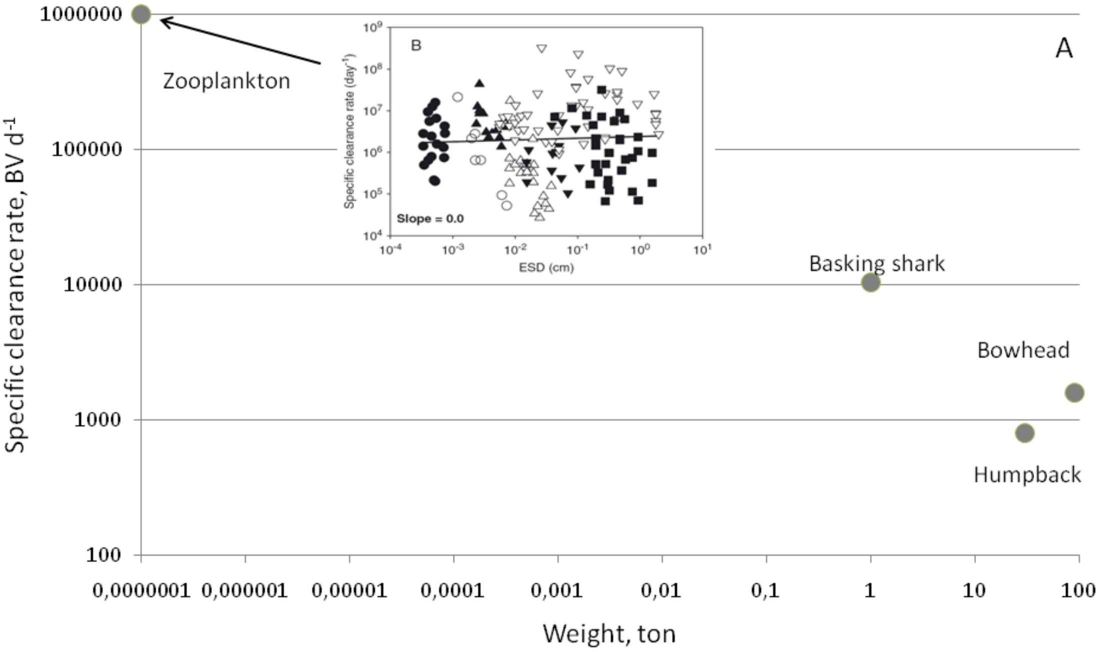


Fig. 14. A. The relationship between the specific clearance rate and body weight for filter feeding zooplankton, sharks and whales. B. The specific clearance rate for nanoflagellates (black round), dinoflagellates (white round), ciliates (black upward triangle), ciliated metazoans (white upward triangle), copepods (black downward triangle), fish larvae (white downward triangle) and jellyfish (black square) is 10^6 body volumes, independent of body size (ESD= equivalent spherical diameter) (modified from Kiørboe 2010).

1.3 Prey localization

Filter feeding baleen whales depend on finding high density aggregations of prey above a certain threshold to sustain their large body size by filter feeding (Brodie et al. 1978; Piatt and Methven 1992). The marine ecosystem off West Greenland is highly dynamic and baleen whale prey are patchy both in time and space (Chapter 7). The sensory means used by baleen whales to find prey patches are largely unknown, but might vary with the temporal and spatial scales from long-distance seasonal migrations over periods of months to minute–by-minute decisions about when to open the mouth (Kenney et al. 2001). Here, I will use the four spatio-temporal categories: *Basin-scale*, *Regional-scale*, *Meso-scale* and *Micro-scale*, defined by Kenney et al. (2001) to outline proposed hypotheses about baleen whale prey localization. Thereafter, I discuss selected hypotheses with most relevance to the topics of this thesis in the light of data from West Greenlandic baleen whales. Finally I will outline and discuss prey-herding as a means of increasing prey density for more efficient prey engulfment.

Basin-scale (1000s of kilometers)

The proposed sensory clues necessary to repetitively navigate half-way around the globe between feeding and breeding grounds in all likelihood include topography (Pike 1962; Norris 1967), the sun as navigational cue (Pilleri and Knuckey 1969), oceanographic conditions (Norris 1967), passive acoustic navigation using natural low-frequency sources (Norris 1967), and coarse-scale echo-location (Norris 1967; Ellison et al. 1987; Würsig and Clark 1993

In addition, Payne and Webb (1971) proposed the theory that fin whales live in a “range-herd” society where individuals are in acoustic contact by their long-range 20 Hz song (described in Chapter 8). They argued that fin whales living in acoustically interconnected range-herd societies would actively search vast areas for high resource patches in a cooperative effort. This would be especially advantageous when feeding on patchy dynamical prey that is not reliably linked to the same geographical area year after year.

Regional-scale (10s to 100s of kilometers)

Baleen whales seasonally navigate from near the Equator to their specific feeding grounds. Matrilineal transfer of knowledge is the primary hypothesis for explaining the site fidelity to the feeding grounds seen in humpback (Weinrich 1998) and right whales (Malik et al. 1999; Brown et al. 2001), where mothers may transfer knowledge on the migratory route and navigation between the breeding and feeding grounds to the calves (Weinrich 1998). This is likely to be aided by similar cues as mentioned under *Basin-scaled* navigation, such as ocean currents, topographical features, passive acoustics for low frequency natural sound sources etc.

Besides sensory cues, maternally transferred knowledge about high quality feeding areas within the feeding grounds may provide whales with a network of places that are worth visiting during the feeding season. The notion of dedicated movements between potentially high quality feeding areas in search for food is supported by the tracks of humpback whales tagged with satellite transmitters in West Greenland. The whales stayed in a focal area for 1-4 weeks and then rapidly moved to another feeding area (Fig. 15, Heide-Jørgensen and Laidre 2007b). The authors hypothesized that the movement pattern could be a response to knowledge about dynamic changes in prey availability.

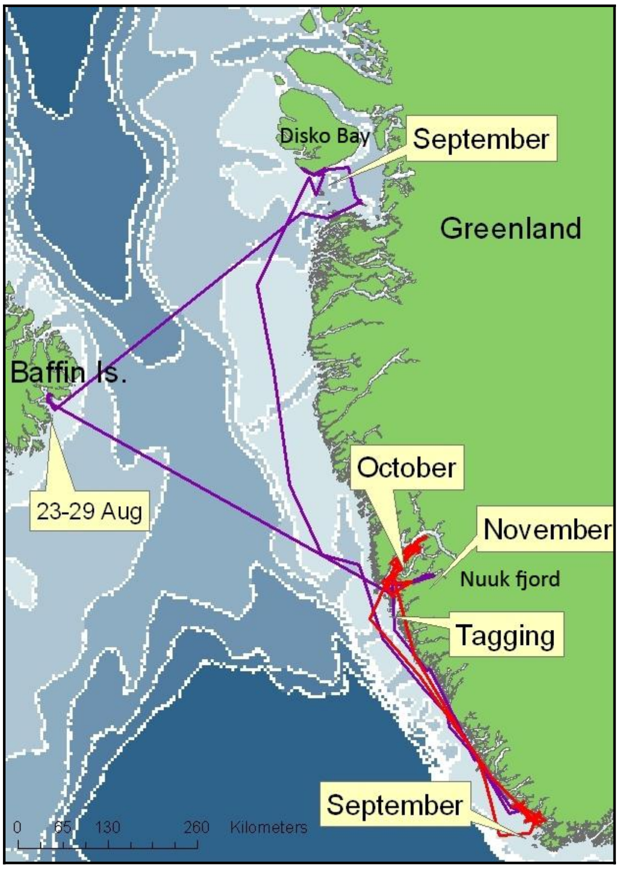


Fig. 15. Tracks of two humpback whales tagged in West Greenland with satellite transmitters. The whales travel long distances to visit potential feeding areas.
Modified from Heide-Jørgensen and Laidre 2007b.

In chapter 7, my co-authors and I combined the data from an aerial survey off West Greenland (Chapter 6), a ship based survey of Southeast and West Greenland (Chapter 5) and a hydroacoustic / trawling survey for capelin and krill (Bergström and Vilhjalmarsson 2007). From this we concluded that, on a regional scale during daytime in September, distribution of large whales was influenced by the distribution of krill at depths larger than 150m. This suggests that the whales are able to sample a large portion of the water column, including depths of more than 150m.

Meso-scale (1 to 10 kilometers)

Baleen whale prey aggregations are highly dynamic in space and time and some areas have a higher probability of containing worthwhile prey patches than others. A feeding ground may consist of a network of feeding sites of various qualities.

To detect prey aggregations on this scale the whales may use chemosensory trails from aggregations of copepods and krill (Thewissen et al. 2010), as tube-nosed sea birds are able to do (Nevitt 2008). In addition, acoustic cues may be important, since information on prey patches may be obtained by eavesdropping on feeding sounds from other predators, by intraspecific communication advertising feeding spots (Vaughn et al. 2008; Payne and Webb 1971; McGregor 2005) or by passively listening for sounds produced by the prey aggregations themselves (Tyack & Clark 2000). Finally, large objects can possibly be detected by their modifications of the ambient noise field, so-called Acoustic Daylight

Ocean Noise Imaging (Buckingham et al. 1992), which may have potential as a way for large whales to detect large prey aggregations in the ocean.

Simultaneously with genetic sampling, Croll et al. (2002) recorded the intense 20-Hz fin whale song (described in Chapter 8) from feeding fin whales and showed that only males were singing. Based on this, he hypothesized that in the mating season fin whale males may find a good feeding patch, and then sing to advertise the patch, attracting possible mates (Croll et al. 2001). Besides a con-specific advertising prey patches, the prey aggregation itself may provide acoustic cues for localization.

Many marine species produce sounds (Richardson et al. 1995) and large aggregations of such animals are likely to generate high sound levels. It has been suggested that baleen whales might use passive listening to find such aggregations of sound producing prey (Tyack and Clark 2000). One initial aim of this PhD was to investigate the possibility of passive listening as a prey localization strategy for baleen whales. However, early on I realized that the task was challenging due to difficulties in localizing and recording the prey animals with the limited boat time I had funding for. I made sound recordings near schools of capelin, a key prey species to most marine predators in West Greenland (Fig. 15; Hedeholm 2010), but I could not unequivocally attribute any detectable sound signals to the capelin before the fish actually physically touched the hydrophone. Thus at present I cannot say if capelin produce any sound signals useful for passive acoustic detection. Besides sensory means, knowledge on good quality feeding areas within the feeding grounds may also be transmitted maternally when the calf is still traveling with the mother. I will now discuss this hypothesis in the light of data from West Greenlandic humpback whales.

Photo identification is a widely used well-established method of identifying individual cetaceans from natural markings on their bodies (Würsig and Würsig 1977; Würsig and Jefferson 1990; Katona et al. 1979). From photo identification pictures we found that some humpback whales show strong small-scale site fidelity to Nuuk Fjord (Chapter 4). Though Nuuk Fjord is one of the largest fjord systems in the world, it still comprises a very small part of the entire West Greenlandic feeding grounds. The results presented in chapter 4 are based only on resightings between 2007 and 2008. However, data from 2009 and 2010 show similar resighting rates and support the conclusion that humpback whales do have small-scale site fidelity to Nuuk Fjord, as has been indicated for other parts of the world (Unpublished data, GINR; Clapham *et al* 1993).

The small scale site fidelity reported in chapter 4 demonstrates that individual migrating humpback whales have navigational skills that allow them to find a fjord entrance that is less than 10 km wide. In chapter 4 we also show that the humpback whales in Nuuk Fjord, despite a

Fig. 16. Local market in Nuuk. Capelin, a key species in the West Greenlandic ecosystem are seasonally abundant near the coast, where all top predators enjoy the abundant fish. Photo: Carsten Egevang/ARC-PIC.com

strong degree of small scale site fidelity, do not reside in the Nuuk area for the entire feeding season but migrate between foraging areas. These results, in combination with resightings from individuals photographed in multiple feeding areas within one season (e.g. Nuuk fjord and Disko Bay) and satellite tracking (Fig. 15, Heide-Jørgensen and Laidre 2007), strongly support the hypothesis that humpback whales transit between a network of high quality feeding areas within the West Greenlandic feeding grounds throughout the season.

Such a foraging behavior makes sense in the view of the dynamic nature of some of the West Greenlandic food resources. For example, capelin is a key species in the ecosystem (Hedeholm 2010) and a key prey species for humpback whales in spring. That notion is supported by stomach samples, surface observations of feeding whales and the fact that humpback whales usually arrive in Nuuk Fjord within the same week when shoals of capelin approach the coast for spawning in spring (Unpublished data, GINR; Kapel 1979). The capelin spawn close to shore in the protected fjords of West Greenland. The spawning is temporally segregated, starting in April at the southern tip of Greenland and ending North of Uummannaq in the fall (Hedeholm 2010). In Nuuk fjord, capelin spawns in May, and top predators including humpback whales, harp seals, predatory fish such as cod, and humans feed on this abundant and rich food source (Fig. 15).

Micro-scale (centimeters to 10s of meters)

Filter feeders have extensive energetic costs from drag when opening their mouths during swimming (Acevedo-Gutiérrez et al. 2002; Werth 2004). To save energy, baleen whales must have a set of sensory means to gather information on when it is worthwhile to engage their filtering apparatus (Chapter 2 and 3). Sensory modalities may include vision, tactile sense, acoustics such as passive listening and echolocation (Kenney et al. 2001). This scale of prey localization is especially relevant to chapter 2 and 3 of this dissertation, dealing with the kinematics of filter feeding humpback and bowhead whales.

Fig. 17. Humpback whale bi-caught in a crab fishery in Nuuk, 2005. The arrow points at a hair sitting at the top of a tubercle. Photo: F. Ugarte

The use of vision might seem obvious and should work for animals feeding near the surface. However, many baleen whales feed at night and at great depths with little light (Goldbogen et al. 2006; Croll et al. 2001; Chapter 3), thus vision is unlikely to be the only cue. Baleen whales have tactile hairs placed at different areas of the head, depending on the species (Fig. 17). These hairs are likely to be of use in sensing the density of a prey field as the foraging whale passes through, probably aiding ram filtrators in deciding when to open and close their mouths and lunge feeders in deciding when to perform a lunge (Kenney et al. 2001).

Finally, cetaceans generally have well developed acoustic senses. Echolocation is well understood in toothed whales that use self-generated echoes for navigation and prey localization (Au 1993;

Madsen et al. 2005). Due to the low frequency long duration characteristics of baleen whale sounds, these signals have mainly been proposed to aid in long-distance detection of large ocean features such as continental shelves and seamounts and icebergs (Patterson and Hamilton 1964; Clark 1989). However, recently Stimpert et al. (2007) recorded clicks produced by foraging humpback whales in the Gulf of Maine with onboard DTAGs (Johnson and Tyack 2003). Based on the temporal pattern in interclick intervals, resembling echolocation clicks of odontocete, the authors suggest that these humpback whales might use echolocation during night time foraging (Stimpert et al. 2007). However, due to the low frequencies, long duration and low intensity, I argue that the signals described by Stimpert et al. (2007) are more useful in herding prey rather than for echolocation. Secondly, I did not record any click sounds like those described by Stipert et al. 2007 from the feeding humpback whales in West Greenland. I will now turn to prey herding

Prey herding

In addition to finding prey concentrated in high densities, predators can pack prey schools into dense prey balls, increasing feeding efficiency. This herding behavior has been described from several species of cetaceans, such as dusky dolphins that cooperatively herd fish into near surface prey balls (Vaughn et al. 2007). Herring-eating killer whales herd herring into tight schools using air bubbles, flashing white parts of their bodies, and emitting loud herding-calls, all of which trigger the schooling behavior of the fish and results in densely packed prey balls (Similä and Ugarte 1993; Simon et al. 2006). Among the baleen whales, the humpback whales are the masters of prey herding behaviors, such as bubble-net feeding, which I also observed from feeding humpback whales in West Greenland. Humpback whales in Alaska produce a long duration, low frequency call when feeding on herring (D'Vincent et al. 1985). The call is similar to the herding-call used by herring-eating killer whales (Simon et al. 2006), tuned to the optimal hearing frequency (i.e. resonance frequency of their swimming bladder) of their prey. The sounds trigger schooling behavior of the fish (M. Wilson pers comn) before prey capture (humpback whale lunge) or immobilization (killer whale tail slap). Packing prey into tight densities provides another explanation for the low clearance rates in baleen whales (Fig 14, section 1.2.). If the whales pack the prey from a larger volume of water, they seem to be filtering just the engulfed volume, but in fact they cleared a volume much larger due to the herding.

During this thesis work, I made 54 hours (n=18) of sound recordings of feeding humpback whales in the hope of documenting a West Greenlandic version of the Alaskan herding calls. These recordings also included cooperative feeding of up to 3 whales. However, the West Greenlandic humpback whales were silent, and the question is then, why? Capelin and sandeel are believed to be the most important prey for West Greenlandic humpback whales (Kapel 1979). They belong to the families of *osmeridae* and *salmonidae* and as such are expected to have very poor hearing abilities (Hawkins and Johnstone 1978). If the fish are unable to hear an acoustic signal it will have no herding effect, possibly explaining the lack of acoustic herding in West Greenlandic humpback whales.

In summary, baleen whales most likely use a combination of several means to locate temporal and spatially dynamic prey aggregations, which is likely to vary with the ecological context such as prey species, distance to prey and ambient noise levels (Kenney et al. 2001). These means may include cultural transmission of knowledge on high quality feeding spots or from own experience, advertising calls from conspecifics, passive listening to prey sounds, chemical cues (smell/taste), tactile sense, etc. Given the few data on baleen whale sensory abilities, reviews of the hypotheses are largely speculative (Kenney et al. 2001). However, I hope that future research will focus on this interesting topic, because the better we understand the suite of means that baleen whales rely upon to migrate and locate food the better we can mitigate disturbances from anthropogenic activities, and understand the ecological driving forces that led to baleen whale feeding in time and space.

I will now turn to discuss correlations in the spatial distribution of baleen whales and their potential prey in the West Greenlandic feeding grounds.

1.4 Spatial distribution and ecological studies of baleen whales and their prey

Distribution and density of prey are likely to be the most important factors controlling baleen whale abundance and distribution in their feeding grounds (e.g. Croll et al. 2005; Friedlander et al. 2006). Despite these presumed direct distributional links between high and low trophic levels, few studies take a multi-species ecosystem-based approach (e.g. Simard & Lavoie 1999; Croll et al. 2005; Friedlaender et al. 2006). One reason for this is the logistic difficulties and costs involved in investigating pelagic marine ecosystems over appropriate temporal and spatial scales. The harsh environment of the Arctic adds to these difficulties. Factors such as primary production, salinity, temperature, currents, distance to sea ice, and topography affect the distribution and abundance of baleen whale prey (Croll et al. 2005). As an alternative to prey distribution, these indirect measures are often used in apparent correlation to the distribution of marine mammal predators when studying pelagic ecosystems (e.g. Harrison et al. 1990; Elphick & Hunt 1993; Kenney et al. 1995; Tynan 1998). However costly, hydroacoustic surveys can indeed be combined with sighting surveys of baleen whales, and several studies have found positive correlations between baleen whale distribution and the distribution of one or more prey species (e.g. Simard & Lavoie 1999; Croll et al. 2005; Friedlaender et al. 2007). These results can provide new levels of insight into the distributional dynamics between predators and lower trophic levels. However, it is important to keep in mind that causality does not necessarily follow from a correlation. For instance, a distributional correlation between predator and prey species does not necessary mean that the spatial patterns in predator abundance were caused by abundance of the prey.

Estimates of baleen whale abundance in West Greenland are aimed at providing management advice for the aboriginal subsistence whaling scheme from the International Whaling Commission (IWC). This was also the primary aim for the surveys presented in chapters 5 and 6. We successfully provided the first reliable baleen whale abundance estimates in more than a decade (IWC 2007). The ship-based survey (Chapter 6) was carried out using a fisheries research boat as a platform of opportunity, following east-west transect lines (Fig 18B). This provided a unique opportunity to combine our data on large whales with the trawl and hydroacoustic backscatter data from krill and capelin, some of the main prey species of balaenopterid whales (Chapter 7). Combined multi-disciplinary ecological studies are rare in West Greenland, and to my knowledge Chapter 7 was the first involving balaeopterid predators.

The simultaneous ship-based and plane surveys (Chapter 5 and 6, respectively) showed that the highest density of whales in September 2005 in the off-shore area in West Greenland was the northern edge of Lille Hellefiske bank between 65°and 67°N, where humpback, fin, sei and minke whales were observed. In addition to this apparent hot-spot, the whales were concentrated north of Paamiut (at 63° N) and in South Greenland in Qaqortoq Bay, between 60° and 61°N (Fig. 18A). This distributional pattern raises the simple question of: Why did these areas stand out with a high presence of baleen whales?

As mentioned above, the observations from the ship-based platform were collected simultaneously with a hydroacoustic survey targeting capelin, but with the multi-frequency echo-sounder collecting backscatter data from krill aggregations as well (Chapter 7). Regression models were developed to identify possible explanatory variables relating the presence, absence, and density of large whales to the physical and biological environment and the two different survey platforms (Chapter 7). Models indicated that the most important parameter in predicting large baleen whale presence was the integrated krill abundance at depths of more than 150m, suggesting a threshold depth below which it is energetically feasible for baleen whales to forage on krill in West Greenland during daylight. As a comparison, figure 18B shows the distributional abundance of krill and capelin in the survey area. The correlation between whale and krill abundance does not necessarily imply that the whales are there feeding on krill. However, the fact that krill made up a substantial part of the stomach contents of humpback and fin whales caught at the offshore West Greenlandic banks in 1956-1976 (Kapel 1979) supports the notion that the observed whales were feeding on krill. The whale observations used for the analysis were made during daylight (Chapter 5 and 7). As krill migrate toward the surface during the hours of dark (Sourisseau et al. 2008) it is likely that the depth of the most predictive krill biomass would shift towards the surface during night-time.

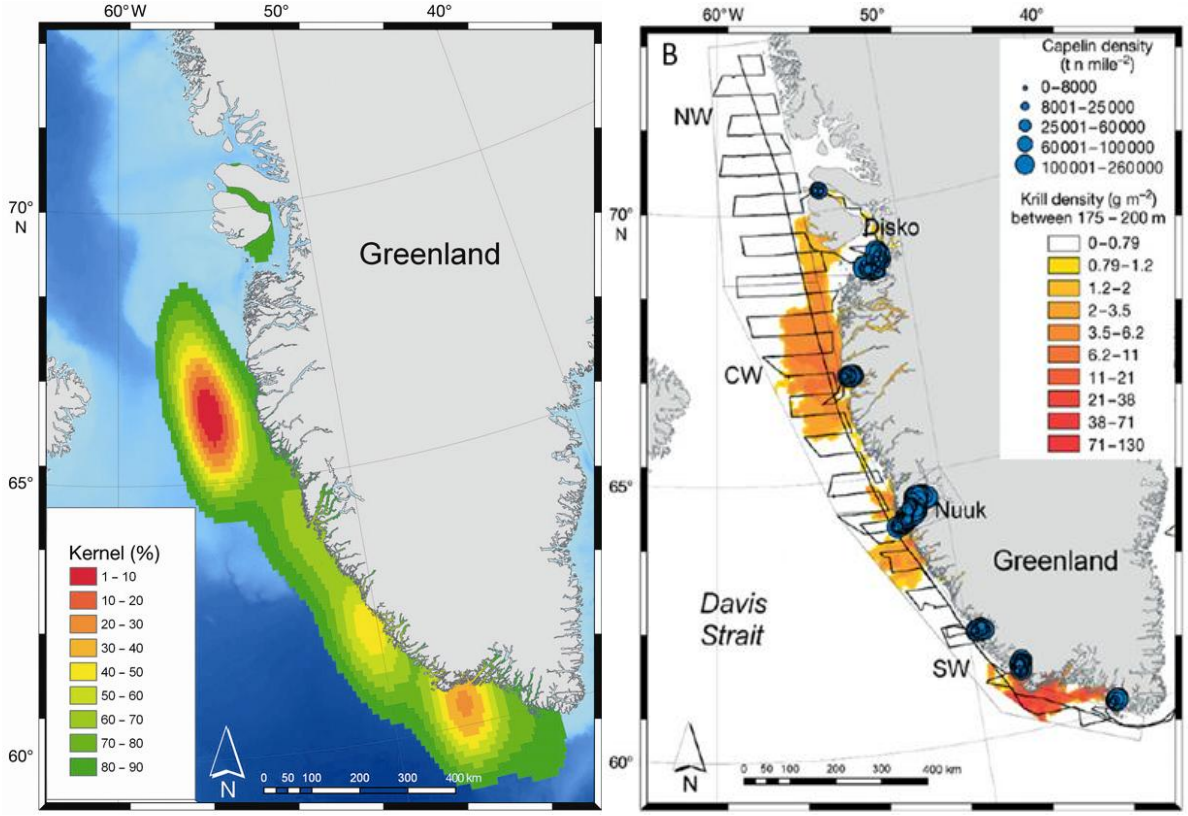


Fig. 18. A. Kernel density estimation in 10% intervals for all sightings of baleen whales from both aerial (Chapter 5) and ship-based surveys (Chapter 5). B. The offshore krill density with the density given in red to yellow color scale. Capelin density given by the blue rings, and the black lines are the transect lines for the krill and capelin survey. Figures from chapter 7.

As an institution that provides the government with management advice, the Greenland Institute of Natural Resources is regularly asked questions such as: How much do the whales eat? And how do whales affect the ecosystem? Should they be seen as competitors to fisheries? How will climatic changes in the ecosystem affect the whales? These questions are very hard to answer, especially on the basis of our poor ecological knowledge of the region. We simply do not know enough about the abundance of different species, prey composition and the quantitative links between trophic levels.

Capelin, krill and sandeel are considered key prey species for balaenopterids in West Greenland. This is based on data from stomach samples (Kapel 1979) and surface observations. Other than this basic knowledge, little is known about the prey composition of balaenopterid whales in Greenland. Chapter 5 and 6 provide abundance estimates for four species of balaenopterid whales, including the first abundance estimate for sei whales. Chapter 7 provides the first biomass estimates of krill and capelin in West Greenland. The capelin estimate was based on partial survey coverage of only 7 fjords representing a fraction of the entire capelin habitat of fjord systems (Fig. 18B). Thus the estimate of capelin biomass of $2x10^5$ tones is grossly underestimated. Sandeel is also a presumed important prey species for apex predators in West Greenland. However, besides a report from an experimental fishery in 1978 (Andersen 1978) and studies of distribution of larvae (Munk 2002; Simonsen et al. 2006), almost nothing has been published about the abundance and ecology of West Greenland sandeel.

Clearly, there is a large demand for quantitative knowledge about the basic links and processes of the West Greenlandic ecosystem. This knowledge is needed to answer simple ecological questions, to provide more ecosystem-based advice for international management boards (as requested from IWC and NAMMCO) or to predict how climate changes may affect the ecosystem and species composition of lower trophic levels cascading up to the prey composition and availability to large apex predators. With chapters 5-7 my co-authors and I covered some of the unknown ground concerning the diversity, abundance and ecology of balaenopterids in the West Greenlandic feeding grounds.

One way to gain more diverse knowledge on the dynamics of the West Greenlandic ecosystem is to investigate alternative methods and logistical solutions. Traditionally, sighting surveys are used to estimate the abundance and distribution of balaenopterids in West Greenland (E.g. chapter 5 and 6). However, the survey effort is limited by the weather, sea ice, daylight, fog, as well as the great costs involved. Aerial surveys for large whales in West Greenland are carried out in late summer and early fall, when sighting conditions are best. Thus, our knowledge of baleen whale distribution is limited to this period of the year, leading to a severe bias. Passive acoustic monitoring (PAM) has increasingly been used world-wide as an alternative and complimentary method to monitor baleen whale distribution and relative abundance (Clark 1995; Mellinger et al. 2007). Passive acoustic monitoring might be limited on a spatial scale, but contrary to sighting surveys PAM gives a good temporal resolution and coverage as recordings can be carried out continuously for a whole year in all weather and light conditions. In chapter 7, my co-authors and I tested the potential for PAM in West Greenland by deploying four moorings across the Davis Strait.

1.5 Tracking the seasonality of baleen whale song in the Davis Strait with PAM

Passive acoustic monitoring (PAM) is increasingly used as a tool to study the presence, relative abundance, migratory movements and behavior of large baleen whales (e.g. Moore et al. 2006; Mellinger et al. 2007). In addition, PAM has recently proven useful in combination with remote sensing and oceanographic data loggers to investigate the relation between marine mammal behavior as inferred from acoustic data and environmental factors such as chlorophyll a, temperature and sea ice (Stafford et al. 2009; Chapter 8). Acoustic data loggers moored on the seabed provide a continuous record of the occurrence of vociferous animals over long time periods. Due to the low frequencies of their species-characteristic sounds, baleen whales are especially suitable for long-term acoustic monitoring, as sampling frequency can be kept low, increasing the monitoring period. Furthermore, due to the low frequency and high intensity, signals of baleen whales propagate for long distances, allowing for monitoring large areas (e.g. Payne and Webb 1971; Clark and Ellison 2004).

FIG. 19. Acoustic recorder deployed from KNORR R/V in Davis Strait, 2006.
Photo: K. Stafford

In my PhD I set out to investigate the potential for monitoring baleen whales in West Greenland and the Davis Strait with the use of passive acoustics. The published and preliminary results were promising and indicate that there is a large unexplored potential in investigating the distributional and behavioral ecology of baleen whales and other vociferous marine mammals in the area with the use of PAM.

Acoustic and oceanographic instruments were deployed as part of a large bottom-moored oceanographic array across the Davis Strait (Fig. 19 and 20). Three recorders were deployed in 2006 and recovered in 2007, and a single recorder was redeployed in 2007-08 (see Chapter 8 for details of the methodology). So far, signals from five species of baleen whales have been identified in the recordings: blue, sei, humpback, fin and bowhead whales. Due to lack of time minke whale sounds have not yet been analyzed, and thus may or may not have been recorded. In addition, calls of bearded seals and the lower frequencies of some toothed whale signals were recorded, but they were not analyzed for the present work, where I am focusing on the baleen whales.

Species identification

Given the species composition of the Davis Strait, it is generally straight forward to identify the species from their calls. However, bowhead and humpback whale songs seem more challenging. Likewise, the sei whale low frequency calls can be confused with the 20 Hz fin whale song (Watkins 1981; Thompson et al 1992; Cummings et al 1986; Rankin & Barlow 2003). When I was in doubt about the species, I looked at temporal cues, such as inter-call- intervals, and discussed the signals with collaborators with long-term experience with PAM on baleen whales. I was not expecting any confusion between bowhead and humpback whale song because the bowhead is an ice-associated species that uses the eastern part of Davis Strait during the winter and spring, while the humpbacks come to Greenland during summer and fall. However, we recorded humpback whale song in the late winter, and not bowheads. I did not expect this and was therefore uncertain about the species identification of the signals. However, it was verified that the sounds were indeed humpback whale songs, as they were similar to humpback whale song recorded on Stellwagen Bank, US, in the same year (S. Van Parijs, Pers comm). The recordings during late fall and early winter of conspicuous summer visitors such as fin and humpback whales are clear examples that we should avoid making assumptions based on previous knowledge of seasonality during the species identification process, even though it may be tempting to do so.

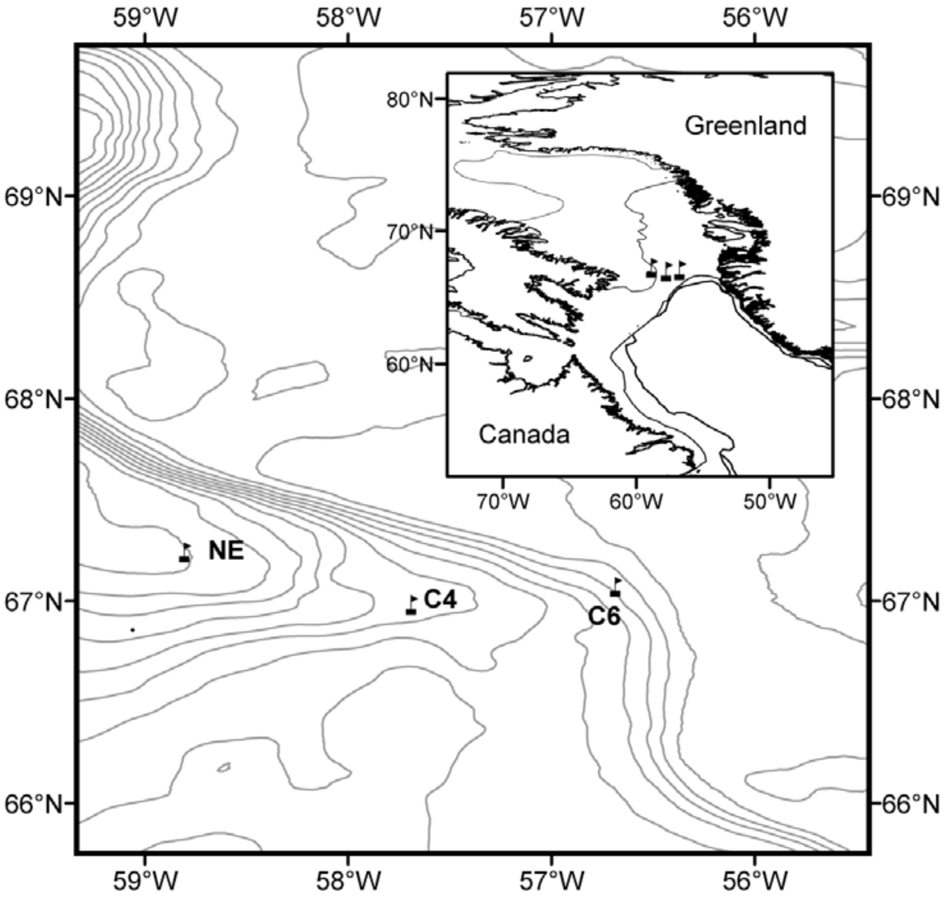


Fig. 20. Locations of the three instruments deployed at 300m depth in the Davis Strait. The monthly extension of the sea ice edge from November 2006 to March 2007 is shown as lines in the inset map.

Acoustic detection of baleen whales in Davis Strait

For this thesis I mainly focused on fin whale song (Chapter 8), revealing new information about the seasonality, behavioral ecology and correlation between acoustic activity and sea ice. The recordings in the Davis Strait constitute a large data set on the seasonality and behavioral ecology of baleen whales. In the future, my collaborators and I intend to analyze the detection patterns of the other four species; bowhead, humpback, sei and blue whales using similar methodology as for fin whales in Chapter 8. Here I will first outline the main findings from the detailed analysis of fin whale song. Secondly, I will present the results of the preliminary analysis of seasonal patterns in the acoustic activity from the other four species of large baleen whales in the Davis Strait.

Fin whale: Fin whales were acoustically active in the Davis Strait from June to December. The acoustic power in the fin whale call frequencies peaked in November–December, showing that fin whales are present in relatively large numbers much later in the year than previously thought. A clear annual peak in fin whale singing activity lasting for about four months has been reported from the northern and southern hemisphere (Watkins et al. 2000, Sirovic et al 2009). This seasonal peak in fin whale song coincides with the estimated conception time of fin whales, suggesting that the song is part of a mating display, possibly to attract mates (Watkins et al. 1987; Croll et al. 2002). This hypothesis has been further supported by the fact that only males have been reported to sing (Croll et al. 2002). The contemporaneous peaks in song activity and estimated conception time in the Davis Strait suggest that not all fin whales migrate south to mate, but rather that some stay at high latitudes perhaps to exploit food niches that are not available at lower latitudes while mating (Chapter 8). This notion is supported by the fact that the singing activity of fin whales in the Davis Strait is strongly linked to daylight hours, and could be controlled possibly by the vertical migratory behavior of their prey (Stafford et al. 2005; Chapter 8). This suggests that fin whales might feed during the few daylight hours of the late fall and early Arctic winter. Finally, there was a negative correlation between fin whale calling and sea ice coverage, suggesting that fin whales remain in the Davis Strait until the sea ice covers the area, after which they move south (Fig. 21).

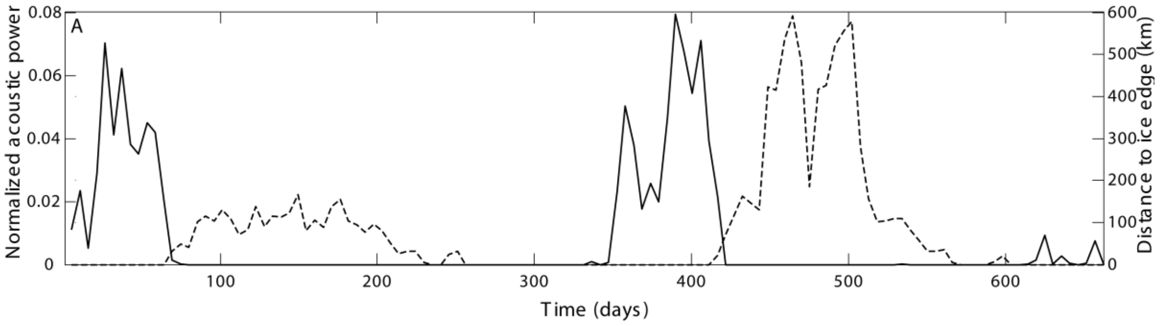


Fig. 21. Dynamics of normalized power in the fin whale frequency bands and the distance to the ice edge (broken line) when the sea ice edge has covered the mooring. The distance was set to zero when the sea ice edge was north of the mooring. All data was computed as the mean of 5 days.

Blue and sei whales: The acoustic detection of blue and sei whales had a strong seasonal pattern that overlapped in time (Fig. 22 RED and GREEN). Both species were acoustically active in the Davis Strait in August-September. Sei whales were also observed from the sighting surveys in West Greenland in August-September (Chapter 5). Few observations has been reported on blue whales in the Davis Strait and West Greenland and they were not observed during the years the West Greenland surveys were conducted (Chapter 5-6). The most recent visual report was in May 2009 in Disko Bay (K. Laidre pers. comm).

Humpback whales: Humpback whales produce a large variety of sounds, ranging from long mating songs at the breeding areas (Payne and McVay 1971; Tyack 1981) to grunts, moans and pulse trains at the feeding grounds (Thompson et al. 1986; Stimpert et al. 2007). In the Davis Strait, we have not detected any feeding sounds from our recordings. However, we have not yet thoroughly searched for feeding sounds of humpback whales either. It is worth mentioning though, that during the 54 hours (n=18) of recordings I made near feeding humpback whales during other field work for this PhD, I detected no feeding sounds. This suggests that the humpback whales actually are silent while feeding in West Greenland. Possible explanations for this could be the poor hearing abilities of the prey (Section 1.3) or killer whale predation (Section 1.1), as discussed earlier in this introduction.

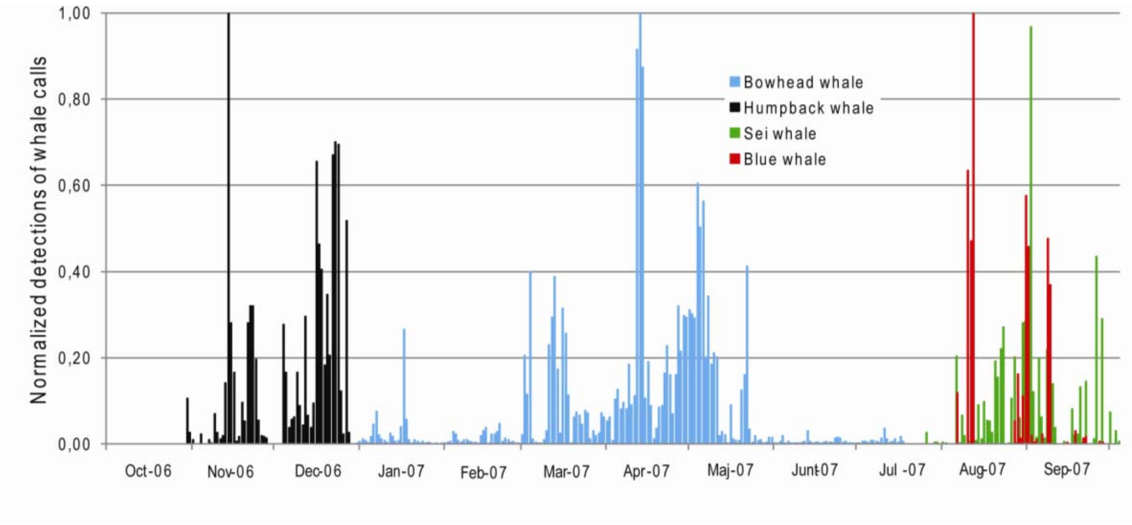


Fig. 22. Seasonality in the detection of Blue whales (red), sei whales (green), humpback whales (black) and bowhead whales (blue).

Even though no feeding sounds were detected, we did detect humpback song. Through November and December humpback whale song was recorded on all three recorders (Fig. 22 BLACK). Humpback whale song is related to courtship behavior where the males sing at the low latitude feeding grounds to attract possible mates (Payne and McVay 1971; Tyack 1981). Although, song at high latitudes has been reported (Clark and Clapham 2004; Stafford et al. 2007), it has to my knowledge not been reported as far north as the Davis Strait and it is an interesting question why these individuals are singing while being so far away from their mating grounds. One explanation could be that they start singing before leaving to the mating grounds. Another, is that the singers are young non-breeding individuals singing due to rise in testosterone levels, even if they are not migrating to the mating grounds (Clark and Clapham 2004). However, these speculative hypotheses would have to be tested and a first step could be to measure hormone levels and identify the sex from biopsy samples taken during winter. Ingebrigtsen (1929) describes a possible breeding ground for humpback whales off Finmark, Norway, north of the Arctic Circle during the start of modern whaling at the turn of the last century. Thus, there is a possibility that humpback whales may indeed mate in the Arctic. However, the fact that the singers recorded in Davis Strait were apparently few suggests that these are more likely to be stragglers leaving late for their southwards migration, or skipping the migration altogether.

Bowhead whales: In contrast to the humpback whales, bowheads are known for their frequency modulated songs in the Arctic (Würsig and Clark 1993; Stafford et al. 2008). In the Davis Strait, bowhead whales were detected from January to May (Fig. 22 BLUE), which is a complete match to the visual data from Disko Bay (Fig. 24). Despite the limitations in frequency range of these recordings, only detecting the lower frequencies of the bowhead whale song (Stafford et al. 2008; Tervo et al. 2009), the preliminary analysis revealed nine different bowhead whale songs. None of the song types occurred in both years. Stafford et al. (2008) recorded three distinct song types from bowhead whales in Disko Bay in 2007. Three of the song types recorded in the Davis Strait matched the three song types recorded in Disko Bay by Stafford et al. (2008) in the same season. The recordings from the Davis Strait strongly indicate that bowhead whales sing during migration across the Davis Strait. This represents a promising potential for using PAM to reveal the presently poorly known path of the bowhead whale migratory route from the Canadian Arctic to West Greenland. The route from West Greenland to Canada in early summer has been well documented with satellite telemetry (Heide-Jørgensen et al. 2006).

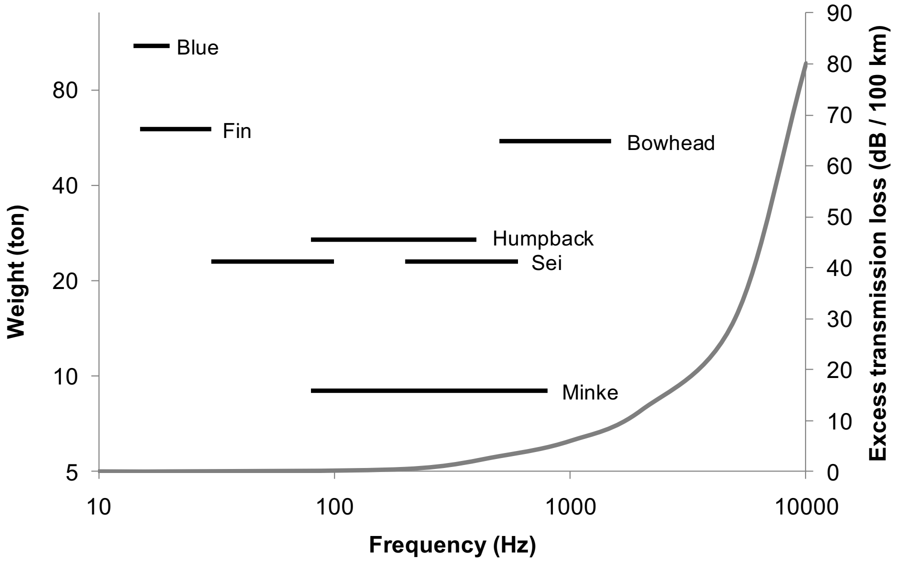


Fig. 23. Relationship between the weight of singing whales and signal frequency. The grey line is the absorption per 100 km at the different frequencies.

Generally there is a negative relationship between the body weight of a baleen whale and the frequency content of their song (Fig. 23; Fletcher 2004); the larger the body mass, the lower frequency the signals. Bowhead whale song covers a broad band of frequencies, higher than would have been expected from the large body mass of bowhead whales (Fig. 23). To investigate the active space of bowhead whale song, my collegues and I recorded singing bowhead whales with a GPS-linked large aperture array deployed from the ice in Disko Bay, March, 2009. Preliminary results show that the source level is about 190 dB re 1µPa rms. This is comparable to source level estimates of fin whale song of 170-190 dB re 1µPa rms (Charif et al. 2002; Thomson and Richardson 1995). However, due to the high frequencies of the bowhead whale song, for which the excess transmission loss is high, the active space is much lower than that of the similar sized fin whales, for example (Fig. 23).

As in all PAM studies, it is important to keep in mind that a lack of acoustic detection does not necessarily mean that no whales are present, only that they are not singing. However, here I showed that a comparison between timing of visual sighting reports and the seasonal patterns in acoustic detection provides a better overview of the presence of marine mammals in the Davis Strait than either of the two methods could do alone (Fig. 24). This is especially true for fin and humpback whales that were detected acoustically outside the time that they were previously thought to be in the Davis Strait. A preliminary comparison revealed a fine temporal match between visual sightings and acoustic detection of blue (though few), sei and bowhead whales (Fig. 24). After describing the seasonality of the acoustic detection, it is natural to ask which factors shape the occurrence of these temporal patterns. In the following paragraphs I will describe how we used PAM to investigate how sea ice may influence the seasonality of fin whales in the Davis Strait.

PAM and sea ice

Širović et al. (2004) reported a negative correlation between the occurrence of fin and blue whale calls and sea ice cover in the Antarctic, implying that the whales move towards lower latitudes when the sea ice forms. Our data corroborated this finding. Starting in November the sea ice expands in the Davis Strait from the northeast, and all three instruments were covered with sea ice from December 2006 to June 2007 (Fig. 20). The differences in the intensity of fin whale signals on the three intruments, with a weak signal on the northern instrument (NE, Fig. 20) compared to instrument C6, suggests that the singing whales were closer to instrument C6, south of the sea ice edge during the peak singing period. This

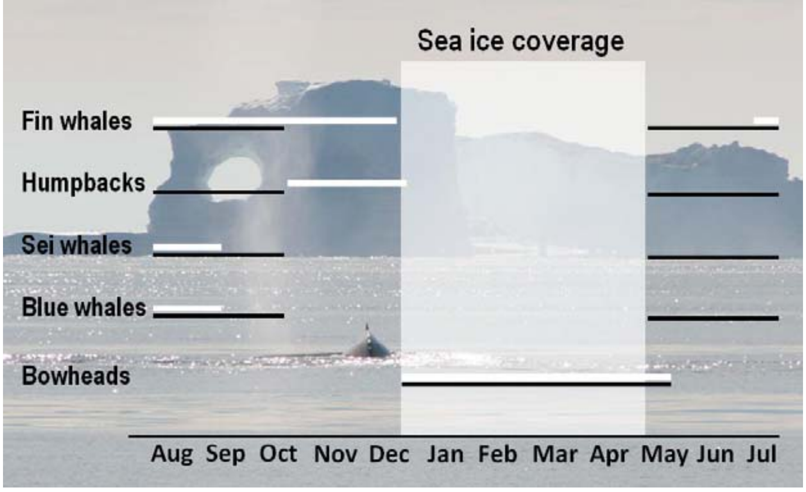


Fig. 24. Seasonality of acoustic detection (white bars) in relation to the visual observations (black bars) and sea ice coverage.

indicates that sea ice dictates the northern limit of the distribution of singing fin whales in the Davis Strait during winter (Chapter 8). We also observed that the short period of intense singing activity ended abruptly by the end of December. Thus, both Antarctic and Davis Strait fin whale calling activity is strongly negatively correlated with the expansion of sea ice (Širović et al. 2009 and Chapter 8), suggesting that similar circumstances exist for singing fin whales near the two poles, where sea ice limits their distribution toward higher latitudes. Changes in the sea ice cover may therefore lead to changes in the distribution of singing fin whales in the Arctic. We showed that PAM is useful in detecting and exploring distributional changes in vocalizing marine mammals in relation to environmental changes such as sea ice coverage. Ice constitutes an environmental feature unique for polar areas, important in forming the habitat of the marine mammals living at high-latitudes. But there is also a significant challenge in the logistics of working in the Arctic as discussed below.

Arctic challenges for passive acoustic monitoring

In the Arctic we face a set of additional challenges when using PAM and icebergs are one of these. Unfortunately, long-term moorings are at serious risk of being dragged away or the intrumentation damaged by passing icebergs. Therefore, icebergs should be accounted for when preparing a PAM project in Arctic locations. However, icebergs are not the only type of ice to affect the animals and PAM. All ice types are highly dynamic structures, and the movement, breaking and melting makes a lot of noise, in some cases dominating the ambient noise level (Richardson et al. 1995).

To illustrate the differences in ambient noise levels in arctic areas, I made several snapshot (10 min) recordings of ambient noise in three different habitats, one of them in two different seasons. Ambient noise levels are normally reported as statistical distributions for long periods covering natural noise level dynamics. Thus the data presented here is not an estimate of the ambient noise in these locations, but an attempt to illustrate the possible ambient noise variations between locations.

The recordings were made with two different calibrated recording systems:

1. B&K-8101 hydrophone (sensitivity: -184 dB re 1V/µPa) on a Digital Audio Tape recorder (DAT, Sony TDC-8)
2. Reson 4032 hydrophone (Sensitivity: -172 dB re 1V/µPa) onto an M-Audio digital recorder.

Each location and season had a set of ambient noise characteristics (Fig. 25):

- Disko Bay in August was characterized by melting ice with a lot of high frequency noise from microbubbles released from the ice (solid blue line)
- Disko Bay in May was characterized by icebergs and no sea ice cover (blue broken line)
- Nuuk fjord in August was characterized by shipping and small-boat traffic (red line)
- Kobbefjord in August was characterized by no ice or traffic (green line)

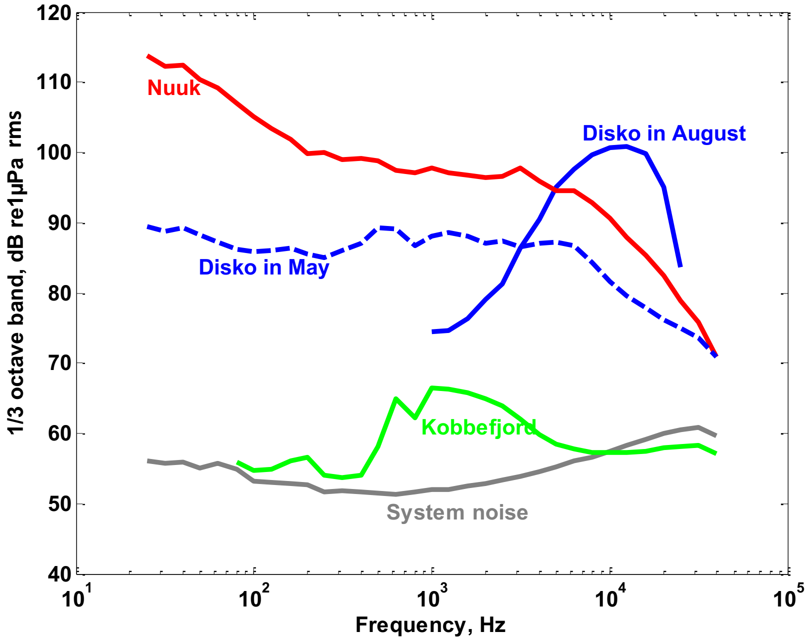


Fig. 25. Snap-shots of ambient noise from different habitats and seasons in West Greenland. The difference in bandwidths is due to differences in recording systems. System noise was measured in an anechoic room at the Danish Technical University of Denmark.

There was a very large variation in the ambient noise profiles between the locations (Fig. 25) with melting ice mainly contributing to the high frequency spectrum (Disko in August), traffic increasing the lower frequencies of the spectrum (Nuuk) and a very low noise level, near system noise (GREY, Fig. 25), in the protected Kobbefjord. Animals moving between these habitats experience large differences in ambient noise affecting the detection ranges of sound signals from e.g. con-specifics and prey. However, these different ambient noise levels and profiles will also affect detection distances by PAM instruments and should be taken into account when investigating detection ranges and relative abundance using PAM. Finally, if we want to evaluate the noise impact from human activities, we need to take these large variations in ambient noise into account and make sure that we have a good base-line description of the ambient noise dynamics in the Arctic.

1.6 Future research

In this dissertation I aimed at answering questions regarding baleen whale acoustics, foraging behavior and distributional patterns of the whales and their prey in West Greenland using multisensor archival tags (D-TAGS), passive acoustic monitoring (PAM) and more traditional techniques, such as sighting and hydroacoustic surveys, theodolite observations and photo-identification. However, many interesting questions still remain unanswered within this field of research, some of which I would like to address in the future. Here, I outline what are to me the most interesting unanswered questions and unmeasured variables of importance in advancing our knowledge of Arctic baleen whales.

Foraging behavior

I presented an analysis of the detailed kinematics and dive behavior of feeding bowhead and humpback whales with estimates of their filtration rates. The next obvious step is to put these results into an ecological framework investigating the overall energy budget of feeding whales while in the West Greenlandic feeding grounds. To do this, three basic questions present themselves: 1. What is the proportion of different prey species? 2. What is the prey density in the filtered water? 3. What is the energetic cost of lunge feeding/ram filtration? Here I will suggest means of addressing these three questions:

1. The proportion of the different prey species in, for example, the humpback whale diet could be identified from fatty acid and stable isotope analysis of biopsy samples. Another, older approach would be to analyze the species identification of prey in stomach contents from the subsistence catches.

2. To estimate the prey density in the patches that may trigger the whales to open their mouths, we would have to develop some way of measuring prey density right in front of the gape. If not impossible, this task is a major logistical and technical challenge that perhaps could be met by onboard cameras. Alternatively, trawls and echo-sounders near feeding whales could provide an estimation of the overall density of prey in the area. However, this method is likely to underestimate the prey densities.

3. To answer the question of how much biomass a baleen whale consumes while in the West Greenland feeding grounds, we need to know more about their behavioral time budget. Clearly, whales perform different behavioral activities in the feeding grounds. The dive profile from a humpback whale tagged with a DTAG for 25 hours showed that the whale first spent about 6 hours lunge feeding at depth, 3 hours non-feeding near the surface, followed by 6 hours continuous lunge feeding divided into 3 hours surface lunges and 3 hours lunge at depth (Fig. 26). Finally, the whale spent 10 hours non-feeding near the surface with a few deep dives (Fig. 26). The whale went through hour-long periods of different behavioral activities, probably searching, resting and feeding at different depths. Long tag-outs of instruments with sensors (such as accelerometers) sampling at a high rate to identify lunge signatures are necessary to investigate how much time they spend on

actually feeding and searching for food patches. This brings me to the unanswered questions regarding prey localization.

Prey localization

It is clear that baleen whales must be very good at finding high density prey patches over vast oceanographic areas, but we are still facing the conundrum of what modalities and means they employ to localize their prey. To me this is a very interesting question, though difficult to answer. Play-back experiments with the sounds of prey could be carried out to investigate if baleen whales react to these acoustic cues. But first the possible sound signals have to be unequivocally identified and recorded, which is not trivial. Even if good sound recordings of prey are obtained and broadcasted faithfully, the whales' behavior must be observed and quantified during the experiment. One way of doing that would be to tag them with a DTAG before a playback experiment.

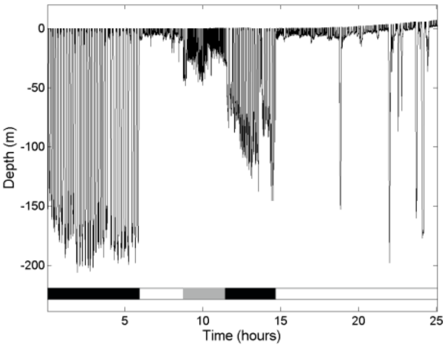


Fig. 26. Dive profile of humpback whale tagged with a DTAG. The 25hr tag-out shows that the whale shifts between hour long feeding bouts (deep lunges: black bar, surface lunges: grey bar) and non-feeding bouts (white bar)

Means other than acoustics can be used by whales to localize prey patches or good feeding areas. In chapter 4, analysis of photo id suggests that humpback whales search known areas for food availability along the Greenlandic coast and that they might time this to coincide with high concentrations of prey availability, such as spawning capelin. However, this study is based on a very small dataset. To further investigate the temporal patterns in habitat use by individual whales on a broader scale, photo ID should be gathered in several areas along the coast over a period of many years. The resighting rates will help reveal any patterns in individual whales revisiting certain areas to feed. In addition, satellite telemetry can be used to track the spatial search-pattern of individual whales.

PAM in West Greenland

As part of investigating the potential in passive acoustic monitoring (PAM) in West Greenland, an extensive analysis of temporal patterns in fin whale calls in Davis Strait was presented (section 1.5 and Chapter 8). It turned out that PAM is an efficient tool in studying the distribution and behavior of fin whales (Chapter 8). Many other species were recorded (section 1.5) and there was a clear seasonal variation in the occurrence of vocalizing individuals. My collaborators and I intend to use similar analytical methods as outlined in Chapter 8 to investigate the spatial and temporal distribution of blue, sei, bowhead and humpback whales and relate this to environmental factors, such as sea ice and temperature. These analyses will provide a better understanding of the relative abundance, seasonality, habitat use and acoustic behavior of these animals outside the periods where sighting surveys are possible. Finally, we showed that sea ice limits the northern distribution of fin whales. This analysis showed that, in combination with remote sensing of environmental parameters such as sea ice, PAM is useful for monitoring distributional changes in vocal marine mammals related to environmental and climatic changes.

Cited litterature

ACEVEDO-GUTIÈRREZ A, CROLL DA AND TERSHY BR. 2002. High feeding costs limit dive time in the largest whales. J Exp Biol 205: 1747-1753

ALERSTAM T, HEDENSTRÖM A AND ÅKESSON S. 2003. Long-distance migration: evolution and determinants. Oikos 103: 247-260

ANDERSEN OGN. 1985. Forsøgsfiskeri efter tobis I Vestgrønland 1978. Grønlands Fiskeri- og Miljøundersøgelser. Pp. 1-54.

AU WWL. 1993. The sonar of dolphins. 1st edition. Berlin, Heidelberg,New York: Springer-Verlag. Pp 1-277.

AU WWL. 2000. Hearing in Whales and Dolphins: An overview. (Eds. Au WWL, Popper AN and Fay RR). In. Hearing by Whales and Dolphins. Springer-Verlag New York Barlin Heidelberg. Pp 1-43.

BANNISTER J, PASTENE LA and BURNELL SR. 1999. First record of movement of a southern right whale (*Eubalaena australis*) between warm water breeding grounds and the Antarctic Ocean, South of 60°S. Mar Mammal Sci 15: 1337-1342.

BAUMGARTNER MF, COLE TVN, CAMPBELL RG, TEEGARDEN GJ AND DURBIN EG. 2003. Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales Mar Ecol Prog Ser 264: 155–166

BEARDSLEY R, EPSTEIN AW, CHEN C, WISHNER KF, MACAULAY MC AND KENNEY RD. 1996. Spatial variability in zooplankton abundance near feeding right whales in the Great South Channel. Deep Sea Res. Part II. Topical Stud Oceanogr. 43: 1601–1625.

BERGSTRÖM B AND VILHJALMARSSON H. 2007. Cruise report and preliminary results of the acoustic/pelagic trawl survey off West Greenland for capelin and polar cod 2005. Technical report no. 66, Pinngortitaleriffik, Greenland Institute of Natural Resources.

BRODIE PF. 1975. Cetacean energetics, an overview of intraspecific size variation. Ecology 56(1): 152-161.

BRODIE PF, SAMEOTO DD AND SHELDON RW. 1978. Population densities of Euphausiids off Nova Scotia as indicated by net samples, whale stomach contents and sonar. Limnol Oceanogr 23(6): 1264-1267.

BROWN MW, BRAULT S, HAMILTON PK, KENNEY RD, KNOWLTON AR, MARX K, MAYO CA, SLAY CK AND KRAUS SD. 2001. Sighting heterogeneity of right whales in the western North Atlantic, 1980-1992. J Cetacean Res Manage (special issue) 2:245-250.

BUCKINGHAM MJ, BERKHOUT BV AND GLEGG SAL. 1992. Imaging the ocean with ambient noise. Nature 356: 327-328

CHARIF RA, MELLINGER DK, DUNDSMORRE KJ, FRISTRUP KM AND CLARK CW. 2002. Estimated source levels of fin whale (*Balaenoptera physalus*) vocalizations: Adjustments for surface interference. Mar Mammal Sci. 18: 81–98.

CHRISTENSEN I, HAUG T AND ØIEN N. 1992. Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. ICES J Mar Sci. 49: 341-355.

CLAPHAM PJ, BARAFF LS, CARLSON CA, CHRISTIAN MA, MATTILA DK, MAYO CA, MURPHY MA AND PITTMAN S. 1993. Seasonal occurrence and annual return of humpback whales in the southern Gulf of Maine. Can J Zool. 71: 440–443.

CLAPHAM PJ. 1996. The social and reproductive biology of humpback whales: an ecological perspective. Mamm Rev. 26: 27-49.

CLARK CW. 1995. Application of US Navy underwater hydrophone arrays for scientific research on whales. Rep Int Whal Comm. 45: 210-212.

CLARK CW. 1989. The use of bowhead whale call tracks based on call characteristics as an independent means of determining tracking parameters. Rep Int Whal Comm. 39: 111-113.

CLARK CW AND CLAPHAM PJ. 2004 Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring Proc R Soc Lond B. 271: 1051–1057.

CLARK CW AND Ellison WT. 2004. Potential use of low-frequency sounds by baleen whales for probing the environment: Evidence from models and empirical measurements. In Echolocation in Bats and Dolphins. Eds. J Thomas, C Moss, and M Vater. Chicago, IL: Univ. of Chicago Press. pp. 564–582

CORKERON PJ AND CONNOR RC. 1999. Why do whales migrate? Mar Mammal Sci. 15: 1228-1245.

CROLL DA, ACEVEDO-GUTIÉRREZ A, TERSHY B AND URBÁN-RAMÍREZ J. 2001. The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? Comp Biochem Physiol A. 129: 797–809.

CROLL DA AND TERSHY B. 2002. Filter feeding. In. Encyclopedia of marine mammals. Eds. Perrin WF, Würsig B. and Thewissen JGM. Academic Press London.

CROLL DA, CLARK CW, ACEVEDO-GUTIÉRREZ A, TERSHY B FLORES S, GEDAMKE J AND URBAN J. 2002. Only male fin whales sing loud soungs. Nature. 417: 809.

CROLL DA, MARINOVIC B, BENSON S, CHAVEZ FP, BLACK N, TERNULLO R AND TERSHY BR. 2005. From wind to whales: trophic links in a coastal upwelling system. Mar Ecol Pro Ser. 289: 117-130.

CUMMINGS WC, THOMPSON PO AND HA SJ. 1986. Sounds from Bryde, *Balaenoptera edeni*, and finback, *B. physalus*, whales in the Gulf of California. Fish B_NOAA. 84: 359-370.

D'VINCENT CG, NILSON RM AND HANNA RE. 1985. Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. Sci Rep Whales Res Inst. 36: 41-47.

DOLPHIN WF. 1987. Observations of humpback whale, *Megaptera novaeangliae*-killer whale, *Orcinus orca*, interactions in Alaska: Comparisons with terrestrial predatorprey relationships. Canadian Field-Naturalist. 101: 70-75.

ELLISON WT, CLARK CW AND BISHOP GC. 1987. Potential use of surface reverberation by bowhead whales, *Balaena mysticetus*, in under-ice navigation: preliminary considerations. Rep Int Whal Comm. 37: 329-32.

ELPHICK CS AND HUNT GL Jr. 1993. Variations in the distributions of marine birds with water mass in the northern Bering Sea. Condor 95: 33–44

EVANS PGH. 1987. The natural history of whale and dolphins. Christopher Helm, London. Pp 1-105.

FISH FE. 2002. Speed. In. Encyclopaedia of marine mammals. Eds. WF Perrin, B Würsig and JGM Thewissen. San Diego, CA: Academic Press. Pp. 1161–1163.

FLETCHER NH. 2004. A simple frequency-scaling rule for animal communication. J Acoust Soc Am 115 (5): 2334-2338.

FRIEDLANDER AS, HALPIN PH, QIAN SS, WIEBE PH, THIELE D, READ AJ. 2006. Whale distribution in relation to prey abundance and oceanographic processes in the Western Antarctic Peninsula shelf waters. Mar Ecol Prog Ser. 317: 297–310.

GILL PC AND THIELE D. 1997. A winter sighting of killer whales (*Orcinus orca*) in Antarctic sea ice. Polar Biology. 17: 401-404.

GOLDBOGEN JA, CALAMBOKIDIS J, SHADWICK R E, OLESON EM, McDONALD MA AND HILDEBRAND JA. 2006. Kinematics of foraging dives and lunge-feeding in fin whales. J Exp Biol. 209: 1231–1244.

GOLDBOGEN JA, PYENSON ND AND SHADWICK RE. 2007. Big gulps require high drag for fin whale lunge feeding. Mar Ecol Pro Ser. 349: 289-301.

GOLDBOGEN JA, POTVIN J, SHADWICK RE. 2009. Skull and buccal cavity allometry increase mass-specific engulfment capacity in fin whales. Proc R Soc London. doi: 10.1098/rspb.2009.1680

GOLEYP D AND STRALEY JM. 1994. Attack on gray whales (*Escbricbtius rodustm*) in Monterey Bay, California, by killer whales (Orcinus orca) previously identified in Glacier Bay, Alaska. Can J Zool. 72: 1528-1530.

HARRISON NM, HUNT GLJ, COONEY RT. 1990. Front affecting the distribution of seabirds in the northern Bering Sea. Polar Res. 8: 29–31

HAWKINS AD AND JOHNSTONE ADF. 1978. The hearing of the Atlantic salmon, *Salmo salar*. J Fish Biol. 13: 655-673.

HEDEHOLM RB. 2010. The importance of small pelagic fishes to the energy flow in marine ecosystems: the Greenlandic capelin. PhD dissertation, Aarhus University. Pp 104.

HEIDE-JØRGENSEN MP, LAIDRE KL, JENSEN MV, DUECK L, POSTMA LD. 2006. Dissolving stock discreteness with satellite tracking: bowhead whales in Baffin Bay. Mar Mamm Sci. 22(1): 34–45.

HEIDE-JØRGENSEN MP, LAIDRE KL, LOGSDON ML AND NIELSEN TG. 2007a. Springtime coupling between chlorophyll a, sea ice and sea surface temperature in Disko Bay, West Greenland. Progr Oceanogr. 73: 79–95.

HEIDE-JØRGENSEN MP AND LAIDRE KL. 2007b. Autumn-space use patterns of humpback whales (*Megaptera novaeangliae*) in West Greenland. J Cetacean Res Manage. 9(2): 121-126.

HEIDE-JØRGENSEN, M.P., GARDE, E., NIELSEN, N.H. AND ANDERSEN ON. 2010. Biological data from the hunt of bowhead whales in West Greenland 2009 and 2010. 7pp. SC/62/BRG.

HIND AT AND GURNEY WSC. 1997. The metabolic cost of swimming in marine homeotherms. J Exp Biol. 200: 531–542.

HOCHACHKA PW AND SOMERO G. 1984. Biochemical Adaptation. Princeton: Princeton University Press. Pp

INGEBRIGTSEN A. 1929. Whales caught in the North Atlantic and other seas. ICES Reports. 563-26.

IWC. 2007. International Convention for the Regulation of Whaling, 1946; Schedule. In: Annual Report of the International Whaling Commission 2007. Cambridge.

IWC. 2009. Annual Report of the International Whaling Commission 2009. Cambridge.

JOHNSON MP AND TYACK PL. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE J Ocean Eng. 28: 2–12.

KAPEL FO. 1979. Exploitation of Large Whales in West Greenland in the twentieth Century. Rep Int Whale Comm. 29: 197–214.

KATONA SK, BAXTER B, BRAZIER B, KRAUS S, PERKINS J AND WHITEHEAD H. 1979. Identification of humpback whales by fluke photographs. The behavior of marine mammals. In. Behavior of marine mammal science Volume 3, Cetaceans. Eds. HE Winn and BL Olla. New York: Plenum Press. Pp. 33–44.

KELLOG R. 1929. What is known on the migrations of some of the whalebone whales? Smithsonian Institution Annual Report 1929. 467-494.

KENNEY RD, WINN HE AND MACAULEY MC. 1995. Cetaceans in the great south channel, 1979–1989: right whale (*Eubalaena glacialis*). Cont Shelf Res 15: 385–414

KENNEY RD, MAYO CA AND WINN HE. 2001. Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. J Cetacean Res Manage (Special issue). 2: 251–260.

KIØRBOE T. 2010. How zooplankton feed: mechanisms, traits and trade-offs Biol Rev. doi: 10.1111/j.1469-185X.2010.00148.x

KIØRBOE T, ANDERSEN A, LANGLOIS VJ AND JAKOBSEN HJ. 2010. Unsteady motion: Escape jumps in copepods, their kinematics and energetics. J Roy Soc Interface. doi:10.1098/rsif.2010.0176

KOOYMAN GL, WAHRENBROCK EA, CASTELLINI MA, DAVIS RW AND SINNETT EE. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddel seals: evidence of preferred pathways from blood chemistry and behavior. J Comp Physiol. 138: 335–346.

KOOYMAN GL. 1989. Diverse Divers: Physiology and Behavior. Berlin: Springer-Verlag. Pp 200.

KRAMER DL. 1988. The behavioural ecology of air breathing by aquatic animals. Can J Zool. 66: 89–94.

KRAUS SB, PRESCOTT JH, KNOWLTON AR AND STONE GS. 1986. Migration and calving of right whales (*Eubalaena glacialis*) in the western North Atlantic. Rep Int Whal Commn. Special Issue. 10: 139-144.

LAIDRE KL, HEIDE-JØRGENSEN MP AND NIELSEN TG. 2007. Role of the bowhead whale as a predator in West Greenland. Mar Ecol Prog Ser. 346: 285-297.

LAMBERTSEN RH. 1983. Internal mechanism of rorqual feeding. J Mamm. 64: 76-88.

LAMBERTSEN RH, ULRICH N AND STRALEY J. 1995. Frontomandibular stay of Balaenopteridae: A mechanism for momentum recapture during feeding. J Mamm. 76: 877-899.

LAMBERTSEN RH, RASMUSSEN KJ, LANCASTER WC AND HINTZ RJ. 2005. Functional morphology of the mouth of the bowhead whale and its implications for conservation. J Mamm. 86: 342–352.

LAWS RM. 1985. The ecology of the southern ocean. Am Sci. 73: 26-40.

LOWRY LF. 1993. Foods and feeding ecology. In The Bowhead whale. (Eds. Burns, JJ, Montague, JJ, Cowles, CJ) Special Publication No 2. The Society for Marine Mammalogy. Pp 201-238.

LOWRY LF, SHEFFIELD G, GEORGE JC. 2004. Bowhead whale feeding in the Alaskan 479 Beaufort Sea, based on stomach content analyses. J Cetacean Res Manage. 6: 215-223.

MADSEN PT, JOHNSON M, AGUILAR SOTO N, ZIMMER WMX AND TYACK P. 2005. Biosonar performance of foraging beaked whales, *Mesoplodon densirostris*. J Exp Biol. 208: 181-194

MALIK S, BROWN MW, KRAUS SD, KNOWLTON AR, HAMILTON PK AND WHITE BN. 1999. Assessment of mitochondrial DNA structuring and nursery use in the North Atlantic right whale (*Eubalaena glacialis*). Can J Zool. 77(81): 1217-22.

MAYO CA AND GOLDMAN L. 1992. Right whale foraging and the plankton resources in Cape Cod and Massachusetts Bays. In. The right whale in the western North Atlantic: a science and management workshop. Ed. J Hain. Northeast Fish Sci Cent Ref Doc. 92-05. Pp. 43–44.

McGREGOR P. 2005. Animal communication networks. Cambridge University Press. Pp 672.

MEHTA AV, ALLEN JM, CONSTANTINE R, GRRIGUE C, JANN B, JENNER C, MARX MK, MATKIN CO, MATTILA DK, MINTON G, MIZROCH SA, OLAVARRÍA C, ROBBINS J, RUSSEL KG, SETON RE, STIEGER GH, VÍKINGSSON GA, WADE PR, WITTEVEEN BH AND CLAPHAM PJ. 2007. Baleen whales are not important as prey for killer whales Orcinus orca in high latitude regions. Mar Ecol Pro Ser. 348: 297-307.

MELLINGER DK, STAFFORD KM, MOORE SE, DZIAK RP AND MATSUMOTO H. 2007. An overview of fixed passive acoustic observation methods for cetaceans. Oceanography. 20: 36-45.

MIZROCH SA, RICE D, ZWIEFELHOFER D, WAITE J AND PERRYMAN W. 2009. Distribution and movements of fin whales in the North Pacific Ocean. Mam Rev. 39: 193-227.

MOORE SE, STAFFORD KM, MELLINGER DK AND HILDEBRAND JA. 2006. Listening for large whales in offshore waters of Alaska. BioScience 56: 49–55.

MUNK P. 2002. Larval sand lance (*Ammodytes sp.*) in the diet of small juvenile wolffish (*Anarhichas sp.*): predatory interactions in frontal waters off western Greenland. Can J Fish Aq Sci. 59: 1759-1767.

NERINI MK. 1984. A review of gray whale feeding ecology. In. The gray whale. Eds. ML Jones, SL Swartz and S Leatherwood. Academic Press Inc, Orlando, FL Pp. 423-450.

NAMMCO Annual Report 2009. North Atlantic Marine Mammal Commission, Tromsø, Norway. Pp 529.

NEVITT GA. 2008. Review: Sensory ecology on the high seas: the odor world of the procellariiform seabirds. J Exp Biol. 211: 1706-1713.

NORRIS K. 1967. Some observations on the migration and orientation of marine mammals. In. Animal orientation and Navigation. Ed. RM Storm. University of California Press, Berkeley. Pp. 320-380.

OLESON. NJ. 1995. Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove Mar Ecol Prog Ser. 124: 63-72.

PARKINSON CL, CAVALIERE DJ, GLOERSEN P, ZWALLT HJ AND COMISO JC. 1999. Arctic sea ice extents, areas, and trends, 1978–1996. J Geophys Res. 104(C9): 20.837–20.856.

PATTERSON B, AND HAMILTON GR. 1964. Repetitive 20 cycle per second biological hydroacoustic signals at Bermuda. In. Marine bio-acoustics. Ed. W N Tavolga. Pergamon Press, New York, NYY. Pp. 125–145.

PAYNE R. 1995. Among whales. Scribner, New York. Pp 432.

PAYNE RS AND McVAY S. 1971. Songs of Humpback whales. Science 173: 585-597

PAYNE R AND WEBB D. 1971. Orientation by means of long range acoustic signaling in baleen whales. Ann. N.Y. Acad. Sci. 188: 110–141.

PERRYMAN WL, DONAHUE MA, PERKINS PC AND REILLY SB. 2002. Gray whale calf production 1994-2000: are observed fluctuations related to changes in seasonal ice cover? Mar Mammal Sci. 18(1): 121-144.

PILLERI G AND KNUCKEY J. 1969. Behaviour patterns of some Delphinidae observed in the western Mediterranean. Z. Tierpsychol. 26: 48-72.

PIKE GC. 1962. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). J Fish Res Bd Can. 19(5): 815-38.

PIATT JF AND METHVEN DA. 1992. Threshold foraging behavior of baleen whales Mar Ecol Prog Ser 84: 205-210

PIVORUNAS A. 1979. The feeding mechanisms of baleen whales. Am Scientist. 67: 432– 440.

RAY GC AND SCHEVILL WE. 1974. Feeding of a captive gray whale *Eschrichtius robustus*. Mar Fish Rev. 36 (4): 31-38

RANKIN S AND BARLOW J. 2006. Vocalisations of the Sei Whale *Balaenoptera borealis* off the Hawaiian Islands. Bioacoustics 16(2): 137-145

RICHARDSON WJ. GREENE CR, MALME CI, THOMSON DH. 1995. Marine mammals and noise. Academic Press California. Pp. 576.

SAMEOTO DD. Euphausiid distribution in acoustic scattering layers and its significance to surface swarms. J Plankton Res. 5: 129-143.

SANDERSON SL AND WASSERSUG R. 1990. Suspension-feeding vertebrates. Sci. Am. 262: 96–101.

SHEVCHENKO TW. 1975. The Nature of the interrelationships between killer whales and other cetaceans. Morskie Mlekopitayshchie Chast. 2: 173-174. In. Metha AV and 19 others. 2007. Baleen whales are not important as prey for killer whales *Orcinus orca* in high-latitude regions. Mar Ecol Pro Ser. 348: 297-307.

SIMARD Y AND LAVOIE D. 1999. The rich krill aggregation of the Saguenay—St. Lawrence Marine Park: hydroacoustic and geostatistical biomass estimates, structure, variability, and significance for whales. Can J Fish Aquat Sci. 56: 1182–1197.

SIMILÄ T AND UGARTE F. 1993. Surface and underwater observations of cooperatively feeding killer whales in northern Norway. Can J Zool. 71: 1494-1499.

SIMON M, UGARTE F, WAHLBERG M AND MILLER LA. 2006. Icenaldic killer whales *Orcinus* orca use a pulsed call suitable for manipulating schooling behaviour of herring *Clupea harangus*. Bioacoustics. 16: 57–74

SIMONSEN C, MUNK P, FOLKVORD A AND PEDERSEN SA. 2006. Feeding ecology of Greenland halibut and sandeel larvae off West Greenland. Marine Biology DOI 10.1007/s00227-005-0172-5.

ŠIROVIĆ A, HILDEBRAND JA, WIGGINS SM, McDONALD MA, MOORE SE 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. Part II. 51: 2327–2344.

ŠIROVIĆ A, HILDEBRAND JA, WIGGINS SM AND THIELE D. 2009. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. Marine Mammal Sci. 25: 125-136.

SOURISSEAU M, SIMARD Y AND SAUCIER FJ. 2008. Krill diel vertical migration fine dynamics, nocturnal overturns, and their roles for aggregation in stratified flows. Can J Fish Aquat Sci. 65: 574–587.

STAFFORD KM, NIEUKIRK SL AND FOX CG. 1999. Low frequency whale sounds recorded on hydrophones moored in the eastern tropical Pacific. J Acoust Soc Am. 106: 3687–3698.

STAFFORD KM, MOORE SE AND FOX CG. 2005. Diel variation in blue whale calls recorded in the eastern tropical Pacific. Animal Behaviour. 69: 951–958

STAFFORD KM, MELLINGER DK, MOORE SE AND FOX CG. 2007. Seasonal variability and detection range modeling of baleen whale calls in the Gulf of Alaska, 1999–2002. J Acoust Soc Am. 122(6): 3378-3390.

STAFFORD KM, MOORE SE, LAIDRE KL AND HEIDE-JØRGENSEN MP. 2008. Bowhead whale springtime song off West Greenland. J Acoust Soc Am. 124: 3315–3323.

STAFFORD, KM, CITTA JJ, MOORE SE, DAHER MA AND GEORGE JE. 2009. Environmental correlates of blue and fin whale call detections in the North Pacific Ocean from 1997 to 2002 Mar Ecol Prog Ser. 395: 37–53.

STIMPERT AK, WILEY DN, AU WWL, JOHNSON MP AND ARSENAULT R. 2007. ‘Megapclicks’: acoustic click trains and buzzes produced during night-time foraging of humpback whales (*Megaptera novaeangliae*). Biol Lett doi:10.1098/rsbl.2007.0281

TERVO OM, PARKS SE AND MILLER LA. 2009 Seasonal changes in the vocal behavior of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western-Greenland. J Acoust Soc Am. 126(3): 1570-1580.

THEWISSEN GM, GEORGE J, ROSA C AND KISHIDA T. 2010. Olfaction and brain size in the bowhead whale (*Balaena mysticetus*) doi: 10.1111/j.1748-7692.2010.00406.x

THOMPSON PO, CUMMINGS WC AND HA SJ. 1986. Sounds, source levels, and associated behavior of humpback whales, Southeast Alaska. J Acoust Soc Am. 80: 735–740.

THOMPSON PO, FINDLEY LT AND VIDAL O. 1992. 20-Hz pulses and other vocalizations of fin whales, *Balaenoptera physalus*, in the Gulf of California, Mexico. J Acoust Soc Am. 92: 3051–3057.

THOMSON DH AND RICHARDSON WJ. 1995. Marine mammal sounds. In. Marine Mammals and Noise. Eds. WJ Richardson, CR Greene, CI Malme AND DH Thomson. Academic, New York, pp. 159–204.

TYACK P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behav Ecol Sociobiol. 8: 105-1 16.

TYACK PL AND CLARK CW. 2000. Communication and acoustic behavior of dolphins and whales. In: Hearing by Whales and Dolphins. Eds. Au WWL, POPPER AN and FAY RR. Springer-Verlag New York Barlin Heidelberg. Pp. 156-224.

TYNAN CT. 1998. Ecological importance of the southern boundary of the Antarctic Circumpolar Current. Nature. 392:708-710

VAUGHN RL, SHELTON DE, TIMM LL, WATSON LA AND WÜRSIG B. 2007. Dusky dolphin (*Lagenorhynchus obscurus*) feeding tactics and multi-species associations . New Zeal J Mar Fresh. 41: 391–400.

VAUGHN RL, WÜRSIG B, SHELTON DS, TIMM LL. AND WATSON LA. 2008. Dusky dolphins (*Lagenorhynchus obscurus*) influence prey accessibility for seabirds in Admiralty bay, New Zealand. J Mamm. 89(1): 1051-1058.

WATKINS WA AND SCHVILL WE. 1976. Right whale feeding and baleen rattle. J. Mamm. 57: 58–66.

WATKINS WA 1981. Activities and underwater sounds of fin whales. Sci Rep Whales Res Inst. 33: 83-117

WATKINS WA, DAHER MA, REPPUCCI GM, GEORGE JE, MARTIN DI, DIMARZIO NA AND GANNON DP. 2000. Seasonality and distribution of whale calls in the North Pacific. Oceanography. 13: 62–67

WATKINS WA, Tyack P, Moore KE AND Bird JE. 1987. The 20-Hz signals of finback whales (*Balaenoptera physalus*). J Acoust Soc Am. 82(6): 1901-1912.

WATTS P, HANSEN S AND LAVIGNE DM. 1993. Models of heat loss by marine mammals: Thermoregulation below the zone of irrelevance. J Theoretical Biol. 163: 505-525.

WEINRICH M. 1998. Early experience in habitat choice by humpback whales (*Megaptera novaeangliae*). J Mammal .79: 163–170.

WERTH AJ. 2000. Marine Mammals. In Feeding: Form, Function and Evolution in Tetrapod Vertebrates (ed. K. Schwenk), New York: Academic Press. pp. 475-514.

WERTH AJ. 2004. Models of hydrodynamic flow in the bowhead whale filter feeding apparatus. J Exp Biol. 207: 3569–3580.

WILLIAMS TM. 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. Phil Trans R Soc Lond B. 354: 193.

WILLIAMS TM, DAVIS RW, FUIMAN LA, FRANCIS J, Le BOEUF BJ, HORNING M, CALAMBOKIDIS J AND CROLL DA. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. Science. 288: 133–136.

WÜRSIG B AND WÜRSIG M. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science 198: 755-756.

WÜRSIG B, DORSEY EM, FRAKER MA, PAYNE RS AND RICHARDSON WJ. 1985. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: a description. Fish B-NOAA, U.S. 83: 357-377.

WÜRSIG B, DORSEY EM, RICHARDSON WJ AND WELLS RS. 1989. Feeding, aerial and play behaviour of the bowhead whale, *Balaena mysticetus* summering in the Beaufort Sea. Aquat Mamm. 15: 27-37.

WÜRSIG B AND CLARK C. 1993. Behavior. In: The Bowhead whale. Eds. Burns JJ, Montague JJ and Colws CJ Lawrence, Kansas Society Marine Mammalogy, pp. 157-199.

WÜRSIG B AND JEFFERSON TA. 1990. Methods of Photo-identification for small cetaceans. Rep Int Whal Commn (special issue 12) pp- 43-52.

Filter feeding bowhead whales

Chapter 2

Paper I:
Simon M, Johnson M, Tyack P & Madsen PT. 2009

Behaviour and kinematics of continuous ram filtration in Bowhead whales (*Balaena mysticetus*).
Proc R Soc B 276: 3819-3825

PROCEEDINGS OF THE ROYAL SOCIETY B

FirstCite® e-publishing

Proc. R. Soc. B
doi:10.1098/rspb.2009.1135
Published online

Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*)

Malene Simon[1,2,*], Mark Johnson[3], Peter Tyack[3] and Peter T. Madsen[1,3]

[1]*Zoophysiology, Department of Biological Sciences, University of Aarhus, C. F. Møllers Allé, Building 1131, 8000 Aarhus C, Denmark*
[2]*Department of Birds and Mammals, Greenland Institute of Natural Resources, PO Box 570, Kivioq 2, 3900 Nuuk, Greenland*
[3]*Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*

Balaenid whales perform long breath-hold foraging dives despite a high drag from their ram filtration of zooplankton. To maximize the volume of prey acquired in a dive with limited oxygen supplies, balaenids must either filter feed only occasionally when prey density is particularly high, or they must swim at slow speeds while filtering to reduce drag and oxygen consumption. Using digital tags with three-axis accelerometers, we studied bowhead whales feeding off West Greenland and present here, to our knowledge, the first detailed data on the kinematics and swimming behaviour of a balaenid whale filter feeding at depth. Bowhead whales employ a continuous fluking gait throughout the bottom phase of foraging dives, moving at very slow speeds (less than 1 m s^{-1}), allowing them to filter feed continuously at depth. Despite the slow speeds, the large mouth aperture provides a water filtration rate of approximately 3 m^3 s^{-1}, amounting to some 2000 tonnes of water and prey filtered per dive. We conclude that a food niche of dense, slow-moving zooplankton prey has led balaenids to evolve locomotor and filtering systems adapted to work against a high drag at swimming speeds of less than 0.07 body length s^{-1} using a continuous fluking gait very different from that of nekton-feeding, aquatic predators.

Keywords: filter feeding; bowhead whale; kinematics

1. INTRODUCTION

Air-breathing aquatic animals display a number of adaptations to access two spatially separated, but vital resources: oxygen at the surface and food at depth. To get a sufficient net uptake of energy, aquatic carnivores must balance the metabolic costs of locomotion and prey acquisition against their oxygen reserves while foraging (Kramer 1988; Williams 1999). Most breath-holding marine predators capture food in discrete feeding events (Ropert-Coudert *et al.* 2006; Hassrick *et al.* 2007; Aguilar Soto *et al.* 2008), where they reduce oxygen consumption by gliding during parts of either ascent or descent (Williams *et al.* 2000) and employ a stroke-and-glide gait at depth to prolong foraging time (Crocker *et al.* 1997; Croll *et al.* 2001; Williams 2001; Wilson *et al.* 2002; Watanuki *et al.* 2003). Thus, locomotion is a major oxygen-consuming activity using up oxygen reserves while diving, and the stroke-and-glide strategy of most air-breathing marine animals allows them to perform longer breath-hold dives, maximizing access to food resources (Crocker *et al.* 1997; Williams *et al.* 2000; Watanuki *et al.* 2003).

In contrast to the discrete foraging events seen in most air-breathing marine predators, the large balaenids (right and bowhead whales) feed on aggregations of zooplankton through what has been termed continuous ram filtration, similar to the feeding behaviour of basking-, whale- and megamouth sharks (Pivorunas 1979; Diamond 1985; Sims 1999; Lambertsen *et al.* 2005).

The large head of bowhead whales comprises approximately one-third of its total body length and, with a mouth aperture of more than 4 m^2, it forms an enormous filtering apparatus with the high curved maxillary and premaxillary bones supporting up to 4 m long baleen plates (Werth 2001, 2004; Lambertsen *et al.* 2005). When foraging at the surface, balaenid whales have been reported to swim with mean speeds of 1.1–2.5 m s^{-1} (Mayo *et al.* 2001; Baumgartner & Mate 2003; Werth 2004), which is comparable to their migration speeds (Heide-Jørgensen *et al.* 2006). Owing to lack of data, these speeds have been presumed to be maintained by whales feeding under water (Baumgartner & Mate 2003; Werth 2004). Swimming with an open mouth to force water past a dense curtain of baleen changes the hydrodynamic shape of the animal and increases the drag significantly (Sanderson & Wassersug 1990; Werth 2004). Despite this increased drag, balaenid whales perform long foraging dives lasting between 10 and 40 min (Werth 2004; Laidre *et al.* 2007). Given the expected large drag increment resulting from an open mouth, balaenids face a trade-off between the benefits of filtering large volumes of water per second and the

---

[*] Author and address for correspondence: PO Box 570, Greenland Institute of Natural Resources, 3900 Nuuk, Greenland (masi@natur.gl).

Received 30 June 2009
Accepted 31 July 2009

energetic costs of swimming faster, thus reducing foraging time. This trade-off brings into question the assumption that whales diving to feed with their mouth open will swim as fast as those travelling with mouth closed or feeding at the surface: how can bowhead whales maintain high speeds while continuously working against a high drag during long breath-hold dives? One possible explanation is that balaenids do not employ continuous ram filtration when submerged, but only open their mouth in discrete events when the food density is particularly high. Drag would be reduced during the mouth-closed swimming, which, in combination with an energy-saving stroke-and-glide gait, could explain the long dive times at high mean speeds. An alternate hypothesis is that balaenids employ continuous ram filtration while at depth, but swim much slower than previously estimated from surface feeding whales, thereby reducing the drag forces and hence oxygen consumption during breath-hold dives.

Here, we test these two alternative hypotheses using multi-sensor archival digital tags (DTAGs) on filter feeding bowhead whales in West Greenland and provide, to our knowledge, the first detailed account of the behaviour and biomechanics of filter feeding in balaenid whales with implications for filtration rates and prey location. We show that feeding bowhead whales employ a continuous fluking gait and swim slowly at less than 0.07 of body length s^{-1}, allowing them to ram filter feed continuously at depth during long breath-hold dives.

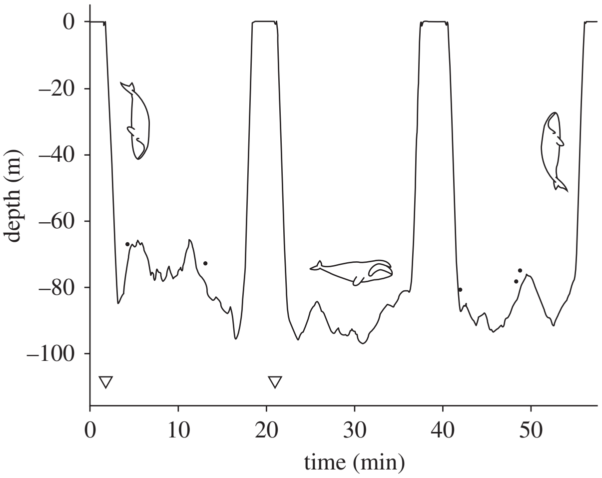


Figure 1. Dive profile from a feeding bowhead whale tagged with a DTAG in Disko Bay, West Greenland. Small dots at the bottom of dives indicate the times at which rattle-like sounds were detected. The two triangles indicate the bottom depth measured with an echo-sounder from the tag boat.

2. MATERIAL AND METHODS

Bowhead whales south of Disko Island were tagged with DTAGs (Johnson & Tyack 2003) in the period from 2–16 May 2008. The whales were approached slowly with a dinghy, and the DTAGs were attached to the middle of their backs with four suction cups, using an 8 m hand-held carbon fibre pole. The DTAG released from the whale after a pre-programmed time period, and the tags were retrieved using VHF tracking (Johnson & Tyack 2003). Given the challenging field conditions of partial ice cover, variable weather and uncertain whale residence time in the area, we programmed tags to release after 3 h.

The DTAG contains a pressure sensor and three-axis magnetometers and accelerometers, each sampled at 50 Hz with 16-bit resolution (Johnson & Tyack 2003). For analysis, the sensor data were down-sampled to 5 Hz, and the accelerometer and magnetometer data were corrected for tag orientation on the whale by rotating each three-element vector to provide orientation data in whale frame coordinates (Johnson & Tyack 2003). All sensors were compensated for drift from the changing temperatures using a built-in temperature sensor (Johnson & Tyack 2003).

Following previous tagging studies of balaenids, two broad types of dives were identified: U-shaped and V-shaped dives (Baumgartner & Mate 2003; Laidre *et al.* 2007). Dives were divided into three phases: descent, bottom and ascent. Descents started when the whale left the surface and ended when the whale's pitch angle first became positive, indicating the first upward-pointing orientation (figure 1). Ascents started when the whale pitch last became negative and ended when the whale reached the surface (Sato *et al.* 2003; Miller *et al.* 2004; Watwood *et al.* 2006). The bottom phase of U-dives was the interval between the descent and ascent phases (figure 1). V-dives lacked a bottom phase and consisted of only ascent and descent phases. To compare speed estimates and fluke rates of U-dives with an equivalent part of V-dives, we defined a 'bottom phase' in V-dives. On average, the bottom time made up 79 per cent of the deepest samples of each U-dive. Based on this, we defined the bottom phase of V-dives as the 79 per cent deepest samples of each V-dive.

The oscillations from fluke strokes of a swimming whale undulate through the whole body (Fish *et al.* 2003) and can be detected as cyclic variations in the pitch angle of the tag (Johnson & Tyack 2003). Using this signal, the fluking rate was computed as the inverse of the time between peaks in the pitch record averaged over 30 s bins and reported in Hertz (fluke strokes s^{-1}).

Swimming speed is difficult to measure accurately for a submerged animal using a small tag without external localization methods such as acoustic tracking (Johnson & Tyack 2003). Swim speed is generally defined as the forward-directed movement along the longitudinal axis of the animal per unit of time. However, the body of a swimming whale undulates with each fluke stroke accelerating the tag perpendicular to the body axis, complicating speed measurements. In addition, animals moving in three dimensions are affected by lift, buoyancy and gravity forces influencing their forward speed. Therefore, we estimated swimming speed using two methods. In the first method, vertical speed, derived from the depth sensor, was multiplied by the arcsine of the pitch angle (Miller *et al.* 2004) and smoothed with a Kalman filter following Zimmer *et al.* (2005). This approach is a good proxy for speed provided (i) that the whale's specific acceleration is low (a requirement for the pitch estimate to be accurate), (ii) that the whale moves anteriorly in the direction of its body axis, and (iii) that the absolute pitch angle is far from zero. During the bottom phase of U-dives, bowhead whales regularly swim with pitch angles close to zero, rendering the speed estimate unreliable at these times. Therefore, following previous studies (Fletcher *et al.* 1996; Burgess *et al.* 1998; Goldbogen *et al.* 2006; Aguilar Soto *et al.* 2008), we used the low-frequency flow noise recorded by the tag as an alternative proxy for speed. For each tag placement, we computed the flow noise (noise power at 500 Hz band-pass filtered with a 2-pole Butterworth filter) during descents in 5 s bins along with the mean speed, in that bin derived from the mean vertical speed multiplied by the arcsine of the mean pitch angle over the same interval. We used descent for the speed–noise calibration because the tagged whales all fluked during descent and in the bottom phases, whereas many ascents had little fluking. Using regression analysis (*sensu* Goldbogen *et al.* 2006), we fitted a function $k+\alpha(20\log(\text{noise power}))$ with a mean r^2 value of 0.65 to the noise and speed data during descents for each whale. This flow noise/speed correlation was used to estimate the swimming speed in the bottom phases in U-dives. The speed estimate is probably an overestimate as any low frequency sounds associated with feeding, such as increased flow noise because of the changed body form when compared with the calibration epoch, will add to the noise level and thus the apparent speed.

The sound of baleen plates rattling during feeding has been described from surface-skimming Northern right whales (Watkins & Schevill 1976). We listened through the tag sound recordings using custom software and marked possible baleen rattles to identify the time and depth of these sounds. All analyses were performed using MATLAB 6.5 (Mathworks).

3. RESULTS

Seven bowhead whales were tagged, and a total of 13.9 h of dive data were obtained containing 52 dives, of which 33 and 19 were classified as V- and U-dives, respectively.

The maximum depth of V-dives ranged from 15 to 221 m, with a mean of 69 m (s.d. = 37). V-dives had an average duration of 9.0 min (s.d. = 5.1), with a range of 1.6–19 min (statistics for each animal are summarized in table 1). The maximum depths of U-dives varied across whales with an overall mean of 79 m (s.d. = 64) and range of 17–127 m. The duration of U-dives was 15.2 min (s.d. = 4.1), with a range of 7–21 min (table 1). When the whales left the surface descending on a typical U-dive, they pitched downwards and fluked continuously for the first 24–90 m (figure 2). One whale continued fluking throughout descents, but other whales adopted a stroke-and-glide gait, resulting in overall mean (over the dive phase) fluking rates of 0.08 Hz (s.d. = 0.03) during descent and 0.06 Hz (s.d. = 0.02) during ascent (table 1). The instantaneous fluking rate computed in the bouts of fluking during the initial part of the descent was 0.79 Hz (s.d. = 0.11), 10 times higher than the mean descent fluking rate (0.08 Hz, table 1). In comparison, whales fluked almost continuously during the bottom phases of U-dives, with a mean fluking rate of 0.12 Hz (s.d. = 0.08) (figure 2*b* and table 1). The mean fluking rate in the bottom phase was significantly higher than the overall mean descent and ascent fluking rate (non-parametric ANOVA $p < 0.05$, descent: $H = 6.8$, ascent: $H = 9.1$, d.f. = 1). However, the mean of the instantaneous fluking rate during the first part of the descent was significantly higher than the U-dive bottom-phase fluking rate (non-parametric ANOVA $H = 55$, $p < 0.05$, d.f. = 1). Despite the higher mean fluking rate during the bottom phase, the estimated swim speeds were 0.7 m s^{-1} (s.d. = 0.11) and 0.8 m s^{-1} (s.d. = 0.08) (Kalman-filtered and noise-based estimates, respectively), about one-half of the speeds of descent (1.4 m s^{-1}) and ascent (1.2 m s^{-1}) as estimated with the Kalman approach (table 1). The pitch angle was consistently close to zero (within ±10°) during the bottom phase, making the Kalman speed estimate suspect in this phase, but the general agreement with the noise-based speed estimate was good (table 1). The mean noise speed estimate of bottom phase in U-dives (0.8 m s^{-1}) was significantly lower than the mean speed estimates of the bottom phase in V-dives (1.3 m s^{-1}, s.d. = 0.39) (non-parametric ANOVA $H = 25.21$, $p < 0.001$, d.f. = 1). At the end of the bottom phase, the whales pitched towards the surface and switched to a stroke-and-glide gait. While all of the tagged whales fluked during at least part of the descents, some glided all the way to the surface presumably powered by positive buoyancy. The roll angle was ±10° during the bottom phase of all U-dives (figure 2).

To evaluate the speed estimates during U-dives, we logged the geo-referenced position and time at the beginning and end of two U-dives. Knowing the pitch angles and speeds during the descent and ascent phases of these dives, we subtracted the distance covered during descent and ascent from the total distance covered during the dive to derive the distance covered during the bottom time. The mean speed during the bottom phase in the two U-dives derived in this way was below 0.8 m s^{-1} and hence close to the speed estimates calculated from flow noise and corrected vertical rate with a Kalman filter (0.8 and 0.7 m s^{-1}, respectively; table 1).

The speed estimates during descents and ascents of V-dives (mean 1.3 m s^{-1}) were not significantly different from speeds in U-dive descents and ascents (non-parametric ANOVA, $H = 5.1$, d.f. = 3, $p = 0.2$; table 1). The descent and ascent phases of V-dives were similar to those described earlier for U-dives and thus were characterized by stroke-and-glide gait, with a higher overall mean fluking rate during descent (0.09 Hz, s.d. = 0.02) than during ascent (0.07 Hz, s.d. = 0.03) (figure 3 and table 1). Thus, the only dive phase in which whales fluked continuously was during the bottom phase of U-dives (figure 2).

Distinct rattle-like sounds were heard in six of the seven tag recordings. The remaining tag recording (Bm137a) contained only V-dives. The rattle sound pulses occurred with variable levels and pulse intervals and had a frequency range of 300–600 Hz. Except for recording Bm126a, in which rattle-like sounds were detected throughout the dive profile, rattles were only heard during the bottom phase of U-dives (figures 1,2 and 4). Tagged whales did not produce any detectable vocalizations while foraging, and the soundscape was dominated by cracking ice, and occasional calls from non-tagged bowheads.

4. DISCUSSION

Major questions when studying the behavioural ecology and field physiology of free-ranging animals pertain to when, how and by what energetic investments they acquire food (Costa & Sinervo 2004). Previous tagging studies on Northern right whales and bowhead whales

Table 1. Dive statistics of foraging and non-foraging bowhead whale dives. (Numbers in brackets indicate standard deviation.)

		Bm123a	Bm126a	Bm126b	Bm127a	Bm129a	Bm130a	Bm137a	mean
U-shaped foraging dives	*n*	1	1	3	3	1	10	0	
	maximum depth (m)	90	105	99	115	127	45	—	
	mean maximum depth (m)	90	105	97 (2.3)	90 (36.1)	127	31 (9.4)	—	
	range maximum depth (m)	90	105	94–99	49–105	127	17–45	—	
	mean dive time (min)	20.6		11.2	13.4	18.4	12.5	—	15.2
	speed (m s^{-1}), descent	1.6	1.3	1.7 (0.26)	1.5 (0.29)	1.4	1.0 (0.17)	—	1.43
	speed (m s^{-1}), ascent	1.3	1.5	1.0 (0.32)	1.5 (0.54)	1.4	0.8 (0.07)	—	1.24
	speed (m s^{-1}), bottom	0.8		0.6 (0.33)	0.6 (0.18)	0.8	0.6 (0.08)	—	0.67
	noise calibration speed (m s^{-1})	0.8 (0.2)		0.9 (0.1)	0.9 (0.2)	0.7 (0.1)	0.8 (0.1)	—	0.82
	fluking rate (Hz), descent	0.05 (0.03)		0.07 (0.03)	0.13 (0.003)	0.09 (0.01)	0.07 (0.04)	—	0.08
	fluking rate (Hz), ascent	0.08 (0.13)	0.03	0.05 (0.01)	0.07 (0.02)	0.09	0.05 (0.05)	—	0.06
	fluking rate (Hz), bottom	0.13	0.07	0.11 (0.01)	0.13 (0.01)	0.13	0.15 (0.01)	—	0.12
V-shaped search dives	*n*	2	11	0	13	0	0	7	
	maximum depth (m)	81	124	—	80	—	—	221	
	mean maximum depth (m)	76 (6.29)	66 (42.5)	—	33 (18.2)	—	—	173 (43.8)	
	range maximum depth (m)	72–81	15–124	—	16–80	—	—	93–221	
	mean dive time (min)	6.1	8.9	—	4.8	—	—	16.3	9.0
	speed (m s^{-1}), descent	1.6 (0.02)	0.8 (0.26)	—	1.4 (0.27)	—	—	1.3 (0.33)	1.27
	speed (m s^{-1}), ascent	1.5 (0.03)	1.2 (0.38)	—	1.1 (0.27)	—	—	1.6 (0.42)	1.34
	fluking rate (Hz), descent	0.07 (0.03)	0.07 (0.02)	—	0.12 (0.03)	—	—	0.09 (0.02)	0.09
	fluking rate (Hz), ascent	0.10 (0.02)	0.05 (0.05)	—	0.08 (0.04)	—	—	0.04 (0.03)	0.07

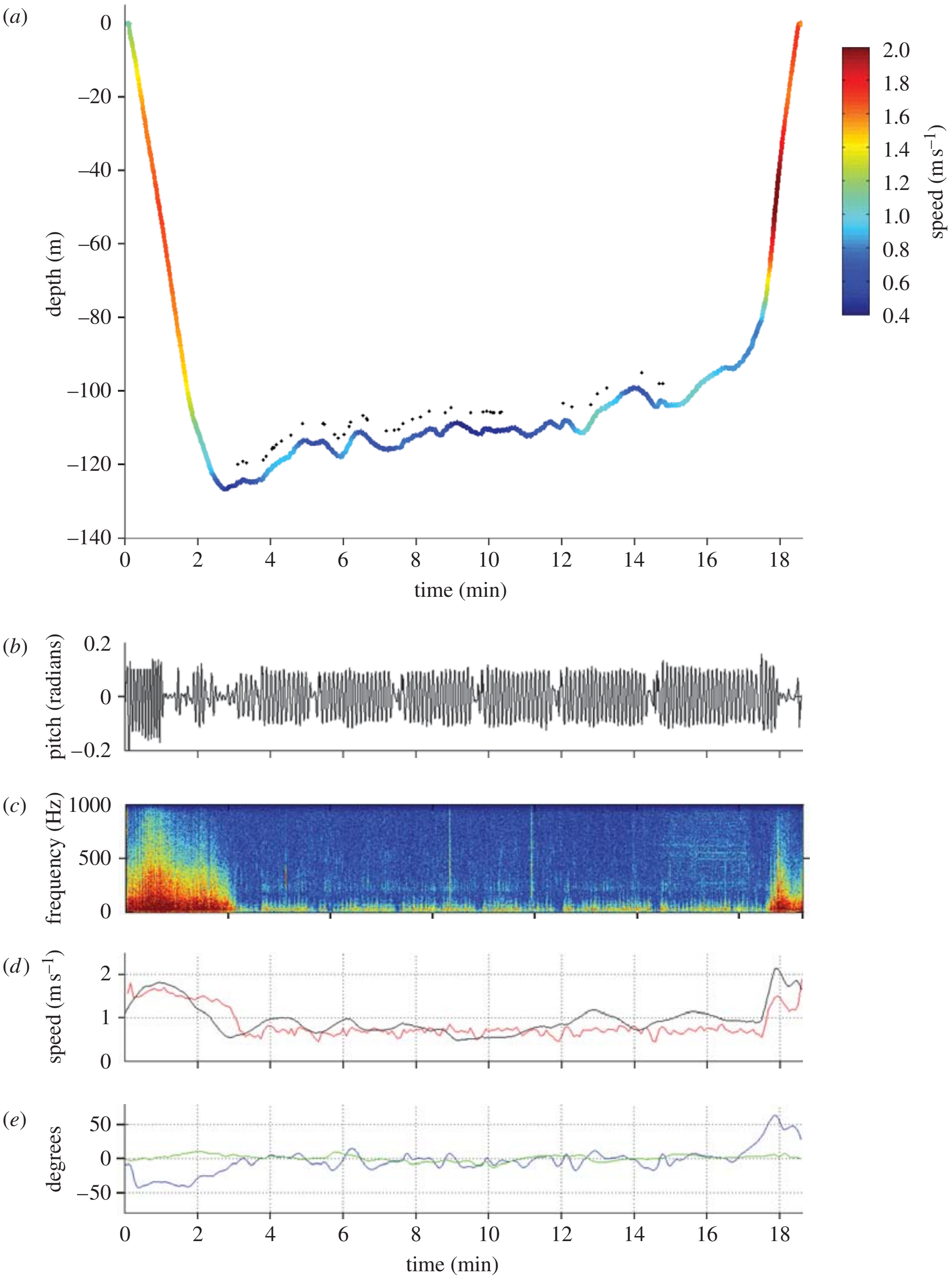


Figure 2. Bowhead whale foraging dive. (*a*) Dive profile showing the slow estimated speed in the bottom phase of the dive compared with the descent and ascent phases (colour bar). The dots indicate the time of recorded rattle-like sounds. (*b*) Cyclic variation in the pitch angle because of fluke strokes, indicating constant fluking during the bottom phase of the dive. (*c*) Spectrogram of the sound recording showing the higher levels of low frequency sound during the fast descent and ascent phases (fast Fourier transform (FFT) size 1024). (*d*) Speed estimated from the change in depth corrected for the pitch angle, filtered with a Kalman filter (black) and speed estimated from the low-frequency flow noise (red). (*e*) Pitch angle (blue) and roll angle (green).

have divided dives into two types—U- and V-dives—and suggested that balaenids employ ram filtration during the bottom phase of the U-dives (Nowacek *et al.* 2001; Baumgartner & Mate 2003; Laidre *et al.* 2007), whereas V-dives serve for travel and search for food (Laidre *et al.* 2007). Dive data presented here from bowhead whales in Greenland also follow a similar pattern of U- and V-dives, but the sensor array of the DTAG allowed us to test the assertion that U-dives are feeding dives.

An air-breathing diver should adopt an energy-efficient gait, matched to its instantaneous body form and behaviour throughout foraging dives so as to maximize net energy return. A filter-feeding balaenid passes through several body forms in a foraging dive from high buoyancy near the surface when the lungs are full of air to a lower buoyancy, more streamlined body form at greater depths (Nowacek *et al.* 2001). A third change in body form occurs when the whale opens its mouth to

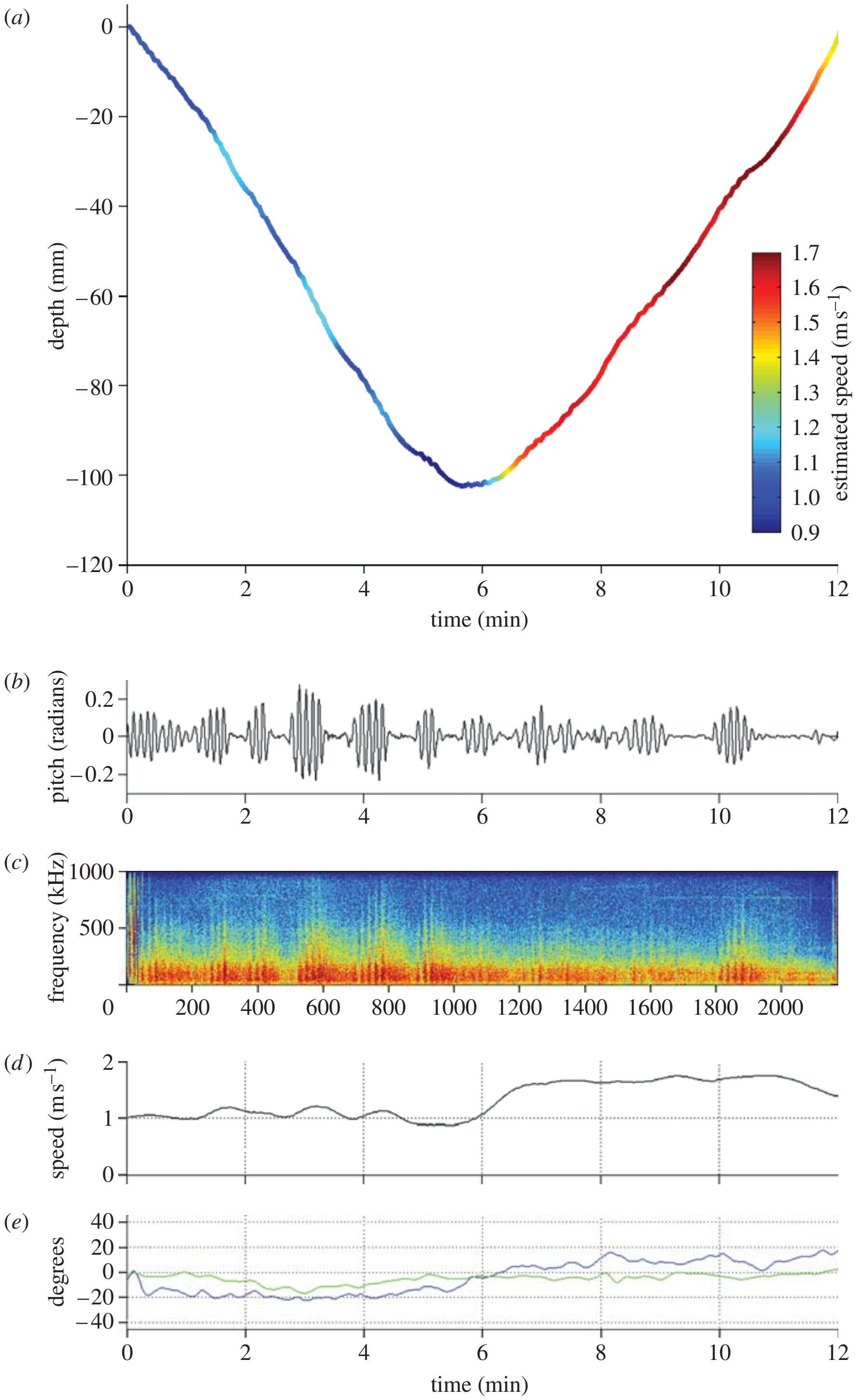


Figure 3. Bowhead whale non-foraging dive. (*a*) Dive profile showing the estimated Kalman-filtered speed in the colour bar. (*b*) The cyclic variation in pitch angle shows the bouts of fluke strokes, typical of a stroke-and-glide gait. (*c*) Spectrogram of sound recording showing the low-frequency sound recorded during descent and ascent of a non-foraging dive (FFT 1024). (*d*) Speed estimated from the change in depth corrected for pitch angle, filtered with a Kalman filter. (*e*) Pitch angle (blue) and roll angle (green).

filter water, probably incurring a drastic increase in the drag coefficient (Werth 2001, 2004). Tagged bowhead whales showed clear changes in gait associated with these changes in body form. When leaving the surface, whales performed a burst of rapid fluking (0.79 Hz instantaneous), giving way to a stroke-and-glide gait with slower fluking (0.08 Hz average during descent). The bottom phase of U-dives had significantly higher mean fluking rates compared with the descents and ascents of both V- and U-dives; whales fluked almost continuously at the bottom of U-dives with only very short breaks in the fluking effort. However, the instantaneous fluking rate of 0.12 Hz during the bottom phase was substantially lower than during bursts of fluking in the descent and ascent, and only half of the 0.25 Hz fluking rate predicted from scaling across a wide range of air-breathing marine vertebrates (Sato *et al.* 2007).

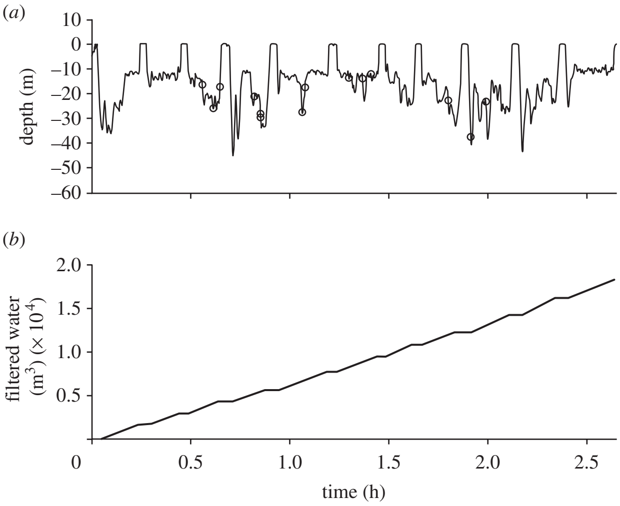


Figure 4. Filtering capacity of a feeding bowhead whale. (*a*) Dive profile from a bowhead whale feeding at 10–50 m depth. Rings indicate time when rattle-like sounds were recorded. (*b*) Accumulated filtered water during a 2.7 h feeding event, assuming a mean effective filter area of 4.23 m^2 and using the estimated swimming speeds in the bottom phases of the dives.

Given the higher average fluking rate during the flat bottom phase of U-dives, one would expect an *increase* in speed compared with the lower mean fluking rates of ascents and descents if the drag coefficient was unchanged. However, the estimated speeds *decrease* to about half of the speeds during descent and ascent. Thus in the bottom part of the U-dives, the whales fluke at least 50 per cent more per unit of time than in descents while almost halving their speeds from 1.4 to 0.8 m s^{-1}. The most parsimonious explanation for this reduction in speed is that their drag coefficient (Vogel 1994) has increased significantly through opening of their mouth for filter feeding (Werth 2004), an inference consistent with previous studies, proposing that whales feed during the bottom phase of U-dives. For this reason, we consider dives with flat bottom profiles, slow estimated speeds and continuous fluking to be foraging dives. Given the near-continuous fluking and slow estimated speeds during the bottom phase of foraging dives, we infer that the tagged whales filtered continuously throughout the bottom phase. That falsifies one of our initial hypotheses: that the relatively long foraging dives of bowheads result from intermittent filtering with the whale swimming with mouth closed in the intervening periods, allowing an oxygen-conserving stroke-and-glide gait. Instead, to cope with the high drag from the open mouth when ram filter feeding on plankton, bowhead whales use a slow continuous fluking gait that is radically different from the stroke-and-glide gait adopted by other nekton feeding air breathers at sea (Williams 2001; Sato *et al.* 2003, 2007; Woodward *et al.* 2006).

The buoyancy of a whale depends on the density of its tissue and the volume of air within its body (Nowacek *et al.* 2001; Miller *et al.* 2004). In this study, whales consistently fluked less but attained higher speeds during ascents (table 1), showing that they are positively buoyant even at depth. In fact, one individual ceased fluking altogether at 120 m depth on the ascent of a V-dive and drifted slowly towards the surface for some seconds, showing that their thick blubber layer may, in some cases, make these whales positively buoyant even when their lungs are compressed (Nowacek *et al.* 2001).

The dive times of large rorquals that employ lunge feeding are surprisingly short (5–10 min), and this has been explained by the high energetic costs of the lunges used to inflate their large buccal pouch with prey laden water (Acevedo-Gutiérrez *et al.* 2002). In comparison, foraging bowhead whales perform long foraging dives: the mean duration of 15.2 min (range 7–21 min, table 1) reported here is comparable to the mean dive times reported in another study of bowhead whales, 3–18 min (mean of U- and V-dives, Laidre *et al.* 2007), and of Northern right whales, 12.7 min (Baumgartner & Mate 2003). The dive duration varies with individual and, although the mean dive duration is just below 15 min, extreme dives of up to 48 min have been reported from some individuals (Laidre *et al.* 2007). Breath-hold dives of 12–15 min, in which the whale is continuously fluking for some 80 per cent of the time with an open mouth, would be very energetically costly if they happened at the normal swimming speeds of 1.5–2 m s^{-1} reported for cetaceans in general and adopted by balaenids feeding near the surface (Watkins & Schevill 1976; Mayo *et al.* 2001; Werth 2004). Instead, our speed estimates from the bottom phase of foraging dives support the alternate hypothesis of this paper, proposing that whales reduce the energetic cost of swimming with an open mouth by reducing their swimming speed and therefore their drag. As seen from figure 2 and table 1, both the Kalman-filtered speed estimates and speed estimates based on flow noise indicate that the speed drops significantly during the flat part of foraging dives, with mean speed estimates around 0.75 m s^{-1}, which is some 60 per cent of the speed during ascent and descent phases.

We therefore conclude that feeding bowheads move forward at an average speed of less than 1 m s^{-1} at depth. More specifically, our data indicate a mean speed of some 0.75 m s^{-1}, demonstrating that bowheads swim significantly slower when feeding at depth than reported in previous studies of whales observed at the surface (Watkins & Schevill 1976; Mayo *et al.* 2001; Werth 2004). It is also about half the stable average swim speeds between 1 and 2 m s^{-1} found across sizes ranging from 0.5 kg birds to 30 000 kg sperm whales (Sato *et al.* 2007). As drag increases with the square of speed at the Reynolds numbers in play here (Vogel 1994), a halving of speed should give a drag that is four times smaller for the same body shape. In our study, filter feeding bowhead whales swam at about one half of their descent and ascent speed while foraging, and yet needed an average fluking rate 1.5 times higher to maintain this low speed. This suggests that the drag coefficient increases by a factor of around 6 (1.5 × 4) when the whales swim with an open mouth, assuming a constant thrust per fluke stroke. For a given drag coefficient, the power, and hence oxygen consumption required to swim, increases with the cube of the swimming speed (Hind & Gurney 1997; Fish 2002). As the oxygen consumption sets the aerobic dive time (Kooyman *et al.* 1980), the slow swim speeds of feeding bowheads may represent an attempt to maximize dive time by reducing drag and hence oxygen consumption while swimming with the mouth open. Swimming at double the speed would, all other things being equal, increase oxygen consumption eightfold, while only doubling the volume of filtered water and prey.

It may seem ironic that one of the largest carnivores on the planet can capture enough prey by moving forward at less than 0.07 body length s^{-1}. However, whereas many nekton-eating predators need to swim at high speeds to locate and subdue agile but calorific prey, the copepod prey of bowhead whales moves slowly (approx. 4 mm s^{-1}, Wong 1988) and is found in extensive patches. Nonetheless, these small prey must be acquired in large numbers, calling for a large filter aperture that, in turn, creates a large drag coefficient and requires a lower foraging speed to maximize net energy gain. This implies that the minimum cost of transport for feeding bowheads occurs at speeds about one half of those found for similar sized fusiform marine endotherms (Sato *et al.* 2007). We conclude that balaenid ram filter feeding is a highly specialized behaviour, where not only the morphology of the filter apparatus of the predator is optimized for the capture of its slow small prey in dense patches (Werth 2004; Lambertsen *et al.* 2005), but also the locomotor system and the physiology that fuels it are adapted to work against a high drag at slow speeds using a continuous fluking gait very different from other air-breathing predators at sea.

The filter apparatus of an adult bowhead whale has an estimated mean effective cross-sectional area of 4.23 m^2 (Werth 2004). If we assume that the whales keep a constant gape and a mean swimming speed of 0.75 m s^{-1} (table 1) while feeding, the filtration rate is around 3.2 $m^3 s^{-1}$. So despite the slow swimming speed, the large mouth aperture can filter a remarkable volume of water over time. Figure 4 shows the estimated filtered water volume using the estimated speeds during ram filtration of one of the tagged whales. Over a period of 2.7 h, an estimated water volume of 18 000 m^3 passed through the filter of the whale. That raises the questions of how much food the whales collect over time and how often they must empty their filtering apparatus.

Overall, the whales in this study spent 29 per cent of the total tagged time feeding (i.e. at the bottom of a foraging dive moving at a slow speed with continuous fluking), resulting in an estimated daily filtering rate of some 80 000 m^3 of water per whale, assuming that the short tagging periods are representative of time allocation over a diurnal cycle. Based on a copepod concentration of 0.001 kg m^{-3}, Laidre *et al.* (2007) concluded that a bowhead whale should filter more than 800 000 m^3 of water per day just to meet its estimated field metabolic rate (FMR). If a whale spends only 7 h d^{-1} (29% of the time) with its mouth open, it would have to filter 31.7 m^3 of water s^{-1} when feeding at these copepod densities. With a mean effective filter area of 4.23 m^2, it would translate into a mean swimming speed of 7.5 m s^{-1}. This is about an order of magnitude above our estimate and highly unlikely given the 100-fold higher drag force at such a speed. While the 29 per cent foraging time may be an underestimate, it is evident that either the FMR is widely overestimated or that the prey density where the whales feed has been grossly underestimated, as suggested by Laidre *et al.* (2007). Assuming that the FMR estimate of Laidre *et al.* (2007) is correct, whales moving at 0.75 m s^{-1} would require copepod patches with a mean density of 0.01 kg m^{-3}, 10 times higher than Laidre's figure but in line with the prey densities reported in the vicinity of foraging Northern right whales (Mayo & Goldman 1992; Beardsley *et al.* 1996).

During the bottom phase of foraging dives, we observed brief pauses in fluking with durations around 2 s (i.e. the duration of about half a fluke stroke when feeding) at fairly regular intervals with a mean interval of 2.4 min (s.d.=0.65) (figure 2). Similar brief pauses have also been observed in ram filtering Northern right whales (Nowacek *et al.* 2001). Although ram filter feeding whales are believed to be able to continuously filter for hours (Baumgartner & Mate 2003; Laidre *et al.* 2007), they will probably need to clean the collected prey from the baleen plates periodically to ingest prey and maintain water flow through the baleen (Werth 2001). Cleaning could be achieved by shaking the head, using the muscular tongue to scrape off prey, back flushing trapped prey, or a combination of all three methods (Werth 2001). If we interpret the regular pauses in the fluking correctly to be cleaning of the baleen, our data suggest that this happens every 2.5 min, corresponding to some 480 m^3 of filtered water. The regularity of the gesture suggests that prey is acquired at a fairly constant rate consistent with the idea that the whales are feeding in an extensive patch with sufficiently high prey density to support continuous filtration.

Other ram filter feeding animals carefully balance food uptake with energy consumption and oxygen assimilation over the gills (Sims & Quayle 1998; Sims 1999). For example, basking sharks decrease locomotion in low food concentrations to save energy when food concentrations are low (Sims & Quayle 1998; Sims 1999). Herring switch from ram filtering to particulate feeding when food densities drop and the increased food uptake of filter feeding no longer compensates the increased energetic cost of ram filter feeding (Gibson & Ezzi 2006). Similarly, it seems energetically important that bowhead whales only open their mouths in areas of high food density and keep the mouth shut when energetic costs of ram filter feeding are too high relative to the food intake (Mayo & Marx 1990). The non-foraging dives observed here generally reach the same depth as feeding dives and may reflect that the whales search for food patches in some of those dives, but that they do not encounter prey densities worth targeting. We have shown that the bowhead whales feed in all parts of the water column, not only close to the surface or bottom where there are physical boundaries to guide the whales to the food patches or constrain the prey (figures 1 and 4). This fact, along with the need for much higher copepod densities than found on average, suggests that bowhead whales employ sensory cues to locate high density food patches and guide them as to when to open their mouth. How and with what means they locate these food patches offers an intriguing challenge for future studies on these large, slow filter feeders of the Arctic.

The research was conducted under a permit granted by the Greenland Government to GINR.

We thank A. Brandt, A. Isaksen, Arctic Station and F. Ugarte for invaluable help in the field. F. Ugarte, A. Werth, M. Baumgartner, D. Costa, M. P. Heide-Jørgensen,

K. L. Laidre and two reviewers are thanked for helpful discussions and critique. M.S. was funded by the Oticon Foundation and KIIIN, Greenlandic Home Rule, P.T.M. by Steno and frame grants from the National Danish Science Foundation and M.J. and P.L.T. by NOPP and SERDP grants.

REFERENCES

Acevedo-Gutiérrez, A., Croll, D. A. & Tershy, B. R. 2002 High feeding costs limit dive time in the largest whales. *J. Exp. Biol.* **205**, 1747–1753.

Aguilar Soto, N., Johnson, M., Madsen, P. T., Díaz, F., Domínguez, I., Brito, A. & Tyack, P. 2008 Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *J. Anim. Ecol.* **77**, 936–947. (doi:10.1111/j.1365-2656.2008.01393.x)

Baumgartner, M. F. & Mate, B. R. 2003 Summertime foraging ecology of North Atlantic right whales. *Mar. Ecol. Prog. Ser.* **264**, 123–135. (doi:10.3354/meps264123)

Beardsley, R., Epstein, A. W., Chen, C., Wishner, K. F., Macaulay, M. C. & Kenney, R. D. 1996 Spatial variability in zooplankton abundance near feeding right whales in the Great South Channel. *Deep Sea Res. Part II. Topical Stud. Oceanogr.* **43**, 1601–1625. (doi:10.1016/S0967-0645(96)00050-1)

Burgess, W. C., Tyack, P. L., Le Boeuf, B. J. & Costa, D. P. 1998 A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Deep Sea Res. II* **45**, 1327–1351. (doi:10.1016/S0967-0645(98)00032-0)

Costa, D. P. & Sinervo, B. 2004 Field physiology: physiological insights from animals in nature. *Annu. Rev. Physiol.* **66**, 23.1–23.30.

Crocker, D. E., Le Boeuf, B. J. & Costa, D. P. 1997 Drift diving in female northern elephant seals: implications for food processing. *Can. J. Zool.* **75**, 27–39. (doi:10.1139/z97-004)

Croll, D. A., Acevedo-Gutiérrez, A., Tershy, B. & Urbán-Ramírez, J. 2001 The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? *Comp. Biochem. Physiol. A* **129**, 797–809. (doi:10.1016/S1095-6433(01)00348-8)

Diamond, J. A. 1985 Filter-feeding on a grand scale. *Nature* **316**, 679–680. (doi:10.1038/316679a0)

Fish, F. E. 2002 Speed. In *Encyclopaedia of marine mammals* (eds W. F. Perrin, B. Würsig & J. G. M. Thewissen), pp. 1161–1163. San Diego, CA: Academic Press.

Fish, F. E., Peacock, J. E. & Rohr, J. J. 2003 Stabilization mechanism in swimming odontocete cetaceans by phased movements. *Mar. Mamm. Sci.* **19**, 515–528. (doi:10.1111/j.1748-7692.2003.tb01318.x)

Fletcher, S., Le Boeuf, B. J., Costa, D. P., Tyack, P. L. & Blackwell, S. B. 1996 Onboard acoustic recording from diving northern elephant seals. *J. Acoust. Soc. Am.* **100**, 2531–2539. (doi:10.1121/1.417361)

Gibson, R. N. & Ezzi, I. A. 2006 The relative profitability of particulate- and filter-feeding in the herring, *Clupea harengus* L. *J. Fish Biol.* **40**, 577–590. (doi:10.1111/j.1095-8649.1992.tb02607.x)

Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A. & Hildebrand, J. A. 2006 Kinematics of foraging dives and lunge-feeding in fin whales. *J. Exp. Biol.* **209**, 1231–1244. (doi:10.1242/jeb.02135)

Hassrick, J. L., Crocker, D. E., Zeno, R. L., Blackwell, S. B., Costa, D. P. & Le Boeuf, B. J. 2007 Swimming speed and foraging strategies of northern elephant seals. *Deep Sea Res. II* **54**, 369–383. (doi:10.1016/j.dsr2.2006.12.001)

Heide-Jørgensen, M. P., Laidre, K. L., 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.

Hind, A. T. & Gurney, W. S. C. 1997 The metabolic cost of swimming in marine homeotherms. *J. Exp. Biol.* **200**, 531–542.

Johnson, M. P. & Tyack, P. L. 2003 A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Ocean Eng.* **28**, 2–12. (doi:10.1109/JOE.2002.808212)

Kooyman, G. L., Wahrenbrock, E. A., Castellini, M. A., Davis, R. W. & Sinnett, E. E. 1980 Aerobic and anaerobic metabolism during voluntary diving in Weddel seals: evidence of preferred pathways from blood chemistry and behavior. *J. Comp. Physiol.* **138**, 335–346.

Kramer, D. L. 1988 The behavioural ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89–94. (doi:10.1139/z88-012)

Laidre, K. L., Heide-Jørgensen, M. P. & Nielsen, T. G. 2007 Role of the bowhead whale as a predator in West Greenland. *Mar. Ecol. Prog. Ser.* **346**, 285–297. (doi:10.3354/meps06995)

Lambertsen, R. H., Rasmussen, K. J., Lancaster, W. C. & Hintz, R. J. 2005 Functional morphology of the mouth of the bowhead whale and its implications for conservation. *J. Mamm.* **86**, 342–352. (doi:10.1644/BER-123.1)

Mayo, C. A. & Goldman, L. 1992 Right whale foraging and the plankton resources in Cape Cod and Massachusetts Bays. In *The right whale in the western North Atlantic: a science and management workshop* (ed. J. Hain), pp. 43–44. Northeast Fish Sci Cent Ref Doc. 92-05.

Mayo, C. A. & Marx, M. K. 1990 Surface foraging behaviour of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Can. J. Zool.* **68**, 2214–2220. (doi:10.1139/z90-308)

Mayo, C. A., Letcher, B. H. & Scott, S. 2001 Zooplankton filtering efficiency of the baleen of a North Atlantic right whale, *Eubalaena glacialis*. *J. Cetacean Res. Manag. Special Issue* **2**, 225–229.

Miller, P. J. O., Johnson, M. P., Tyack, P. L. & Terray, E. A. 2004 Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J. Exp. Biol.* **207**, 1953–1967. (doi:10.1242/jeb.00993)

Nowacek, D. P., Johnson, M., Tyack, P., Shorter, K. A., McLellan, W. A. & Pabst, D. A. 2001 Buoyant balaenids: the ups and downs of buoyancy in right whales. *Proc. R. Soc. Lond. B* **268**, 1811–1816. (doi:10.1098/rspb.2001.1730)

Pivorunas, A. 1979 The feeding mechanisms of baleen whales. *Am. Sci.* **67**, 432–440.

Ropert-Coudert, Y., Kato, A., Wilson, R. P. & Cannell, B. 2006 Foraging strategies and prey encounter rate in free-ranging Little Penguins. *Mar. Biol.* **149**, 139–148. (doi:10.1007/s00227-005-0188-x)

Sanderson, S. L. & Wassersug, R. 1990 Suspension-feeding vertebrates. *Sci. Am.* **262**, 96–101.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. & Naito, Y. 2003 Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J. Exp. Biol.* **206**, 1461–1470. (doi:10.1242/jeb.00265)

Sato, K. *et al.* 2007 Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc. R. Soc. B* **274**, 471–477. (doi:10.1098/rspb.2006.0005)

Sims, D. W. 1999 Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge? *Proc. R. Soc. Lond. B* **266**, 1437–1443. (doi:10.1098/rspb.1999.0798)

Sims, D. W. & Quayle, V. A. 1998 Selective foraging behaviour of basking sharks on zooplanton in a small-scale front. *Nature* **393**, 460–464. (doi:10.1038/30959)

Vogel, S. 1994 *Life in moving fluids. The physical biology of flow.* Princeton, NJ: Princeton University Press.

Watanuki, Y., Niizuma, Y., Gabrielsen, G. W., Sato, K. & Niato, Y. 2003 Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proc. R. Soc. Lond. B* **270**, 483–488. (doi:10.1098/rspb.2002.2252)

Watkins, W. A. & Schevill, W. E. 1976 Right whale feeding and baleen rattle. *J. Mamm.* **57**, 58–66. (doi:10.2307/1379512)

Watwood, S. L., Miller, P. J. O., Johnson, M., Madsen, P. T. & Tyack, P. 2006 Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J. Anim. Ecol.* **75**, 814–825. (doi:10.1111/j.1365-2656.2006.01101.x)

Werth, A. J. 2001 How do mysticetes remove prey trapped in baleen? *Bull. Mus. Comp. Zool.* **156**, 189–203.

Werth, A. J. 2004 Models of hydrodynamic flow in the bowhead whale filter feeding apparatus. *J. Exp. Biol.* **207**, 3569–3580. (doi:10.1242/jeb.01202)

Williams, T. M. 1999 The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Phil. Trans. R. Soc. Lond. B* **354**, 193. (doi:10.1098/rstb.1999.0371)

Williams, T. L. 2001 Intermittent swimming by marine mammals: a strategy for increasing energetic efficiency during diving. *Am. Zool.* **41**, 166–176. (doi:10.1668/0003-1569(2001)041[0166:ISBMAS]2.0.CO;2)

Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J. & Croll, D. A. 2000 Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**, 133–136. (doi:10.1126/science.288.5463.133)

Wilson, R. P., Ropert-Coudert, Y. & Kato, A. 2002 Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. *Anim. Behav.* **63**, 85–95. (doi:10.1006/anbe.2001.1883)

Wong, C. K. 1988 The swimming behavior of the copepod *Metridia pacifica*. *J. Plankt. Res.* **10**, 1285–1290. (doi:10.1093/plankt/10.6.1285)

Woodward, B. L., Winn, J. P. & Fish, F. E. 2006 Morphological specializations of baleen whales according to ecological niche. *J. Morphol.* **267**, 1284–1294. (doi:10.1002/jmor.10474)

Zimmer, W. M. X., Johnson, M., Madsen, P. T. & Tyack, P. 2005 Echolocation clicks of free-ranging Cuvier's beaked whales (*Ziphius cavirostris*). *J. Acoust. Soc. Am.* **117**, 3919–3927. (doi:10.1121/1.1910225)

Kinematics of humpback whale lunges

Chapter 3

Paper II:
Simon M, Johnson M & Madsen PT. *In prep*.

Keeping momentum with a large mouthful of water: Behavior and kinematics of humpback whale lunge feeding.
Manuscript prepared for submission to J Exp Biol

Keeping momentum with a large mouthful of water: Behavior and kinematics of humpback whale lunge feeding

Simon, M. (1,2)*, Johnson, M. (3) and Madsen, P.T. (1,3).

1. Zoophysiology, Department of Biological Sciences, Aarhus University, C. F. Møllers Allé, Build 1131, 8000 Aarhus C. Denmark.
2. Department of Birds and Mammals, Greenland Institute of Natural Resources, P.O. Box 570, Kivioq 2, 3900 Nuuk, Greenland.
3. Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.
*email of corresponding author: masi@natur.gl

Short title: Kinematics of lunging humpback whales

Keywords: humpback whale, *Megaptera novaeangliae*, lunge, kinematics, feeding, behavior

Summary

Rorqual baleen whales lunge feed by rapid engulfment of many tons of prey-laden water in a large and expandable buccal pouch. This process is energetically costly and probably accounts for the strikingly short dive times of large rorquals. According to the currently held view on lunge feeding, the lunge feeding whale accelerates prior to mouth opening to attain a high speed to expand and fill the buccal pouch with water. The increased drag from the open mouth then decelerates the whale to a near halt after which the engulfed water is filtered through the baleens as the whale flukes to pick up speed for the next lunge. Here, we use archival tags (DTAGs) in a fine-scale kinematic study of lunge feeding in humpback whales to investigate the paradox that such large animals that attain high Reynolds numbers while moving should develop a feeding strategy that involves a near stop hundreds of times a day. Analysis of 357 lunges from 6 whales reveals a high degree of stereotypy and consistent timing in the choreography of lunging indicating that this behavior is controlled by biomechanical limitations rather than by food density. We show that lunge feeding humpback whales time their fluking through the lunge so as to accelerate the engulfed water mass and keep momentum thereby avoiding a near or complete stop despite the high drag. We conclude that it is not the drag of the open mouth but rather the acceleration of the large volume of engulfed water that primarily makes lunge feeding costly and limits the dive time in rorquals.

Introduction

Air-breathing marine animals display physiological and behavioral adaptations to a life in water where two vital resources are separated in space: air at the surface and food at depth (Kramer 1988). To increase time at foraging depth, breath-hold diving animals employ a range of oxygen conserving measures, including a fluke and glide gait which reduces the cost of transport and hence the consumption rate of oxygen (Williams et al. 2000; Watanuki et al. 2003). Rorquals, to which blue, fin and humpback whales belong, include the largest animals ever to have evolved. A number of advantages accrue from large body sizes when economizing oxygen stores in breath-hold foraging: Larger animals have a higher ratio between the carrying capacity of oxygen (Hochachka and Somero 1984; Kooyman, 1989) and the mass-specific metabolism compared to smaller animals (Kooyman et al. 1980), and a lower mass-specific drag (higher Reynolds number), favoring efficient fluke and glide swimming (Williams et al. 2000). Accordingly, the dive times for marine mammals generally increase with body size (Hochachka and Somero 1984; Kooyman, 1989). However, the large rorquals and balaenids seem to break this rule by performing much shorter dives than would be expected given their size (Croll et al. 2001; Acevedo-Gutiérrez et al. 2002). Balaenids and rorquals belong to the baleen whales (Mysticeti), and are specialized in filtering prey from the water with rows of keratinized baleen plates hanging from the roof of the mouth (Croll and Tershy 2002). Their relatively short dive times have been explained by the energetic costs of opposing the high drag of an open mouth when the whales feed (Croll et al. 2001; Acevedo-Gutiérrez et al. 2002). Despite the similarity in filtration apparatus, the two families of baleen whales have adopted very different strategies for prey harvesting. Balaenids generally target slow swimming prey (copepods) using continuous ram-filtration. Their relatively long feeding dives, compared to rorquals, seem to be enabled by extremely slow swimming speeds (<0.1 body lengths s^{-1}) while foraging (Simon et al. 2009). As oxygen consumption increases with the cube of speed, balaenids reduce their drag and hence oxygen consumption dramatically by slow swimming, despite gape areas of more than $4m^2$ (Werth 2004). Rorquals on the other hand target elusive and fast-moving prey, such as schooling fish and must employ foraging methods that are matched to the speed of their prey (Croll and Tershy 2002). The usual rorqual foraging mode is lunge-feeding in which the whale accelerates forward in a burst of energetic fluking to reach a high speed prior to opening the mouth and engulfing a volume of prey-laden water comparable to their own body volume (Goldbogen et al. 2007; 2009). The tissue of the throat and the ventral thorax is pleated into longitudinal furrows, extending from the jaw until one third of the way down the body, forming the highly extendable ventral buccal pouch (Pivorunas 1979). When encountering prey laden water, anatomical specializations in the mandible enable rorquals to increase the mouth aperture; the mandibles rotate outwards as the mouth opens and the frontomandibular stay allows the opening of the jaw to reach nearly 90 degrees to the skull (Lambertsen et al. 1995). After engulfment the mouth closes, and the elastic recoil of the ventral pouch, and muscle contractions of the ventral pouch force the water out through the baleen plates, leaving the prey on the inside of the baleen (Pivorunas 1979; Lambertsen 1983; Orton and Brodie 1987). Thus, in contrast to balaenids, rorquals forage in discrete energetic bursts with each lunge followed by an obligate refractory period in which engulfed water is expelled through the baleen plates and prey are swallowed (Jurasz and Jurasz 1979; Lambertsen 1983; Orton and Brodie 1987).

Until recently, lunge-feeding had only been described from surface observations (Watkins and Schevill 1979; Jurasz and Jurasz, 1979; Orton and Brodie, 1987; Croll et al., 2001). Recently, Goldbogen et al. (2006, 2008) reported the first field measurements from sub-surface lunge feeding fin and humpback whales instrumented with archival tags that log total acceleration, depth and flow noise (which was used as a proxy for speed). Based on these recordings, Goldbogen et al. (2006) proposed an acceleration-deceleration model for lunge feeding in which the whale accelerates in a burst of energetic fluking and then opens its jaws when sufficient speed is attained ($>3\text{ms}^{-1}$). Jaw opening initiates a rapid deceleration of the whale due to the increased drag forces from the open mouth. This deceleration ultimately brings the whale to a near stand-still at the end of the lunge requiring additional fluking for the whale to regain forward way. The lunge cycle is then completed with a period of gliding until a new bout of fluking marks the beginning of the next lunge (Goldbogen et al. 2006, 2007). Reacceleration of the body from close to zero speed after each lunge is energetically costly and may be the key factor determining oxygen consumption in lunge foraging (Goldbogen et al. 2006) if the Goldbogen model is correct. However, the almost complete loss of forward momentum in each lunge predicted by this model raises objections from both energetic and evolutionary considerations.

The large rorquals generally operate at high Reynolds numbers while swimming, meaning that viscous forces are of less importance than inertial forces in keeping momentum (Vogel 1994). Rather, acceleration of a large body mass is energetically expensive for such animals. Rorquals reflect that fact by using a fluke and glide gait: building up momentum from short bursts of fluking and saving oxygen while gliding, taking advantage of the high Reynolds numbers. It therefore seems a conundrum that these large filter feeders that are morphologically adapted to a highly specialized hunting strategy, should bring themselves and the engulfed water to a near stop, when keeping up the speed through a lunge might save energy and increase the valuable foraging time at depth.

The interpretations that have led to the model of Goldbogen and coworkers critically hinges on being able to quantify the right kinematic parameters and their relative timing. The understanding of the biomechanics, kinetics, and timing of rorqual lunge feeding present a key in understanding the functional morphology, life history and eco-physiology of these the largest mammals to ever live. To uncover the fine-scale kinematics of lunge feeding, precise measurements of the whale's speed and the relative timing of the mouth opening and closing are required. However, accurate sensors for forward speed and gape are not currently available. In their study, Goldbogen et al. relied on the low frequency flow noise amplitude recorded by the tag as a proxy for speed while mouth opening state was deduced from the combination of speed and fluking indications derived from an accelerometer in the tag. The relationship between speed and flow noise was derived from measurements on a towed body and data collected on descending or ascending whales where the depth rate is a good speed estimator (Goldbogen et al., 2006). However, the relationship between flow noise and forward speed must depend on the body form and gait, both of which will change during lunges where heaving fluking is taking place and where the whale opens its mouth. Thus speed estimates from flow noise are of uncertain value during lunges calling into question the kinematic models developed from these estimates and inferred timing with mouth opening and closure. The Goldbogen study was also limited by a low sensor sampling rate of 1 Hz which gives rather few samples to work with during the critical acceleration/deceleration phases of a lunge. Given these limitations, the details, and therefore the energetic implications of what has aptly been coined the largest biomechanical action on earth (Brodie 1993) remain in our view open to debate.

To examine the fine-scale timing and development of forces in balaenopterid lunge feeding, we applied suction cup attached DTAGs (Johnson and Tyack, 2003) to 6 humpback whales. The tags sampled triaxial accelerometers, magnetometers and a pressure sensor at 50 Hz allowing fine-scale reconstruction of body movements due to fluking and changes in posture. More specifically we I. investigate the relative timing of lunge events of a rorqual lunge introducing the concept of jerk signatures as a proxy for mouth opening, II test the hypothesis that the highly specialized rorquals brings themselves to a near standstill hundreds of times a day at great depths. We show that humpback whale lunges have a high degree of stereotypy and follows strickt timing in the choreography, indicating that the biomechanical restrictions and not prey density limit the lunging frequency. Further we demonstrate that humpback whales do not perform an acceleration-deceleration behavior, but fluke to accelerate the engulfed water and exploit their high Reynolds numbers to keep momentum while gliding between lunges.

Materials and methods

Humpback whales in Nuup Kangerlua (Godthaab Fjord), West Greenland (N 64.2, W 51.8) were tagged with non-invasive, archival tags (DTAG, Johnson and Tyack, 2003) to record data on their three-dimensional movements during lunge feeding. Humpback whales were located either from a vantage point on land or by searching the fjord with two small boats. Whales were approached slowly, and the tag was delivered to the dorsal surface of the whale using a 7m hand-held carbon fiber pole (2007) or a 12m cantilevered carbon pole (2008) (Moore et al. 2001). Tags attached rigidly to the skin surface, approximately midway between the anterior and posterior end of the whale using four soft silicone suction cups. The cups detached after a pre-programmed period and the tag was retrieved using VHF tracking.

DTAG

The DTAG is an archival tag that streams sound and orientation data to a 3-18GB solid state memory using loss-less compression (Johnson and Tyack, 2003). Three-axis magnetometers and accelerometers provide signals relating to the orientation and acceleration of the animal in three dimensions and a pressure sensor provides depth information. All sensors are sampled at 50Hz with 16 bit resolution and decimated to a sampling-rate of 25Hz in post-processing. Each sensor channel has a single pole anti-alias (low-pass) filter at 5Hz and decimation is achieved using identical 24-tap symmetric FIR filters on each channel. The accelerometer and magnetometer data were corrected for the tag orientation on the whale by rotating each three-element vector by a direction-cosine matrix derived from the tag orientation when the whale surfaces. The resulting rotated vectors represent the sensor measurements that would be made if the tag axes coincided with the body axes of the whale (Johnson and Tyack, 2003). Sounds were recorded continuously from a build-in hydrophone with a sampling rate of 96kHz, 16 bit resolution, and a flat (±3dB) frequency response from 0.5 to 47kHz (Johnson and Tyack, 2003).

Detecting fluking, lunging and orientation

Fluke movements during cetacean swimming cause undulations through most of the body (Fish et al. 2003) and are therefore detectable in on-animal accelerometer data as cyclical variations (Johnson and Tyack, 2003; Goldbogen et al., 2006). The duration of each fluke stroke was measured from the time lapse between pairs of peaks in the high-pass filtered dorsal-ventral acceleration signal. The magnitude of the acceleration signal recorded during fluking is dependent on both the orientation change of the body (i.e., due to pitching motions) and the specific acceleration of the animal at the tag location (i.e., the acceleration other than gravity due to, for example, surge and heave). Both of these two acceleration components have energy at the fluking rate and cannot be separated, in general, without additional information, e.g. from gyroscope measurements (Johnson et al. 2009). This means that the acceleration cannot be integrated to give a speed estimate. Both orientation and specific components in the measured acceleration are also dependent on the position of the tag on the body and the gait of the whale, making the magnitude of the accelerometer signal only useful as a relative (i.e., intra-individual) estimator of fluking strength. Nonetheless, the energetic fluking during rorqual lunges produces distinctive accelerometer signals (Goldbogen et al., 2006) that can be used to define movement events within lunges. The acceleration due to gravity is 1g or $9.8ms^{-2}$, and so measured accelerations that differ from this are reliable indicators of specific accelerations. Although it is not possible to estimate the specific acceleration accurately, an under-bound on its magnitude can be obtained from the norm of the measured tri-axial acceleration $||A|| = \text{sqrt}\ (ax^2+ay^2+az^2)$. The acceleration measured by the tag, A, can be expressed in g's as:

$$A_t = Q_tG + D_t \qquad (1)$$

where G is the gravitational acceleration vector $[0,0,1]^T$ (defined here in a right-hand frame with axes North, West and Down), Q_t is a direction cosine matrix defining the orientation of the tag with respect to the inertial frame as a function of time t, and D_t is the specific acceleration vector, also a function of t. Re-arranging (1) and taking the norm of both sides gives:

$$||D||^2 = ||A||^2 + ||QG||^2 - 2A^TQG$$

Re-arranging and applying the Schwarz inequality (Golub and Loan, 1996) gives:

$$||D||^2 >= ||A||^2 + ||QG||^2 - 2||A||\ ||QG|| \qquad (2)$$

As direction cosine matrices are unitary (Grewal et al. 2001), $||QG|| = ||G|| = 1$ g. So (2) becomes:

$$||D||^2 >= ||A||^2 - 2||A|| + 1$$

or $$||D|| >= |\ ||A||-1\ | \qquad (3)$$

Thus, the magnitude of the specific acceleration is under-bound by $|||A||-1|$ g and we call this quantity the excess acceleration. Using this result, we considered a lunge to take place whenever there was an isolated group of fluke strokes with a large well-defined excess acceleration (>0.3 G) and time 'zero' of the lunge was initially defined as the time of the maximum excess acceleration. Secondly, to create timing information independent of the inertial sensor suite for analysing the timing of lunge-events, we derived a second set of time cues using the flow noise profile, defining time 'zero' of the lunge at the half power end point in flow noise in a lunge.

In lunges performed at depth similar forces from e.g. gravity, buoyancy and drag acted on the whales throughout the lunge. This is in contrast to surface lunges where the whale brings part of the body out of the water at the end of the lunge and a new set of counter directional forces affect the speed and behavior of the lunging whale when moving from water to air. To avoid complication by the forces affecting the animal breaking the surface, we only analyzed lunges below 40m (approx 3 body lengths) of depth.

Goldbogen et al. (2006) estimated speed from the low frequency flow noise over the tag using a third octave filter at 50Hz (i.e., 13Hz bandwidth) to process the sound. They considered a peak in the flow noise corresponding to a speed greater than 2ms^{-1} to indicate a lunge. The tag used here includes a single-pole high pass filter at 400Hz precluding replication the method of Goldbogen. Instead, we low-pass filtered the sound recording (4th order Butterworth filter at 500Hz) and computed the root-mean-square (RMS) level in 40ms blocks to obtain a low frequency noise level estimate with the same sampling rate as used for the non-acoustic tag sensors. The noise level at 400Hz is still dominated by fluke-movement and flow noise but may also contain contributions from boat noise and vocalizations.

Speed estimation

Fine time-scale speed estimation of animals swimming underwater is challenging. Usually, measurements can only be made at a single location on the animal (i.e., the tag position) and vectorial measurements are rarely feasible due to size constraints. A number of indirect methods have been used to measure speed on marine animals: paddlewheels (Blackwell et al. 1999), bending filaments (Shepard et al. 2007) flow-noise (Burgess et al. 1998) and orientation-corrected depth rate (Miller et al., 2004). However, two sources of error impact these sensors. The first results from the flexibility of the animal. By 'speed' we typically mean the rate of progress of an animal along its mean trajectory. However, during swimming a majority of the body undulates with each point following its own trajectory around the mean trajectory (Fish et al., 2003). For a cetacean, most of the body displacement from fluking is in the plane formed by the longitudinal and dorso-ventral axes (Fish et al. 2003), moving the tag . The magnitude of the dorso-ventral or heave component depends on the measurement location with the smallest amplitudes at the rostrum (Fish et al., 2003). As it is rarely possible to tag an animal so far forward, the tag will move, to first order, in a sinusoidal trajectory with instantaneous speed of the tag given by:

$$s_t = s_f + d\omega\cos\omega t \qquad (4)$$

where s_f is the forward speed of the whale, d is the peak dorso-ventral body displacement at the measurement point and ω is the fluking rate in radians/s. For a humpback whale fluking energetically, ω could be 3 (i.e., 2π x a fluking rate of 0.5 Hz) and d might be 1 m for a tag located near the dorsal fin during energetic fluking. If the whale has a forward speed of 2ms^{-1}, the instantaneous speed of the tag will vary between 2 and 3.6ms^{-1} during each fluke stroke. That is, a non-directional speed sensor such as one based on flow noise level, will tend to overestimate the forward speed during strong fluking because a significant proportion of the tag motion is in the dorsal-ventral axis.

Another source of error, impacting directional speed sensors or speed estimates derived from the orientation corrected depth rate is due to lift. With lift, the mean axis of movement does not coincide with the longitudinal axis of the whale leading to underestimation of speed. The extent to which whales exploit lift is not well known, but lift angles of less than 30° seem likely resulting in maximum speed errors of around 15%.

Given these relative error magnitudes, we used orientation-corrected depth-rate for speed estimation rather than flow noise. This estimate is formed from (Miller et al., 2004):

$$\hat{s}t = 1/\sin(\theta t).\ dpt/dt \qquad (5)$$

where p is the depth (i.e., pressure) and θ is the pitch angle with $\theta=0$ representing a nominally horizontal body position and $\theta=-90$ representing a vertically downward body orientation. To get a reliable measure of the overall pitch of the whale during a lunge, we computed the mean of the low pass filtered (0.5Hz, 4 poles) accelerometer signal over ten seconds (time zero of the lunge ±5sec). The accuracy of this speed estimator is not only impacted by lift, but also by errors in θ due to specific acceleration during fluking. In the absence of specific acceleration, $\sin(\theta)$ is given by the caudal-rostral acceleration, a_x, but when the whale changes speed rapidly such as during lunges this is a poor estimator. However, these intervals can be detected fairly reliably using the excess acceleration defined above. For small errors in a_x (e.g., due to undetected specific acceleration or misalignment of the tag), the fractional error in speed will be approximately equal to the fractional error in a_x. At absolute pitch angles greater than 30°, an error in ax of $1 ms^{-2}$ will result in a speed error of less than 25%. Thus, eqn (5) is a fair proxy for speed provided that (i) the absolute pitch angle is not close to zero, (e.g., $|\theta|>20^\circ$ or $|ax| > 3.4 ms^{-2}$) and (ii) the excess acceleration is low ($<1 ms^{-2}$).

To estimate the speed of the animals during descent and ascent of foraging dives we applied a Kalman filter (Zimmer et al., 2005) on instantaneous speed estimates (Equation 5). The inherent smoothing of a Kalman filter and the large error potential at low pitch angles render Kalman filtered speed data unsuited for uncovering the potentially fast speed changes around lunges. Due to the large specific acceleration of the body at time zero of the lunge (by the above definition), it is not possible to measure the speed at the peak acceleration of the lunges. Instead we calculated the depth rate (differential of the output of the pressure sensor) at time 0 ±5sec, providing a lower bound on the actual speed. To quantify the absolute speed development in the last phase and immediately after a lunge (when pitch was still high and the excess acceleration was low due to less energetic fluking), we calculated the mean speed 10 seconds after time zero as the depth rate in each bin (1 sec) divided with the sine of the mean pitch in each bin (1sec) (using Equation 5).

Jerk signatures

The acceleration rate or jerk, estimated by the differential of the triaxial acceleration signal, is a useful indicator of dynamics in orientation and movement of the whale. To combine this vectorial signal into a more easily visualized scalar, we computed the norm of the differentiated acceleration, i.e., $j_t = ||A_t - A_{t-1}||*f_s$. Steady fluking will give rise to cyclical variations in j at the fluking rate while gliding will give low jerk values. Unsteady forces on the whale such as mouth opening/closing or sharp maneuvers will cause high frequency transients in the jerk signal.

Results

Six humpback whales were tagged in Nuup Kangerlua between 2nd and 25th July 2007 (ID mn180a, mn192a mn203a) and 25th May to 4th July 2008 (ID mn146a, mn155a and mn156a). The tags stayed on the whales for periods of 4.7 - 25.2hrs. The tags mostly came off after the preprogrammed period but one stayed on for more than 24 hours.

Diving behavior

A total of 168 foraging dives (defined as dives deeper than 40 m with lunges, detected as peak excess acceleration) were recorded (4-49 foraging dives per individual), with maximum depths ranging from 81 to 267m. Several hour-long feeding bouts were performed by all 6 whales with consecutive dives targeting the same depth layer ±20m (Fig. 1). Descent started when the whale left the surface and ended when the whale's pitch angle first became positive, indicating the first upward-pointing orientation (Fig. 2A). Ascents started when the whale pitch last became negative and ended when the whale reached the surface (Sato et al. 2003; Miller et al. 2004; Watwood et al. 2006). The bottom phase was the interval between the descent and ascent phases (Fig. 2A). Whales fluked continuously with a mean fluking rate of 0.3 Hz) in the first 30-40m of the decent after which fluking became occational or ceased until the foraging depth was reached (Fig. 2A-B). When ascending, whales fluked at about 0.3Hz until they reached 30-40m of the depth, at which depth fluking became occational or ended and the whale glided to the surface (Fig. 2A-B, Table 1). Pitch angles in descent and ascent were relative constant within and between whales. Means across the six whales were -44.2°, descent, and 53.0°, ascent (Table 1). The mean Kalman filtered speed estimates were uniformly high during descent ($2.3ms^{-1}$) and ascent ($2.1ms^{-1}$), with peak speeds reaching more than $3ms^{-1}$ (Table 1).

No vocalizations from the tagged whales or from other nearby whales were detected in the tag sound recordings. The dominant source of noise in the tag recording was from water flow over the tag although occasional noise from passing boats was also recorded

Lunges

Tagged whales performed several vertical excursions of 10 to 4 m amplitude during the bottom phase of most dives deeper than 40m. These depth dynamics coincided with signatures of lunges (Fig. 2). The depth of lunges was fairly constant within individuals (Fig. 1), but varied widely from 54 to 236 m, across animals, likely reflecting differences in the depth of the prey layer. The lower limit of the lunge depth rage is restricted by our definition of subsurface dives (40m) and does not reflect the actual minimum depth limit. One whale (mn203a) performed two separate feeding bouts each lasting several hours and targeting different prey layers with mean depths of 84 and 171m suggesting that lack of intra-individual variability in other tag recordings may relate to short recording times.

The number of lunges per foraging dive ranged from 1 to 9 with a mean of 3.0 (±0.77 sd) (Table 2). The time intervals between lunges were fairly similar across the six whales, with means ranging from 47.1 to 63.5s (Table 2). The mean pitch angle during lunges (mean calculated over the time of peak excess acceleration ±5s, excluding samples with excess acceleration >1ms^{-2}) varied across whales from 17.5 to 44.1 degrees (Table 2). Most lunges were performed in the ascending phase of depth excursions with the final lunge in each dive being performed on the ascent to the surface. One whale (again, mn203a) was more variable in this, performing 17% of lunges in the descending or bottom part of depth excursions. The mean roll was low for the six whales (-1 to -13 degrees, Table 2) and only whale mn192a seemed to have a preference for consistently rolling a little to one side (left) during lunges (Table 2).

Goldbogen et al. (2006, 2007) described lunges as starting with a bout of fluking that accelerates the whale to high speed, as indicated by increasing flow noise over the tag, followed by a sudden deceleration of the whale (i.e., decrease in flow noise), apparently bringing the whale to a near halt. Goldbogen et al. (2007) defined time zero of the lunge as the time of the peak in flow noise. We first used the peak excess acceleration to identify 551 lunges from the 6 whales (Table 2).Secondly, for these lunges we derived a second set of time cues using the flow noise profile to create timing information independent of the inertial sensor suite, defining time zero at the point of half power in flow noise (n=326 lunges, Table 2).

There was a clear pattern in the flow noise during lunges, with a strong increase correlated with the bursts of fluking (Fig. 1C). Given the low pitch angle and high fluking rate (and therefore high peak dorso-ventral velocities) in lunges, neither the flow noise nor orientation-corrected depth rate methods will yield accurate speed estimates. Instead we used the depth rate as an under bound for speed to establish the minimum speeds in each phase of lunges (Table 2). Whales initiated a lunge with a short burst of fast (0.5Hz) fluke strokes (Fig. 3B). The number of fluke strokes varied from 1 to 7 but rarely exceeded 4. Within the fluking bout, flow noise and absolute depth rate increased, and a clear jerk signal appeared (Fig. 3G, Table 2). At about time -1.2s with respect to the lunge 'zero' time (Fig. 3F and 4), the depth rate peaked at 3-4ms^{-1} (Fig. 3F) and shortly (0.4s) thereafter, the flow noise peaked (Fig. 3D and 4, Table 3). The rapid drop in depth rate despite the continued fluking and relatively stable pitch angles indicates that the whale experienced a sudden increase in drag. The last transient in the jerk signal appeared at second +1.3 of the lunge. The end of the jerk signal indicates that an unsteady force influencing the whale had ceased (Table 3). At this point the depth rate settled to a constant level a little above 1 ms^{-1} and fluking stopped at second 4 of the lunge (Fig. 4, Table 3).

It has been hypothesized that fin whales come to a near halt after the lunge (Goldbogen et al. 2006, 2007). To investigate this hypothesis for humpback whales with the fast sensor sampling rate of the DTAG, we computed the pitch and speed in 1Hz bins starting at lunge-time zero to ten seconds after the lunge. The whale forward speed was estimated by taking the mean over 1 s bins of instantaneous speeds (25Hz sampling) computed from the depth rate divided by the sine of the pitch angle (Fig. 5). During these ten seconds after the lunge the pitch was uniformly high and fluking decreased and stopped completely in the first four seconds (Table 3) making speed estimates from equation 5 in this interval fairly reliable. Figure 5 shows that the whales did not come to a near or complete halt, but rather kept gliding at a constant speed just above 1ms^{-1}. The further away from the head the tag is attached, the larger acceleration the tag experiences from fluking (Fish et al. 2003). Whale mn180 and mn203 were tagged closer to the fluke than the other whales and this resulted in large variations in the speed estimates of those two whales during the first two seconds after the lunge (zero) (Fig. 5C). However, then the estimated speed settled above 1ms^{-1}.

The local depth profiles of all lunges performed by whale mn156 were plotted in figure 6. The plot shows a stereotypic dive behavior with some variation in the beginning and end of the lunge depending on if the lunge was performed in the end of the descent phase, the bottom phase or in the beginning of the ascent phase. Asimilar pattern occurs when plotting lunges from the other whales.

Discussion

The energetic cost of lunge feeding is believed to explain the strikingly short dive times of rorquals (Croll et al. 2001; Acevedo-Gutiérrez et al., 2002). However, though our knowledge on rorqual foraging has increased recently thanks to technological advances (Goldbogen et al. 2006, 2008; Calambokidis et al., 2010), the details of the lunging behavior at depth are still largely based on inferences that hinges on indirect measures of speed and unconfirmed timing assignments of mouth opening and closure (Goldbogen et al., 2006). Here we used fast-sampling multi-sensor DTAGs providing a high resolution insight into the kinematics and behavior of rorqual lunge feeding with implications for the eco-physiology, morphology and life history of these large apex marine predators.

The U-shaped foraging dives performed by the tagged whales in the present study are similar to those reported from blue whales, fin whales and two other tagged humpback whales (Croll et al., 2001; Goldbogen et al., 2006, 2008) with direct descent to the foraging depth, a number of descending-ascending excursions linked to lunges during bottom time, followed by a direct ascent to the surface. Like the humpback whales in this study, fin whales also started descent with intense fluking followed by gliding to the foraging depth, just like ascending was initiated by fluking all the way to about 30 m depth, from where the whales usually glided to the surface in both species (Fig.2; Goldbogen et al., 2006). Similarly, the highest speeds for both fin whales and humpback whales were reached during the descent and ascent phases (Table 1; Goldbogen et al., 2006). So overall, our data are consistent with the behaviour reported for fin whale lunge feeding (Goldbogen et al., 2006, 2007). However, when it comes to the details of the behavior, kinematics and energetics of how rorquals execute a lunge, the interpretations of the present, high resolution data differs in some ways significantly from the conclusions of Goldbogen and coworkers.

Goldbogen et al. (2006, 2007) greatly advanced our knowledge on rorqual lunge behavior. However, the sensor sampling rate of 1Hz, used in their study, limited their ability to follow fast kinematics during lunges. Following the Nyquist sampling theorem, a sampling rate of at least 2 times the maximum frequency of the signal is needed to avoid aliasing and so ambiguity in timing and frequency estimation. In practice, the sampling rate should be >3 times the highest frequency of interest to compensate for non-ideal anti-alias filters. Here we show that lunging humpback whales fluke with a mean frequency of 0.5Hz and can reach instantaneous rates of 1.4Hz for one or two strokes in the lunge (Table 2). These data are taken from sensors sampled at 50Hz with 5Hz anti-alias filters (1 pole) and so are free from aliasing. Goldbogen et al. (2006) reported a mean fluking rate of 0.27Hz during fin whale lunges. This low fluking rate compared to that reported here could be due to size scaling between fin and humpback whales, with the larger fin whales fluking at a slower rate (Sato et al. 2007). However, a nearly 50 % increase is a pronounced difference and there is apparently no scaling effect on the fluking rates of fin and humpback whales during descent and ascent, which are within 0.27-0.29Hz (Goldbogen et al. 2006; this study, Table 1). We show below that increased fluking rate is one way that humpback whales develop increased thrust during lunges. If lunges are as energetic as expected, other rorquals should also increase their fluking rate during lunges as compared to descent or ascent fluking. Goldbogen et al. do not specify if anti-alias filters are associated with the sensors in their tag and, if not, it is possible that their reported fluking rates during fin whale lunges may be tainted by aliasing. This serves to emphasise the importance of high sampling rates and adequate anti-alias filtering when acquiring on-animal sensor signals if the details of dynamic foraging are of interest.

Goldbogen et al. (2006, 2007) used flow noise over the tag as an estimate of speed to argue that fin whales first accelerate strongly but then decelerate during lunges. They associated the deceleration phase with the increased drag of an open mouth by defining mouth opening to happen when the flow noise (and hence inferred speed) started to drop. We observed the same overall pattern of flow noise in on-animal hydrophone recordings of lunge-feeding humpback whales (Figure 1-3). However, analysis of our accelerometer and depth data do not confirm the drastic deceleration reported by Goldbogens model, a difference which has repercussions for the subsequently derived models of the biomechanical and evolutionary forces at play for lunge feeding rorquals (Goldbogen et al., 2010; Potvin et al., 2009). In the following, we will discuss the details of humpback whale lunge feeding revealed in the current study and address implications for the existing models for rorqual feeding behavior and kinematics.

Lunges

Tagged humpback whales produce about 3 energetic fluke strokes during lunges, accelerating to reach a maximum depth rate (an underestimate of forward speed) of about $1.8 ms^{-1}$. The depth rate peaks about 0.7s before time zero of the lunge (Table 3; Fig. 3 and 4) and the depth rate then decreases steadily while the whale delivers a final fluke stroke (Fig. 3). At this point the pitch angle is constant and quite high, suggesting that the loss in vertical speed is not due to a change in orientation but represents a true deceleration. Despite the dropping speed, the flow noise, excess acceleration and jerk all remain high due to the continued fluking. Time zero of the lunge is defined by the drastic decrease in flow noise (this study; Goldbogen et al., 2006), but the jerk signal remains strong. At about 1.3s after the drop in flow noise, the jerk signal and fluking cease, and the depth rate stabilizes thereafter to a level consistent with an orientation-corrected forward speed of around $1 ms^{-1}$ (Fig. 3-5). This shows that the whale, after this point in the lunge, is able to glide forward at a constant speed with a full mouth. Goldbogen et al. (2006) conclude that the sudden decrease in flow noise and hence inferred speed reduction is the result of a high drag from mouth opening. We see a similar decrease in depth rate and flow noise despite continued fluking and agree that this must be a result of the whale experiencing an increase in opposite forces. Given this, the mouth opening must occur no later than the peak in depth rate, 0.7s before the drop in flow noise (Fig. 3 and 4, Table 3), because at this point the whale begins to decelerate strongly despite continued hard fluking. However, it is likely that the mouth opens earlier as we will outline below.

Changes in acceleration or jerk are caused both by rapid movements of the whale and by dynamic forces influencing the body, such as vibration or rapid changes in drag from the open mouth. The strong jerk signal ends abruptly on average about 2.3s after the peak in depth rate (Fig. 4, Table 3) and the termination of the jerk signature likely reflects the moment of mouth closure. This interpretation is further supported by the fact that the drop in jerk coincides with the last fluke upstroke and the apparent end of deceleration (Fig. 3, Table 3), implying that at this point the whale and the engulfed water have reached the same speed of 1ms^{-1} (Fig. 4). Once the mouth is closed, the whale can glide slowly forward until the next lunge, partly aided by a body-weight assisted passive descent in the last part of the lunge cycle (Fig. 5).

If a decrease in jerk indicates mouth closure then perhaps there are similar cues earlier in the lunge which might indicate when the mouth opens. The jerk signal rises rapidly some 5 to 6 seconds before time zero of the lunge but this is hard to interpret as it coincides with a period of intense fluking that accelerates the whale forward. The mouth opening likely happens no earlier than the beginning of the jerk transient and no later than the peak of depth rate. Goldbogen et al. (2007) estimated a time period of 3 s from mouth opening to closure from a video of a lunge feeding Brydes whale. Brydes and humpback whales are of similar size so, if humpbacks open their mouths for a similar interval, and if the end of the jerk signature reflects mouth closure as we have argued, then the mouth opening occurs about 1 sec before the peak speed is reached. In this case, whales continue to accelerate for a short period of time after the mouth is opened, and the peak in depth rate may indicate the point at which the whale starts to accelerate the engulfed water.

The notion that mouth opening happens before the onset of deceleration in a lunge is supported by CRITTERCAM recordings of lunging blue whales showing that the mouth opens before the flow noise begins to drop (defined as desceleration by Calambokidis et al. 2010). In nine lunges, from two different foraging dives, the head of the blue whale was raised (indication of mouth opening, Calambokidis et al. 2010) before the flow noise began to drop (point of mouth opening sensu Goldbogen et al. 2006). It is even possible that the mandibles start opening before the lift of the head is visible in the video recording and therefore the lift of the head must be the latest point of mouth opening. There was a mean of three seconds between the lift of the head to the drop in flow noise (Calambokidis et al. 2010) supporting our interpretation that the main deceleration does not start at the point of mouth opening and filling of the buccal pouch, but when the whale begins to accelerate the engulfed water. We therefore propose that lunge feeding humpback whales open their mouth some 1 sec before peak of depth rate and closes it some 3 seconds later, when speed of the whale is stable around 1ms$^{-1.}$ After the lunge, the speed of the humpback whale and the engulfed water levels at 1 ms^{-1} (Fig. 4) and the whale glides before initiating the next lunge (Fig. 4). This quiet interval following the lunge likely marks the time in which water is filtered through the baleen and swallowed.

Assuming that a new lunge start as soon as the harvesting of the previously engulfed water has ended, the mean inter-lunge-intervals of the 6 whales suggest that filtering and ingestion require from 30 to 47 seconds with a mean of 36 seconds (from mouth closure to the start of fluking in the next lunge (Table 2). Thus it seems that humpback whales spend about an order of magnitude longer time to filter and ingest prey from the water compared to the time it takes to engulf it.

Stereotypy and biomechanical constraints

We have shown that lunges involve a strict sequence of events (i.e., 1. accelerate; 2. mouth opening; 3. filling the buccal pouch, and decelerate while accelerating water in the buccal pouch; 4. mouth closure; 5. glide while filtering water, and 6. collect prey from baleen plates) each of which creates a more-or-less distinct movement signature detectable with wide bandwidth accelerometer and pressure sensors (Figs. 5-6). The surprisingly stable inter-lunge-interval of fin whales (45 ±19 s, n=121 lunges, Goldbogen et al., 2006), humpback whales (53.4 ±5.79 s, n=551 lunges, Table 2) and blue whales (71 ±9 s, n=9, J. Calambokidis Pers. Comm.) suggest that lunging rorquals operate under biomechanical limitations that dictate when a new lunge is possible. This also suggests that the volume of water engulfed, which dictates the filtering time and so probably controls the inter-lunge-interval, is fairly constant: whales do not seem to fit the size of the lunge to the prey density. Instead, rorquals must locate a food layer with a density and size that supports sequential lunges at the rate at which the biomechanics allow them to be executed. This is in contrast to other humpback feeding modes such as bubble net feeding in which prey are concentrated before a lunge (Jurasz and Jurasz, 1979; D'Vincent et al., 1985).

While the lunges examined here are restricted to humpbacks dives deeper than 40 m, the specialized kinematics required to fill the buccal pouch with water must operate within similar biomechanical constraints in shallow feeding and in other rorquals. This is further supported by the fact that data sets from two other species of lunge feeding rorquals share many common features (Goldbogen et al. 2006, 2007; Calambokidis et al. 2010).

Why is a lunge energetically expensive?

It has been suggested that the expensive part of a lunge was a complete deceleration from thehigh drag when the whale opens its mouth (Goldbogen et al. 2006, 2007), resulting in short dive times. Here we used high resolution speed and movement data to show that this is not the case, at least in humpback deep lunging. Instead all 6 tagged whales finished lunges gliding with a speed of about 1ms^{-1} (Figs. 3-4). If the whales do not come to a near or complete stop when lunge feeding at depth, then what is it that limits the dive time so severely when compared to similar sized cetaceans? There are several steps in a lunge that could provide an answer to this: 1. To achieve a high speed of 3ms^{-1} is required to capture fast elusive prey and inflate the buccal pouch (Orton and Brodie 1987). 2. To overcome an increased drag from the changed body form. 3. To accelerate the engulfed water (up to 30t). Goldbogen et al. (2007) estimated the drag from the deceleration of the whale (estimated from flow noise derived changes in apparent speed) and the gape angle. The gape angle as a function time, measured from a video recording of a bryde's whale, then scaled to a fin whale by multiplying by two, was formed as a bell-shaped curve (Goldbogen et al. 2007). To estimate drag, the point of mouth opening (beginning of gape angle curve) was chosen by Goldbogen and coworkers ; (Goldbogen et al., 2007; Potvin et al., 2009) to happen at peak speed (peak in flow noise) with no reported evidence to support that notion. By starting the gape angle curve at top speed, and then estimating the drag forces from the gape angle and the speed, drag forces are bound to come out as the main explanatory variable for the decrease in speed (Goldbogen et al. 2007, Fig. 4). However, as suggested from the above sensor data and crittercam recordings, the beginning of mouth opening likely happens earlier in the lunge. With a shift in time of mouth opening with respect to decelleration, the major drag forces may turn out not to start at the point of mouth opening (Fig. 3). Our observation that lunge feeding humpback whales never come to a full stop at depth, but rather maintain a forward speed of around 1 ms^{-1} after the lunge without fluking does in combination with the evidence for an earlier mouth opening suggest a different scenario for the relative costs of performing a lunge: If the whale opens its mouth before it starts slowing down, it is implied that it initially accelerates around the engulfed water mass, and that the major energetic fluke stroke (Fig. 3) is introduced when the whale accelerates a mass of up to 30 tons of engulfed water to 1 $ms^{-1.}$while it decelerates to the same speed To understand how big a proportion this acceleration plays in the deceleration of the whale we calculated the change in speed from the mass factor. The kinetic energy to accelerate a mass m is given by:

Kinematic energy=0.5m V2 (6)

Rearranging equation 6 the change in speed V is given by:

V=√(2/M) (7)

Given equation 7, if the mass factor (M) equals 2 (the whale engulf a water mass equal to its own mass), the acceleration of the engulfed water mass makes out almost 50 % of the deceleration from $3ms^{-1}$ to $1ms^{-1}$. About 2s after time zero of the lunge, the water is completely engulfed with closed mouth and accelerated to 1 ms^{-1} (Fig. 4 and 5). The rest of the speed reduction can likely be ascribed to drag from the mouth opening and of the tadpole shaped whale after buccal puch filling). Either way, the whale do complete a glide cycle up towards the next lunge moving forward at around

1ms^{-1} while going from a tad pole shape to normal body form while expelling the water over the baleen. For rorquals lunge feeding at the surface, the component of gravity changes the situation dramatically. As soon as the whales put body out of the water, the gravitational forces slows them down to a complete stop. Given that the whales at depth execute their fluke patterns to avoid coming to a stop, it seems that they try to avoid the costs of acceleration a large body from a stand still. If that is indeed relatively costly, it is implied that it costs more oxygen to complete a lunge cycle at the surface compared to at depth. However, the much lower costs of transport between the oxygen at the surface and the near surface prey may to some degree even the oxygen consumption per unit of time in both foraging modes.

Conclusion

Analysis of 357 lunges performed by humpback whales feeding at depth, tagged with fast sampling multiple sensor DTAGs, have provided new detailed insights into the kinematics of rorqual lunge feeding. The consistency in relative timing of accelerometer, flow noise and pressure signatures and the low variance in time between lunges show that lunge feeding is a highly stereotyped behavior dictated by the mechanics and kinematics of engulfing a body weight of water and prey at high speeds. We find that a lunge starts with the whale accelerating with a bout of 3-4 fluke strokes while generally pitching upwards. When reaching a speed of 2-3ms^{-1} the whale opens its mouth and fills the buccal cavity with prey laden water. We conclude that the whale is not slowed down when opening its mouth, but that it rather continues to accelerate or maintain its speed while filling the pouch. The main deceleration of the whale happens when the pouch is full and it starts to move the engulfed water forward. It avoids complete stop by producing a strong fluke stroke at the moment the pouch is full to keep part of the momentum, and move forward after the lunge in a bloated tad pole shape at of 1ms^{-1} without fluking while filtering the engulfed water. When the whale has used some 36 seconds to filter out the engulfed water, it initiates a new bout of fluking while pitching towards the surface initiating execution the next lunge. Hence, lunge-feeding humpback whales do not come to a complete or near halt from increased drag from the open mouth, as previously proposed. Instead they fluke through the lunge to overcome counter directional forces from drag and acceleration of engulfed water masses, keeping a speed of minimum 1ms^{-1} throughout the lunge. After the lunge, these large filter-feeders can keep momentum with a mouthful of water without fluking because of their high Reynolds numbers. By avoiding a stop while lunging at depth, they likely save oxygen to be used in the next lunge, maximizing the number of lunges per unit of time. Biomechanic models (Potvin et al., 2009) and their evolutionary implications (Goldbogen et al. 2009) of hydrodynamic processes and kinematics of lunge feeding based on the acceleration-deceleration hypothesis should be revised in the light of these new findings.

List of symbols and abbreviations

A	acceleration measured by the tag in three axes, $A=[a_x,a_y,a_z]^T$. Axes x, y, and z are defined as the caudal-rostral, ventral-dorsal, and left-right , respectively.
d	peak-to-midline dorso-ventral body displacement in m.
D	specific acceleration vector
f_s	Sensor sampling rate in Hz.
g	acceleration due to gravity (9.81 ms^{-2})
G	gravitational acceleration vector in g's. $G=[0,0,1]T$ in a {North,East,Down} coordinate system.
m	body mass
M	mass factor (or is it (body mass + water)/body mass)
p	pressure
Q_t	direction cosine matrix describing the instantaneous orientation of the whale with respect to the inertial frame
s_f	forward speed of the whale
s_t	instantaneous speed of the tag
t	time (sec)
V	change in speed?
θ	pitch angle (degrees)
ω	fluking rate (radians per second) = 2π x fluking rate in Hz.

Acknowledgements

We thank T. Boye, F. Ugarte, M. Møller, L. Heilman, S. Perez and Teit for help in the field, T. Hurst for tag preparation, and F. Ugarte, M. P. Heide-Jørgensen and P. Tyack for helpful discussions or comments on previous versions of the manuscript. This work is a part of the Nuuk Basis monitoring program at the Center for Marine Ecology and Climate Impact, GINR. The research was conducted under a permit granted by the Greenland Government to GINR. M.S. was funded by the Oticon Foundation and KIIIN, Greenland Home Rule, P.T.M. by Steno and frame grants from the National Danish Science Foundation and M.J. by NOPP and SERDP grants.

References

Acevedo-Gutiérrez, A., Croll, D. A. and Tershy, B. R. (2002). High feeding costs limit dive time in the largest whales. *Journal of Experimental Biology*. **205**, 1747-1753.

Blackwell, S. B., Haverl, C. A., Le Boeuf, B. J., Costa, D. P. (1999). A method for calibrating swim-speed recorders. *Marinre Mammal Science*. **15**, 894-905.

Brodie, P. F. (1993). Noise generated by the jaw actions of feeding fin whales. *Canadian Zoology* 71: 2546-2550.

Burgess, W. C., Tyack, P. L., Le Boeuf, B. J., Costa, D. P. (1998). A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Deep-Sea Research.* **45**, 1327-1351.

Calambokidis, J., Schorr, G. S., Steiger, G. H., Francis, J., Bakhtiari, M., Marshall, G., Oleson, E. M., Gendron, D. and Robertson, K. (2008). Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (Crittercam). *Marine Technology Society Journal*. **41**, 19-29.

Croll, D. A. and Tershy, B. (2002). Filter feeding. In *Encyclopedia of marine mammals*. (ed. Perrin, W. F., Würsig, B. and Thewissen, J. G. M.), pp 428-432. London: Academic Press.

Croll, D. A., Acevedo-Gutiérrez, A., Tershy, B. and Urban Ramírez, J. (2001). The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? *Comparative Biochemestry and Physiology Part A*. **129**, 797-809.

D´Vincent, C. G., Nilson, R. M. and Hanna, R. E. (1985). Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *The Scientific Reports of the Whales Research Institute*. **36**, 41-47.

Fish, F. E., Peacock, J. E. and Rohr, J. J. (2003). Stabilization mechanism in swimming odontocete cetaceans by phased movements. *Marine Mammal Science*. **19**, 515-528.

Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M.A. and Hildebrand, J. A. (2006). Kinematics of foraging dives and lunge-feeding in fin whales. *The Journal of Experimental Biology*. **209**, 1231-1244.

Goldbogen, J. A., Pyenson, N. D. and Shadwick, R. E. (2007). Big gulps require high drag for fin whale lunge feeding. *Marine Ecology Progress Series*. **349**, 289-301.

Goldbogen, J. A., Calambokidis, J., Croll, D. A., Harvey, J. T., Newton, K. M., E., Oleson, E. M., Schorr, G. and Shadwick, R. (2008). Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *The Journal of Experimental Biology*. **211**, 3712-3719.

Goldbogen, J. A., Potvin, J. and Shadwick, R.E. (2009). Skull and buccal cavity allometry increase mass-specific engulfment capacity in fin whales. *Proceedings of the Royal Society of London* doi: 10.1098/rspb.2009.1680.

Goldbogen, J. A. (2010). The ultimate mouthful: lunge feeding in rorqual whales. *American Scientist.* **98:** 124-131.

Golub Loan, V. (1996). *Matrix computations* (Ed. Hopkins, J.). Maryland: University Press.

Grewal, M., Weill, L. R., Andrews, A. P. (2001). Global positioning systems, inertial navigation, and integration. John Wiley & Sons, N.Y.

Hochachka, P. W. and Somero, G. N. (1984). *Biochemical Adaptation.* Princeton: Princeton University Press.

Johnson, M. P. and Tyack, P. L. (2003). A digital acoustic recording tag for measureing the response of wild marine mammals to sound. *IEEE Journal of oceanographic Engineering*. **28**, 3-12.

Jurasz, C. M. and Jurasz, V. P. (1979). Feeding modes of the humpback whales, *Megaptera novaeangliae*, in southeast Alaska. *The Scientific Reports of the Whales Research Institute*. **31**, 69-83.

Kooyman, G. L. (1989). Diverse Divers: *Physiology and Behavior*. Berlin: Springer-Verlag.

Kooyman, G. L., Wahrenbrock, E. A., Castellini, M. A., Davis, R. A. and Sinnett, E. E. (1980). Aerobic and anaerobic metabolism during diving in Weddell seals: Evidence of preferred pathways from blood chemistry and behavior. *Journal of Comparative Physiology.* **138**, 335–346.

Kramer, D. L. (1988). The behavioural ecology of air breathing by aquatic animals. *Canadian Journal of Zoology.* **66**, 89-94.

Lambertsen, R. H. (1983). Internal mechanism of rorqual feeding. *Journal of Mammalogy*. **64**, 76-88.

Lambertsen, R. H., Ulrich, N. and Straley, J. (1995). Frontomandibular stay of Balaenopteridae: A mechanism for momentum recapture during feeding. *Journal of Mammalogy*. **76**, 877-899.

Orton, L. S. and Brodie, P. F. (1987). Engulfing mehcanics of fin whales. *Canadian Journal of Zoology*. **65**, 2898-2907.

Miller, P. J. O., Johnson, M. P., Tyack, P. L. and Terray, E. A. (2004). Swimming gaits, passive drag and boyancy of diving sperm whales *Physeter macrocephalus*. *The Journal of Experimental Biology*. **207**, 1953-1967.

Moore, M. J., Miller, C. A., Morss, M. S., Arthur, R., Lange, W., Prada, K. G., Marx, M. K. and Frey, E. A. (2001) Ultrasonic measurement of blubber thickness in right whales. *Journal of Cetacean Research Management* (Special Issue) **2**, 301–309.

Pivorunas, A. (1979). The feeding mechanisms of baleen whales. *American Scientist*. **67**, 432-440.

Potvin, J., Goldbogen, J. A., Shadwick, R. E. (2009). Passive versus active engulfment: Verdict from trajectory simulations of lunge-feeding fin whales. *Journal of the Royal Society Interface.* 6: 1005-1025

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology* **206,** 1461-1470.

Sato K and 17 other authors (2007). Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proceedings of the Royal Society B*. **274**, 471-477.

Shepard, E. L. C., Wilson, R. P., Liebsch, N., Quintana, F., Laich, A. G., Lucke, K. (2007). Flexible paddle sheds new light on speed: a novel method for the remote measurement of swim speed in aquatic animals. *Endangered Species Research.* **4**, 157-164

Simon, M, J., Johnson, M., Tyack, P. and Madsen, P. T. (2009). Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). *Proceedings of the Royal Society B*. **276**, 3819-3828.

Vogel, S. (1994). *Life in moving fluids. The physical biology of flow.* Princeton, NJ: Princeton University Press.

Watanuki, Y., Niizuma, Y., Gabrielsen, G. W., Sato, K. and Niato, Y. (2003). Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proceedings of the Royal Society B*. **270**, 483–488.

Watkins, W. A. and Schevill, W. E. (1979). Aerial Observations of Feeding Behavior in Four Baleen Whales: *Eubalaena glacialis, Balaenoptera borealis, Megaptera novaeangliae, and Balaenoptera physalus*. *Journal of Mammalogy*. **60(1),** 155-163.

Watwood, S. L., Miller, P. J. O., Johnson, M., Madsen, P. T. and Tyack, P. (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *Journal of Animal Ecology*. **75,** 814-825

Werth, A. J. (2004). Models of hydrodynamic flow in the bowhead whale filter feeding apparatus. *Journal of Experimental Biology*. **207**, 3569–3580.

Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J. and Croll, D. A. (2000). Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**, 133–136.

Zimmer, W. M., Johnson, M., Madsen, P. T. and Tyack, P. (2005). Echolocation clicks of free-ranging Cuviers beaked whales (*Ziphius cavirostris*). *Journal of the Acoustical Society of America*. **117**, 3919-3927.

Tables

Table 1. Dive data summary for the six D-tagged humpback whales. Foraging dives are defined as dives with lunges deeper than 40 m. Standard deviations are given in parentheses.

	Mn180a	**Mn192a**	**Mn203a**	**Mn146a**	**Mn155a**	**Mn156a**	**Mean**
Foraging dives	10	39	49	4	35	31	**28.0 (17.4)**
Descent pitch	-54.0 (10.27)	-47.4 (12.42)	-56.5 (10.40)	-30.7 (5.30)	-41.5 (9.06)	-35.3 (11.00)	**-44.2 (10.25)**
Descent speed (Kalman)	3.0 (0.18)	2.22 (0.31)	2.2 (6.42)	2.5 (0.03)	2.0 (0.22)	2.2 (0.31)	**2.3 (0.36)**
Descent fluking rate (Hz)	0.3 (0.05)	0.3 (0.05)	0.3 (0.48)	0.2 (0.03)	0.2 (0.06)	0.3 (0.12)	**0.3 (0.03)**
Ascent pitch	68.1 (2.07)	54.5 (16.21)	52.5 (8.48)	43.0 (4.30)	51.5 (9.82)	48.6 (12.83)	**53.0 (8.41)**
Ascent speed (Kalman)	2.3 (0.16)	2.0 (0.31)	2.0 (0.36)	1.7 (0.14)	1.8 (0.19)	2.6 (0.36)	**2.1 (0.32)**
Ascent fluking rate (Hz)	0.3 (0.05)	0.2 (0.07)	0.3 (0.30)	0.2 (0.30)	0.3 (0.19)	0.3 (0.11)	**0.3 (0.03)**

Table 2. Summary of lunge data of the six humpback whales D-tagged in Nuup Kangerlua. Only deep lunges (> 40 m) are included in the analysis. Standard deviations are given in parentheses.

	Mn180a	**Mn192a**	**Mn203a**	**Mn146a**	**Mn155a**	**Mn156a**	**Mean**
Number of lunges (excess acceleration)	34	110	212	6	109	80	**91.8 (72.00)**
Number of lunges (noise)	34	102	115	6	30	39	**54.3 (43.7)**
Lunges per dive	3.4 (1.84)	2.8 (1.18)	4.4 (1.71)	2.0 (0.82)	3.5 (1.32)	3.1 (1.61)	**3.0 (0.77)**
Inter lunge interval (s)	53.4 (18.30)	63.5 (23.93)	58.2 (22.62)	47.1 (11.34)	47.8 (16.60)	58.2 (38.04)	**53.4 (5.79)**
Pitch at lunge (degrees)	44.1 (13.92)	31.2 (10.73)	17.5 (17.94)	35.5 (10.27)	25.2 (13.66)	32.4 (17.72)	**31.0 (9.05)**
Roll at lunge (degrees)	-11.2 (12.16)	-10.5 (6.09)	-11.3 (9.66)	-10.3 (6.90)	-0.8 (11.53)	-12.5 (12.53)	**-9.4 (4.30)**
Max depth rate (m/s)	1.6 (0.45)	1.4 (0.43)	2.0 (0.93)	2.0 (0.27)	1.9 (0.47)	2.1 (0.58)	**1.8 (0.27)**
Flukes per lunge	2.5 (0.79)	2.7 (0.78)	2.8 (1.04)	3.7 (0.52)	3.5 (1.07)	3.7 (1.13)	**3.2 (0.54)**
Max fluking frequency (Hz)	0.5 (0.23)	0.66 (0.25)	0.5 (0.22)	0.4 (0.04)	0.4 (0.10)	0.4 (0.05)	**0.5 (0.10)**

Table 3. Timing in seconds of lunge events relative time zero (defined by half power point of flow noise) of the lunges. Standard deviations are given in parentheses. Timing of the lunge events is also illustrated in Fig. 3 and 4).

Time in seconds relative to event	*Mn180*	*Mn192*	*Mn203*	*Mn146*	*Mn155*	*Mn156*	*Mean*
Peak excess acceleration	-0.93	-2.02	-1.86	-1.36	-2.37	-1.96	**-1.75**
	(0.30)	(1.41)	(0.54)	(0.76)	(1.91)	(1.89)	**(0.52)**
Max depth rate	-0.38	-0.30	-1.24	-0.03	-0.80	-1.71	**-0.74**
	(0.35)	(0.54)	(0.57)	(0.45)	(0.96)	(1.74)	**(0.64)**
Max flow noise	-0.58	-0.60	-0.95	-1.56	-0.91	-1.46	**-1.01**
	(0.30)	(1.06)	(0.50)	(0.96)	(0.60)	(1.35)	**(0.42)**
Last Jerk peak	1.66	0.76	1.49	1.31	1.41	1.16	**1.30**
	(0.35)	(0.30)	(0.43)	(0.30)	(0.55)	(0.49)	**(0.31)**
Upstroke	0.63	2.12	2.01	1.21	1.44	1.06	**1.41**
	(0.35)	(1.25)	(0.61)	(0.25)	(0.96)	(0.52)	**(0.57)**
End of fluking	2.67	3.83	3.41	3.85	4.26	3.53	**3.59**
	(0.91)	(0.69)	(0.68)	(0.71)	(0.76)	(0.61)	**(0.54)**
Peak depth rate to Jerk	2.12	1.06	2.65	1.49	2.12	2.72	**2.03**
	(0.35)	(0.74)	(0.47)	(0.55)	(1.01)	(1.88)	**(0.65)**
Peak flow noise to Jerk	2.24	1.36	2.42	2.75	2.17	2.72	**2.28**
	(0.35)	(1.21)	(1.46)	(0.96)	(1.46)	(1.42)	**(0.51)**
Peak depth rate to peak flow noise	0.25	0.30	0.23	1.39	0.23	-0.05	**0.39**
	(0.40)	(0.60)	(1.46)	(1.36)	(1.46)	(1.30)	**(0.50)**

Figure legends

Fig. 1. Depth profile of a D-tagged humpback whale tagged in Nuup Kangerlua, Greenland. The red dots show the lunges and the histogram on the right summarizes the depth distribution of the lunges in % (bin width: 5 m).

Fig. 2. Foraging dive with four lunge feeding events. A. Depth profile of a humpback whale foraging dive, performing four lunges (red dots). B. Pitch deviation in radians filtered to illustrate the fluking effort (0.3 Hz high-pass filter). C. Sound recording sampled at 2 kHz (FFT=512, Hann window, 50% overlap) showing increased flow noise over the tag during descent, ascent and lunge events. D. Excess acceleration, showing clear peaks in the lunge events. E. Body orientation of the diving whale in degrees, Pitch (blue) and roll (green) (0.2 Hz low-pass filter). F. Depth rate showing the minimum speed estimate at any time of the foraging dive (0.5 Hz low-pass filter).

Fig. 3. A single lunge event. A. Depth profile of humpback whale lunge with the estimated speed of a Kalman speed estimator of the whale in color coding. B. Pitch deviation in radians filtered to show fluke strokes (0.3 Hz high-pass filter). C. Sound recording sampled at 2 kHz (FFT=512, Hann window, 50% overlap). D. Normalized flow noise. E. Pitch deviation in degrees (0.5 Hz low-pass filter). F. Depth rate (0.5 Hz low-pass filter). G. Jerk signal, the differential of the excess acceleration. The colors of the arrows correspond to the lunge events in figure 4.

Fig.4. Timing of the lunge events of lunges executed by whale mn203. The colors of the events correspond to the colors of the arrows in figure 3. Timing of lunge events from all 6 whales are summed up in table 3.

Fig. 5. Pitch (A) and speed development 10 seconds after the lunge cue (1 sec bin mean pitch sampled at 25 Hz). B. Depth rate as a mean of each 1 sec bin (sampled at 25 Hz). C. Absolute speed measured as the vertical speed of each bin divided with the sine of the mean pitch in each bin.

Fig. 6. Depth development of all lunges of whale mn156a, showing the high degree of stereotypy in the lunge choreography.

FIGURE 1

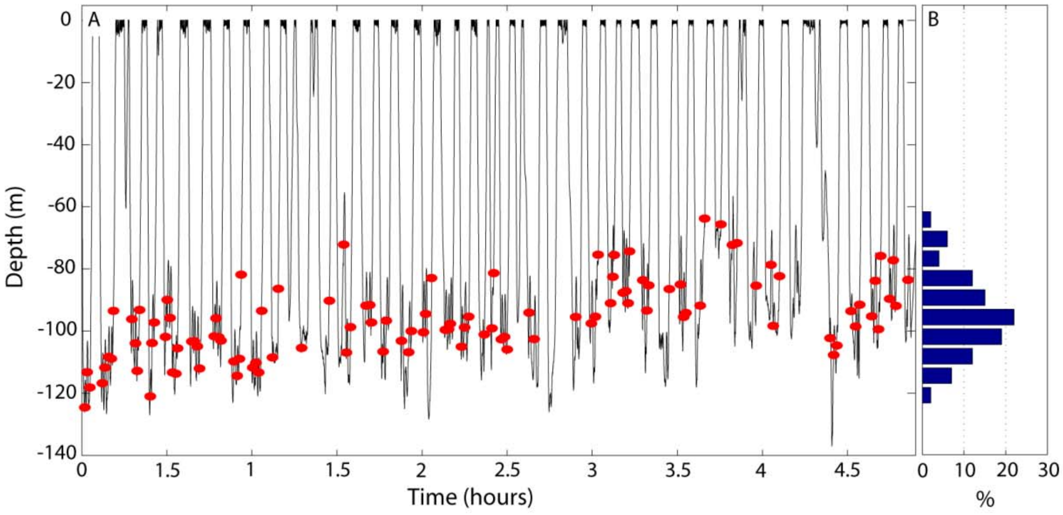

A
B
Depth (m)
0
-20
-40
-60
-80
-100
-120
-140
0
1.5
1
1.5
2
2.5
3
3.5
4
4.5
Time (hours)
0
10
20
30
%

FIGURE 2

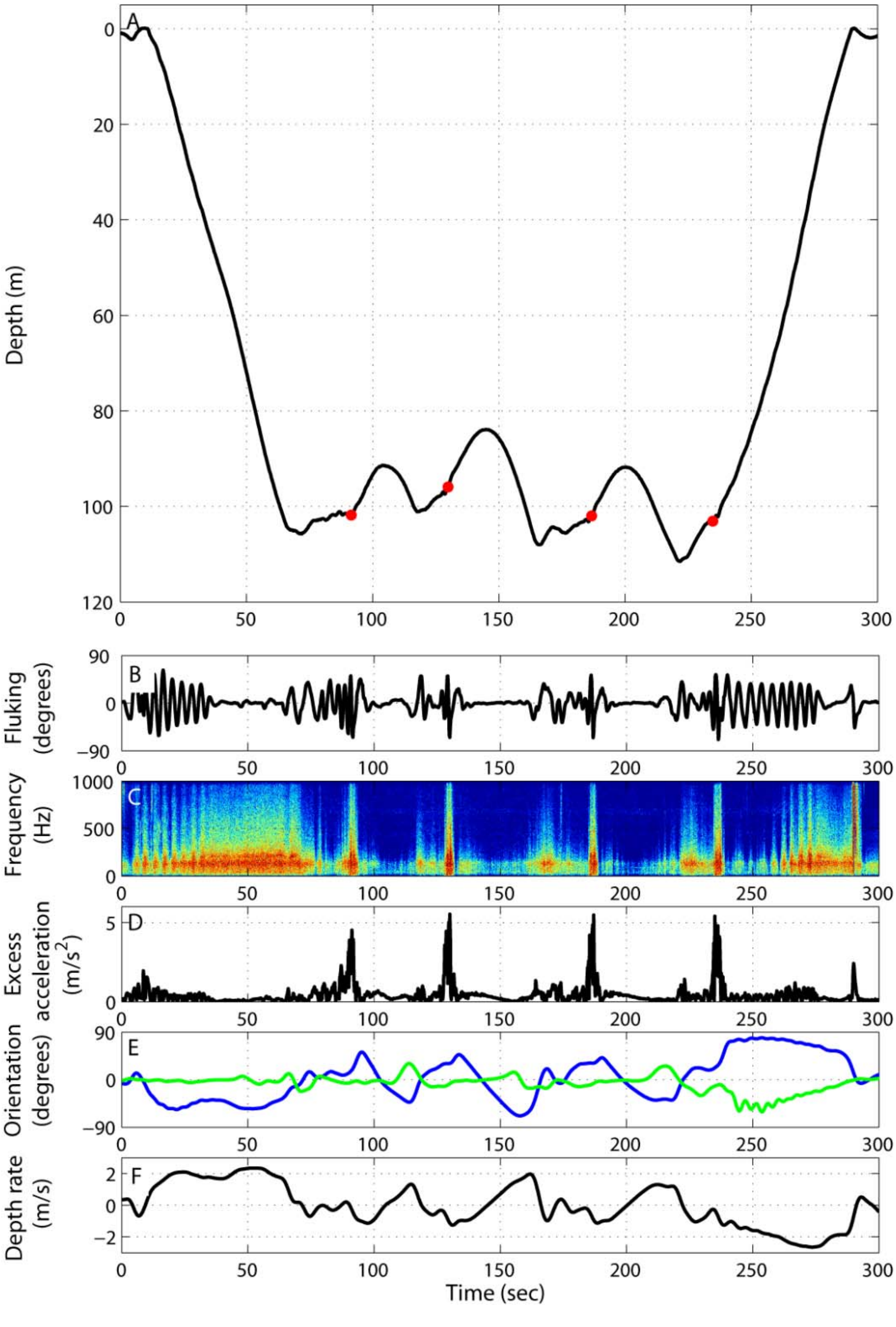
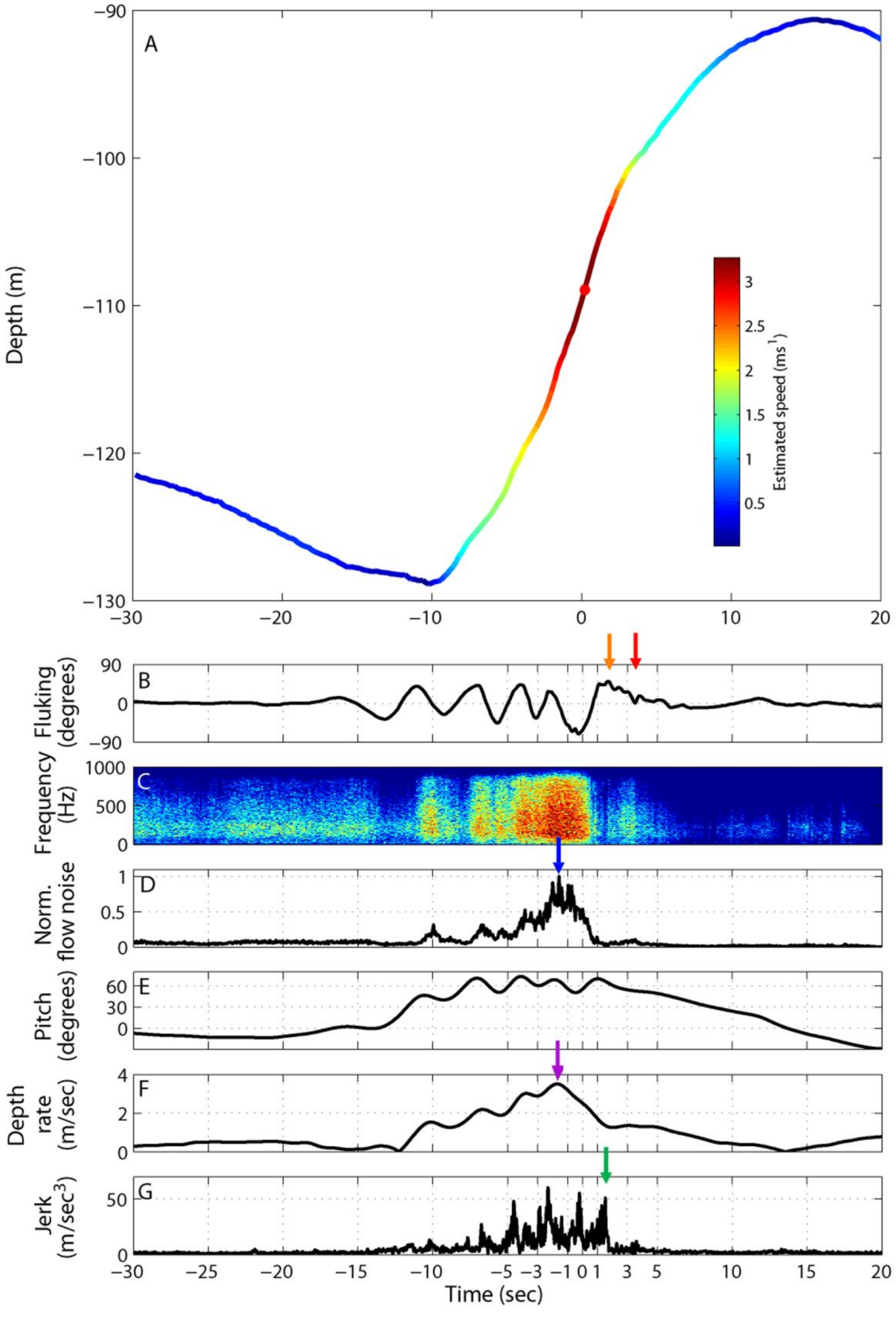

A
Depth (m)
0
20
40
60
80
100
120
B
Fluking (degrees)
90
0
−90
C
Frequency (Hz)
1000
500
0
D
Excess acceleration (m/s^2)
5
0
E
Orientation (degrees)
90
0
−90
F
Depth rate (m/s)
2
0
−2
0
50
100
150
200
250
300
Time (sec)

FIGURE 3



A
Depth (m)
−90
−100
−110
−120
−130
−30
−20
−10
0
10
20
Estimated speed (ms^{-1})
3
2.5
2
1.5
1
0.5
B
Fluking (degrees)
90
0
−90
C
Frequency (Hz)
1000
500
0
D
Norm. flow noise
1
0.5
0
E
Pitch (degrees)
60
30
0
F
Depth rate (m/sec)
4
2
0
G
Jerk (m/sec^3)
50
0
−30
−25
−20
−15
−10
−5
−3
−1
0
1
3
5
10
15
20
Time (sec)

FIGURE 4

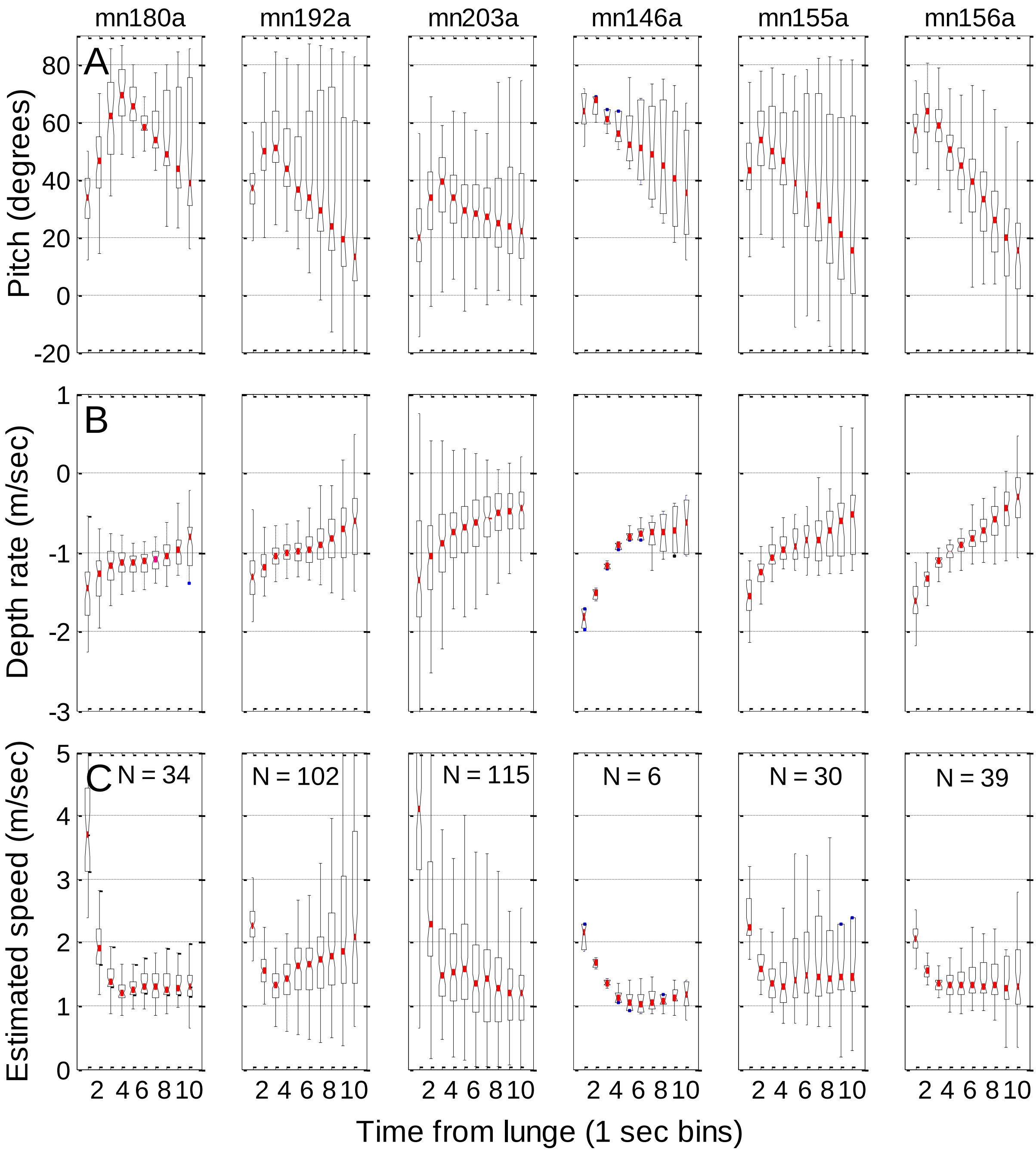

mn180a
mn192a
mn203a
mn146a
mn155a
mn156a
A
B
C
Pitch (degrees)
80
60
40
20
0
-20
Depth rate (m/sec)
1
0
-1
-2
-3
Estimated speed (m/sec)
5
4
3
2
1
0
N = 34
N = 102
N = 115
N = 6
N = 30
N = 39
2 4 6 8 10
Time from lunge (1 sec bins)

FIGURE 5

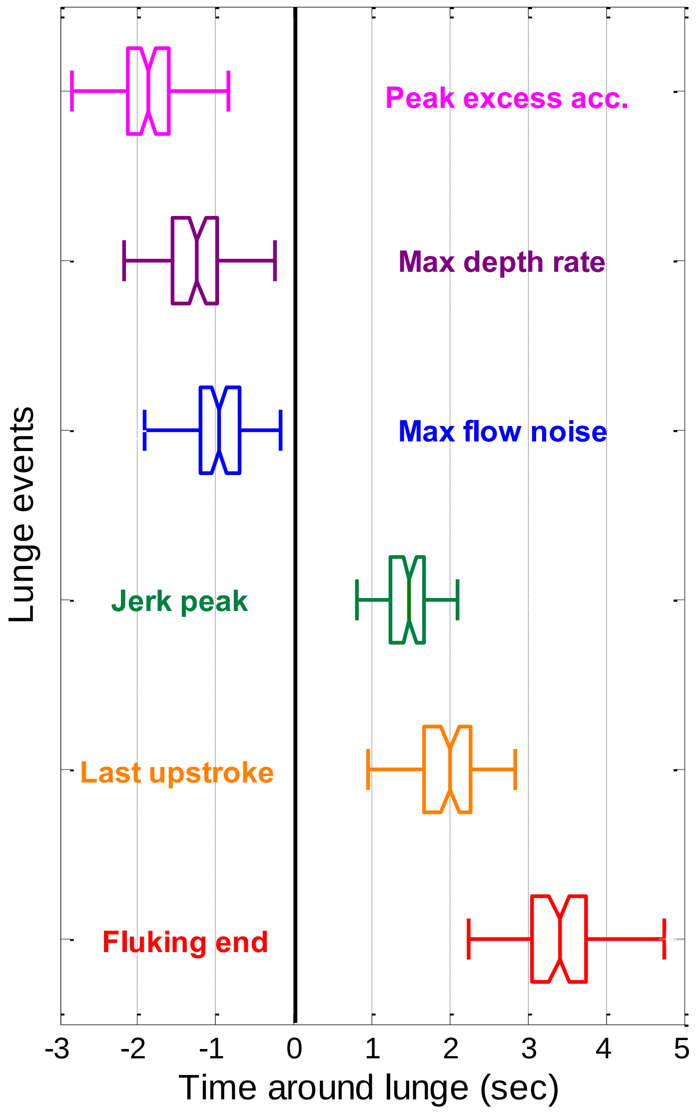
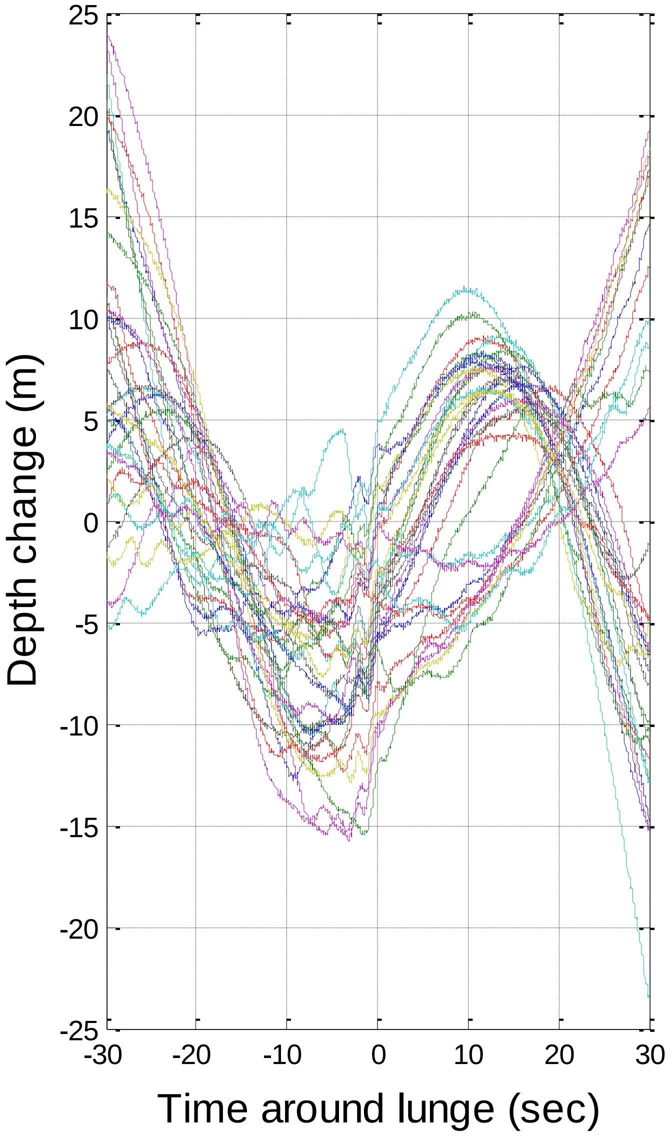

Peak excess acc.
Max depth rate
Max flow noise
Jerk peak
Last upstroke
Fluking end
Lunge events
-3
-2
-1
0
1
2
3
4
5
Time around lunge (sec)

FIGURE 6


Depth change (m)
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-20
-10
0
10
20
30
Time around lunge (sec)

Humpback whale habitat use

Chapter 4

Paper III:
Boye TK, Simon M & Madsen PT. 2010

Habitat use of humpback whales in Godthaabsfjord, West Greenland, with implications for commercial exploitation.
J Mar Biol Assoc UK. 90(8): 1529-1538

Journal of the Marine Biological Association of the United Kingdom, page 1 of 10. © Marine Biological Association of the United Kingdom, 2010
doi:10.1017/S0025315410000755

Habitat use of humpback whales in Godthaabsfjord, West Greenland, with implications for commercial exploitation

TENNA KRAGH BOYE[1], MALENE SIMON[1,2] AND PETER TEGLBERG MADSEN[1]

[1]Zoophysiology, Department of Biological Sciences, Aarhus University, C.F. Møllers Allé, Building 1131, 8000 Aarhus C, Denmark, [2]Department of Birds and Mammals, Greenland Institute of Natural Resources, PO Box 570, 3900 Nuuk, Greenland

North Atlantic humpback whales migrate from breeding grounds to high latitude feeding areas to where individuals display large scale site fidelity. In Godthaabsfjord (Greenland), humpback whales are present from early spring to late autumn. To test for small scale site fidelity and occurrence, identification-photographs were collected from May to September 2007 and 2008 and compared with an older catalogue. We found high small scale site fidelity where 40% of the whales present in 2007 were resighted in 2008. The average resight rate from 1992 to 2008 was 30.2%. Individuals did not remain in the fjord the entire season and the time spent in the fjord was highly variable amongst individuals varying between 7–60% of the time from May to September. Individual humpback whales in the presence and absence of boats were tracked with a land-based theodolite to test for effects of whale watching on whale behaviour. Whale watch vessels were shown to significantly increase whale swimming speed, to shorten long dives and diminish the ratio between surfacings and long dives. It is concluded that the same foraging whales use this fjord system year after year, calling for regulation of whale watching and for consideration when discussing reopening the whaling of humpback whales in West Greenland.

Keywords: humpback whale, photo-identification, site fidelity, habitat use, theodolite tracking, whale watching

Submitted 9 September 2009; accepted 22 February 2010

INTRODUCTION

Most populations of humpback whales (*Megaptera novaeangliae*) migrate annually from low latitude breeding grounds to high latitude feeding areas (Pomilla & Rosenbaum, 2005). They mate and give birth during winter in low productive areas close to the equator with little or no food availability. The whales therefore rely on their fat reserves during winter (Scheidat *et al.*, 2004). As spring approaches the humpback whales migrate to high productive areas at high latitudes, and through the summer they restore their fat reserves to be used at the breeding grounds in the winter. In the North Atlantic five main feeding areas have been identified: Gulf of Maine, Eastern Canada, West Greenland, Nova Scotia and the north-east Atlantic (Stevick *et al.*, 2003). Genetic tagging and photo-identification (photo-ID) studies show that humpback whales display a strong degree of large scale site fidelity towards these areas with little migration between them (Palsbøll *et al.*, 1997; Stevick *et al.*, 2006). However, little is known about small scale site fidelity within these feeding areas, where the same individuals may return annually to the same area within few kilometres (Clapham *et al.*, 1993).

In Godthaabsfjord, West Greenland (64°11 N 51°47 W), humpback whales are present from late spring to late autumn, but it is not clear to what degree it is the same whales targeting food resources in this fjord ecosystem. They come to feed on prey such as sand lance (*Ammodytes dubius*), capelin (*Mallotus villosus*) and euphausiids (Larsen & Hammond, 2004; Stevick *et al.*, 2006). To assess the ecological impact of humpback whales in the Godthaabsfjord ecosystem, data on the time spent in the fjord by individual whales, abundance and the amount of food individual whales consume are needed. Attempts to estimate abundance of humpback whales in Godthaabsfjord have been made (e.g. Heide-Jørgensen *et al.*, 2007) but very little is known about the time spent in the fjord, their ecological role and site fidelity over the summer season.

Knowing a degree of site fidelity is especially important for this stock given the context of potential commercial exploitation. Through time humpback whales have been considered a valuable resource in the Greenlandic society. Due to extensive commercial whaling up until the mid-1900s, commercial hunting of humpback whales was banned by the International Whaling Commission (IWC) in 1966, and only aboriginal hunters in West Greenland and the Lesser Antilles were allowed to continue humpback whaling (Martin *et al.*, 1984). In 1981, Whitehead *et al.* (1983) estimated the population size of West Greenland humpback whales to be 85–200 animals. When it became evident that the West Greenland humpback whales constituted their own feeding aggregation or stock, for which a reliable abundance estimate was lacking, the IWC reduced the West Greenland quota on humpback whales to zero in 1986 (IWC, 1986) and this quota is still in place. During the IWC meeting in 2008, Denmark requested a quota of 10 humpback whales per year for West Greenland (IWC, 2008). The request was not granted and Denmark, on behalf of Greenland, repeated the request in 2009.

Corresponding author:
T.K. Boye
Email: tennaboye@hotmail.com

No settlement has been reached and is up for discussion in the spring of 2010. Today, the population of humpback whales in West Greenland is estimated to increase at 9.4% yr^{-1}. Currently an estimated 3000 (cv = 0.45) humpback whales comprise the West Greenland feeding aggregation stretching from Disko Bay to Arsuk (Heide-Jørgensen *et al.*, 2008).

West Greenland humpback whales also constitute a key species for a growing whale watching industry. The whale watching industry in Greenland is expanding dramatically and in 2007 the industry turned over at least US$ 960,200 on whale watching (O'Connor *et al.*, 2009). Around Nuuk whale watching is restricted to areas within Godthaabsfjord, where the humpback whales are often approached closely by commercial and private whale watching boats. Hence, humpback whales play an important role both ecologically and economically in West Greenland, but little is known about the dynamics and governing factors of their habitat use. Consequently, the increased focus on the use of humpbacks for commercial purposes in the form of whaling where direct takes are involved and whale watching where more subtle long-term effects are possible as seen in dolphins (Bejder *et al.*, 2006; Lusseau *et al.*, 2006) calls for a better scientific basis for policy making around sustainable co-existence and commercial use of humpback whales.

Here we used photo-ID to investigate small scale site fidelity and habitat use of individual humpback whales foraging in Godthaabsfjord. Furthermore, we tracked humpback whales with a land-based theodolite in the absence and presence of whale watching boats to test for possible impacts of the presently unregulated whale watching. We discuss these data in the context of the biological and economic role of humpback whales in West Greenland.

MATERIALS AND METHODS

The study was conducted in Godthaabsfjord, West Greenland (Figure 1), covering the field seasons of May to October 2007 and May to September 2008.

Photo identification

ID-photos of the ventral side of the fluke were taken of humpback whales (Katona *et al.*, 1979) in defined areas in Godthaabsfjord (Figure 1). Searches of whales were conducted from a 5 m boat when weather conditions permitted small boat surveys. When a whale was encountered the boat slowed down to idling and photographs were taken with an EOS 350D Canon digital camera equipped with a Canon EF 75-300mm f/4-5.6 III USM lens. Shutter speed was $>1/1000$. Upon an encounter with a whale (both previously identified and new individuals), GPS position, time, date and number of whales were noted. Photographs were also taken from a local whale watching boat aiming at areas with a high probability to find whales, precluding quantification of effort. Finally, photographs of humpback whale flukes from Godthaabsfjord along with information on date, time and place if possible were provided by the public. Photographs judged to be of suitable quality (Calambokidis *et al.*, 2000) were compared visually and sorted into individual whales by two independent observers with identification experience.

An ID-catalogue of whales in Godthaabsfjord was built from the photographs collected in both field seasons along with photographs from Kook Islands found in an ID-catalogue of humpback whales from the west coast of Greenland (GINR and YONAH projects) from 1988–1993 (Larsen & Hammond, 2004). To investigate site fidelity of the individual humpback whales, ID-photos of the same individuals in Godthaabsfjord were sorted into the years they were taken. The time spent in the fjord, by each whale was determined from the photographs taken of each individual from day to day throughout the entire field season. All photographs were divided into weeks. If two ID-photos of the same individual were separated by one week, the whale was assumed to have been present in the fjord during the full week. The time spent in the fjord by each photo-identified whale was determined by counting how many periods each individual was observed in the fjord. A period was defined by the first and last ID-photos of the same individual taken in consecutive

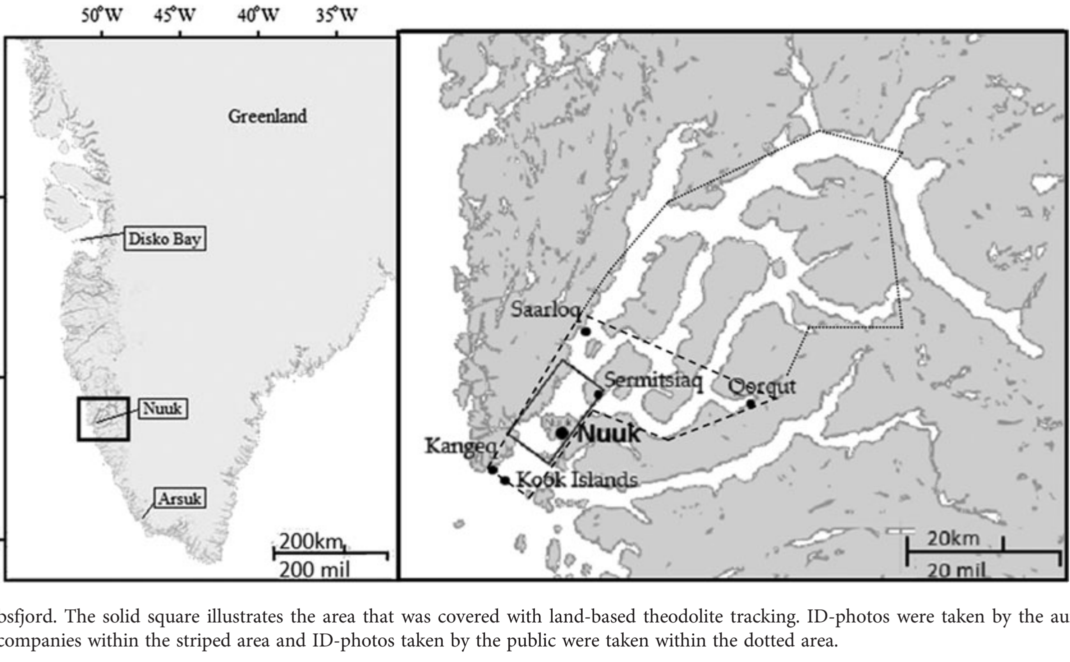


Fig. 1. Godthaabsfjord. The solid square illustrates the area that was covered with land-based theodolite tracking. ID-photos were taken by the authors and whale-watching companies within the striped area and ID-photos taken by the public were taken within the dotted area.

weeks. A new period was counted if two week numbers or more separated ID-photos of the same individual.

Theodolite observations

Humpback whales were tracked with a land-based theodolite from June to October in 2007 and from May to September in 2008. The theodolite (Leica TC1103) was placed at an observation point (64°11.17′N 51°43.95′W), 64.1 m relative to lowest astronomical tide (LAT), overlooking the entrance of the fjord (Figure 1). The position of the station was measured by ASIAQ (Greenland survey) using a high precision GPS (Leica 1200 with RTK). Height of the vantage point was calculated by calibrating the theodolite rendering a height above LAT with the lowest RMS error for distances up to 6000 m away from the land station. This was done, by using a boat as a reference point at logged GPS positions. This resulted in a mean RMS distance error of 0.8% within ranges of 6000 m. The RMS error of the horizontal angle remained stable over all distances and did not exceed 0.3 degrees.

Observations started with a half hour scan survey (Altmann, 1974), carried out daily at 08:00, 14:00 and 19:00. The area was scanned for whales, and if a whale was present, it was fixed by the theodolite, by measuring the horizontal and vertical angle to the whale relative to the observation point. When the half hour survey was done a whale was selected for focal animal sampling (Altmann, 1974) and tracked with the theodolite for at least 1 hour if still present in the study area. If more than one whale was present, one was chosen to be tracked for an hour and afterwards the other whale would be tracked, if still present. If two whales were swimming together (within one body length of each other) they were considered a group and an attempt was made to track only one of the two individuals, based on characteristics such as size, shape of dorsal fin and colour pattern of the fluke. If the two whales separated during tracking, one of the two was chosen for further tracking. The angles to whale watching boats (boats obviously following the whales over longer periods) were measured subsequent to the fluke up of the whale. Surveys were restricted to sea state 4 or less and not carried out during reduced visibility from, e.g. heavy fog or precipitation. From 1 June until 20 June 2007 surveys were carried out without theodolite due to technical problems. During this period only sightings of whales were noted and included in the analysis of temporal distribution.

Data from the theodolite were stored on a laptop and converted into geo-referenced x, y co-ordinates (latitude and longitude) using the equations of Gailey & Ortega-Ortiz (2000) implemented in Matlab 6.5 (Mathworks) and plotted in MapInfo Professional vs. 9.5. To determine the possible effect of whale watching boats on whale behaviour four parameters were quantified using presence/absence of boats as a fixed factor. These parameters were the apparent median surface speed (km/h) of the whales (calculated using the distance between each surfacing and the time taken to cover the distance), difference in duration of long dives (defined as dives exceeding 60 seconds), the ratio between long dives and surfacings and difference in the degree of changes in heading (Williams *et al.*, 2002). Long dives were all likely foraging dives as dives of similar duration by tagged animals showed lunge feeding. All tests were preceded by tests for homoscedasticity and normality, and when these were violated the data were either log transformed or non-parametric tests were applied. To test the difference in ratio between long dives ($\geq$60 seconds) and surfacings ($<$60 seconds) each individual whale was considered as a sample unit while all other tests were performed on the individual data points. As some tracks were longer than others, the tracks were homogenized to ensure that all whales contributed equally to the performed tests. This was done by randomly selecting an equal number of data points from each track. Following this, all data points were pooled in the two groups. Only tracks where whales were either constantly followed by a boat or no boat was present at all were included in analysis on the effect of whale watching.

To support theodolite data, data from a non-invasive, archival tag (DTAG; Johnson & Tyack, 2003) were analysed. One out of three tagged whales was exposed to whale watching, and potential effects of exposure were investigated in the dive profile data. The dive behaviour (time at surface and dive duration) without whale watching boats nearby was compared to the dive behaviour with whale watching boats nearby as recorded in field notes and estimated from boat noise on the tag audio recordings.

RESULTS

Photo-identification

A total of 47 and 126 ID-photos (20 and 56 photographs from the public, respectively) were collected during the two field seasons in 2007 and 2008, respectively. From the photographs collected, 20 individuals were identified in 2007 and 20 individuals were identified in 2008 (Figure 2). Most individuals had been identified by the beginning of July but new individuals were identified throughout both field seasons (Figure 2). Of the 20 individuals identified in 2007, a total of 8 (40.0%) were re-identified in 2008. 86 whales (58 individuals) were identified from ID-photos taken in Godthaabsfjord from 1992 to 2008 (Table 1). Of these, 26 (30.2%) were re-identified in the fjord during the 16 year period. One individual photographed in Godthaabsfjord in 1992 was resighted again in 2008 and at least in 7 other different years over the 16 year period.

Temporal and spatial distribution

In 2007 and 2008, 166 and 174 theodolite surveys (half hour duration) were carried out. This corresponds to a total of 170 hours of surveys (Figure 3A). In both 2007 and 2008 most whales were sighted during the summer months from June–August where June had the majority of whale positive surveys (23.9% and 9.4% respectively). In both years August had a few more whale positive surveys than July (13.2% and 5.6% in July contrary to 17.1% and 5.9% in August of 2007 and 2008 correspondingly). Fewer whales were spotted in May 2008 and October 2007. Mean effort between 2007 and 2008 by time of the day was 60, 58.5 and 51.5 hours at 08:00, 14:00 and 19:00, respectively (Figure 3B). When comparing the two field seasons, no specific pattern was found between time of day and the number of whale positive surveys.

As seen in Figure 3 more whales were sighted in 2007 during the theodolite surveys compared to 2008 (16.9% whale positive surveys in 2007 compared to 6.3% whales positive surveys in 2008). A total of 27 and 10 tracks of humpback

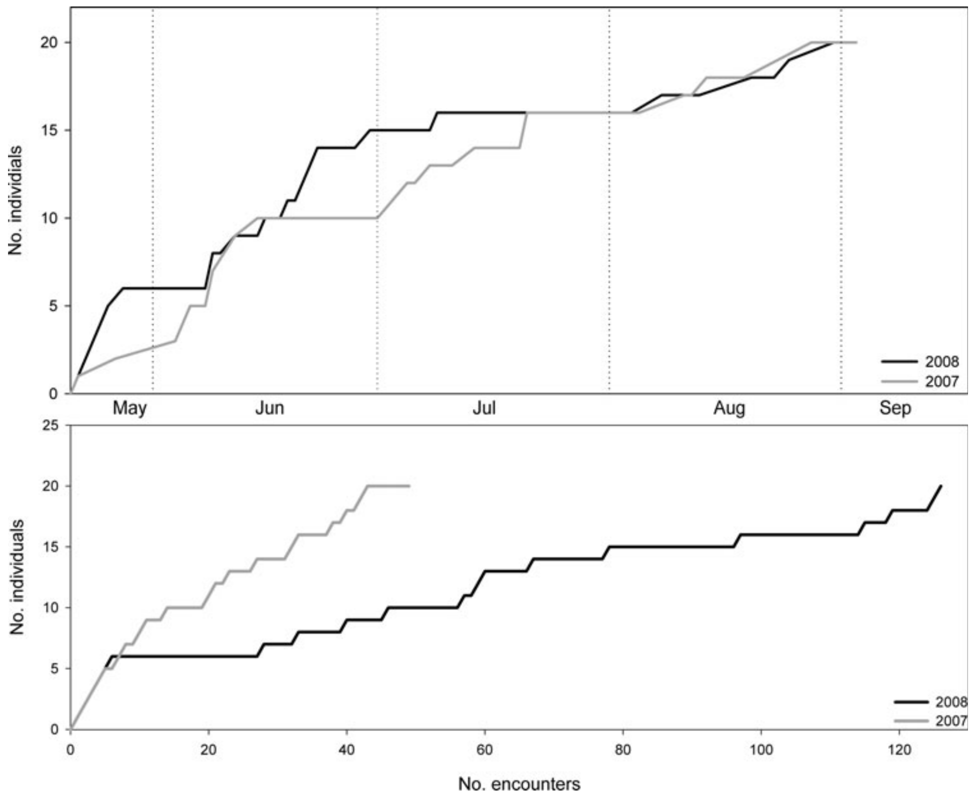


Fig. 2. Discovery curves of humpback whales in Godthaabsfjord. (Top) Number of new individuals identified during the field months (modified Julian days, where 1 May is day 1 to disregard leap year in 2008); (Bottom) number of new individuals identified per whale encounter. Plateaus signify repeated encounters where no new individuals were identified.

whales movements were collected in the season of 2007 and 2008, respectively (Figure 4).

The photo-ID data showed that time spent in the fjord by each whale during the field season varied among individuals, with individuals being present in the fjord from 7% to 60% of the total field season (Figure 5). In both years, the majority of the whales (80%) were photographed during a single period (defined as continuous weeks of observations) within a year. Seven whales were photographed in two different periods in the same year and a single whale was photographed over three different periods (Figure 5).

Effects of whale watching boats on whale behaviour

Sufficient data for analysis of the effect of whale watching were obtained only in 2007. When a whale watching boat was present (from the first time the boat came within 100 m of the whale until the boat left the whale) the median apparent speed of the whales (6.1 km/h ± 4.3, median ± IQR) increased significantly contrary to when no boats were present (5.4 km/h ± 4.5, median ± IQR)) (Mann–Whitney, $P = 0.001$). Furthermore, whales with no boats present

Table 1. Number of whales resighted in the period from 1992 to 2008 in Godthaabsfjord.

Year first seen	ID	N	No. of whales seen in each subsequent year									No. resighted in at least 1 year
			1993	1996	1999	2003	2004	2005	2006	2007	2008	
1992	13	13	2 (15.4)	1 (7.7)	1 (7.7)	1 (7.7)	1 (7.7)	–	1 (7.7)	0 (0.0)	1 (7.7)	2 (15.4)
1993	2	0		1 (50.0)	1 (50.0)	1 (50.0)	1 (50.0)	–	1 (50.0)	0 (0.0)	1 (50.0)	1 (50.0)
1996	2	1			1 (50.0)	1 (50.0)	1 (50.0)	–	2 (100.0)	1 (50.0)	2 (100.0)	2 (100.0)
1999	4	3				1 (25.0)	3 (75.0)	–	2 (50.0)	1 (25.0)	1 (25.0)	3 (75.0)
2003	1	0					1 (100.0)	–	1 (100.0)	–	1 (100.0)	1 (100.0)
2004	9	6						1 (11.1)	3 (33.3)	2 (22.2)	2 (22.2)	4 (44.4)
2005	2	1							–	0 (0.0)	0 (0.0)	0 (0.0)
2006	13	9								5 (38.5)	5 (38.5)	5 (38.5)
2007	20	15									8 (40.0)	8 (40.0)
2008	20	10									–	
Total	86	58										26 (30.2)

No data available is indicated by missing numbers. ID is the number of identified whales from 1992–2008. N is the number of new individuals identified from 1992–2008. The numbers in parentheses are per cent.

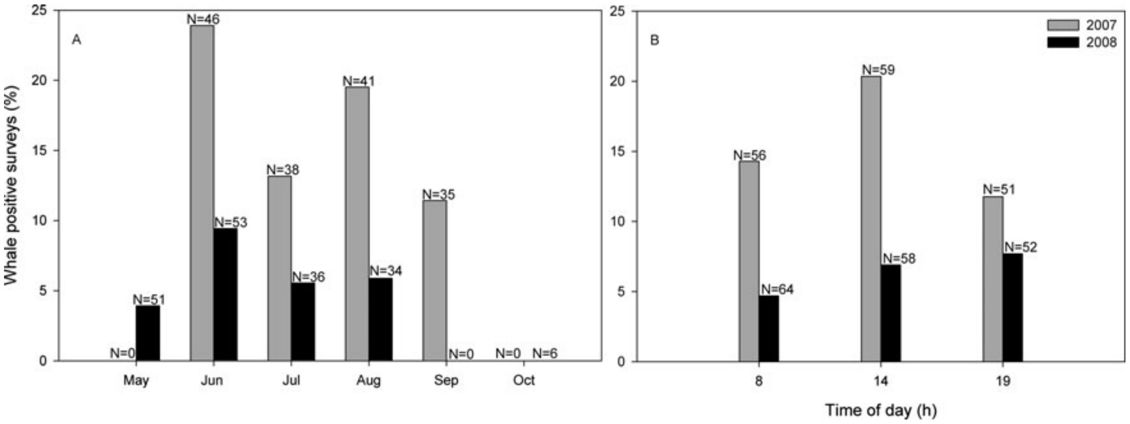


Fig. 3. (A) Number of surveys (%) in the months of both field seasons, where humpback whales were seen. N is the total number surveys conducted in the given month; (B) number of surveys (%) at the different time periods, where humpback whales were seen. N is the total number of surveys conducted at the given time.

carried out long dives of longer duration than whales followed by whale watching boats (Figure 6). Long dives of whales followed by boats were on average 117 seconds shorter than long dives carried out by whales without whale watching boats present (271 ± 195 and 388 ± 222, respectively) (Mann–Whitney, $P = 0.031$). The whales performed less than half the amount of surfacing between long dives when whale watching boats were present contrary to non-whale watching (Student's t-test, $t_{15} = -2.393$, $P = 0.03$). On average only 4.3 surfacings were made contrary to 9.3 surfacings when left undisturbed. Directionality seemed unaffected by presence of whale watching boats (Student's t-test, $t_{342} = 0.774$, $P = 0.439$).

Figure 7 illustrates a dive profile recorded with a DTAG onboard a humpback whale exposed to whale watching. Before exposure (0–110 minutes) the whale made regular long dives between 7 and 9 minutes of length. After some time in presence of a whale watching boat, driving fast towards the whale with closest distances of less than 30 m, long dives became shorter, of decreased depth, and the whale surfaced fewer times before long dives (130–230 minutes) (Figure 7). After exposure (230–350 minutes) a regular dive pattern was resumed, however within the first hour (230–300 minutes) the whale had longer surface times before long dives, compared to pre-exposure.

DISCUSSION

Temporal patterns of habitat use within years

If the population of humpback whales in Godthaabsfjord constituted a closed population, the discovery curve (Figure 2) would gradually level off as no new individuals would enter the fjord and the same individuals would be observed during subsequent encounters. Our discovery curves did not level off in either year. This strongly indicates that the humpback whales foraging in Godthaabsfjord are an open population where individuals from the West Greenland feeding aggregation migrate in and out of the fjord during the summer months. This is not unexpected as Godthaabsfjord is an open fjord system which allows the whales to migrate

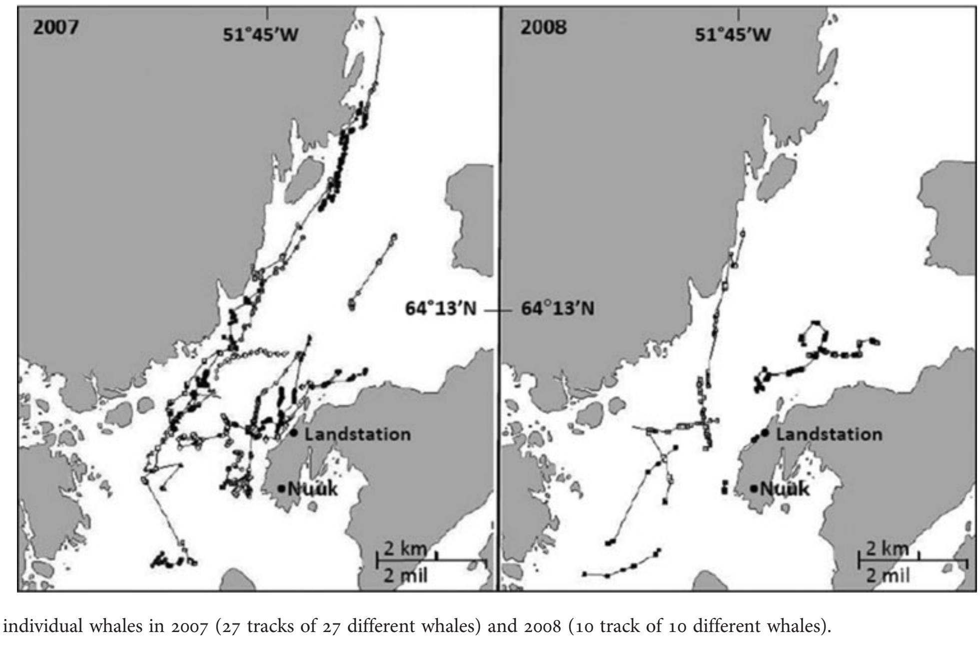


Fig. 4. Tracks of individual whales in 2007 (27 tracks of 27 different whales) and 2008 (10 track of 10 different whales).

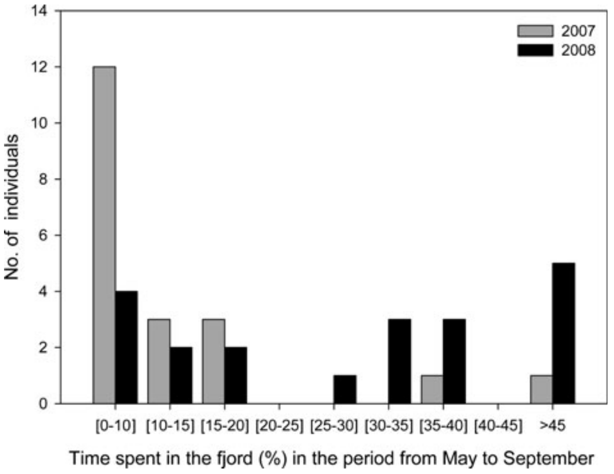


Fig. 5. Time spent in the fjord in both field periods for humpback whales in 2007 and 2008.

in and out easily, making it accessible to all whales travelling along the coast of West Greenland. An interesting feature of the discovery curves for both years is that there are plateaus: periods where no new individuals were added to the catalogue. These plateaus likely represent periods when few whales are entering the fjord system.

The time spent in the fjord amongst each individual was highly variable and we did not observe any whales that stayed in the fjord for the entire season. Moreover, the amount of periods that each whale resided in the fjord varied between one, two and three periods of various lengths. Although this could merely reflect that the individual whales were not photographed within the fjord during consecutive weeks, we believe that if a whale was present in the study area of Godthaabsfjord it was likely to have been photographed due to an almost daily effort on the water by either the whale watching boats or our crew. In addition, other studies have shown that humpback whales do migrate between different feeding areas within the foraging season (Heide-Jørgensen & Laidre, 2007). Normally temporal use of habitat would be quantified using the concept of residence time. However, with the opportunistic collection of photo-ID it was not possible to follow the strict definitions of residence time and we have rather used the term 'time spent in the fjord'. As Godthaabsfjord is open for migration there is a large probability of the whales migrating into the Davis Strait and we cannot assure that individuals were resident in the fjord between sightings. Yet, the fact that an individual is photographed several times in the fjord within a short time window does suggest that the individual has remained in or at least within the proximity of the fjord in those weeks. Although humpback whales can move long distances within a relatively short time period (e.g. Della Rosa *et al.*, 2008), we believe that the time limit set in this study, does not allow the individuals to migrate far distances and reach Godthaabsfjord in time to qualify for more than a single period of occupancy.

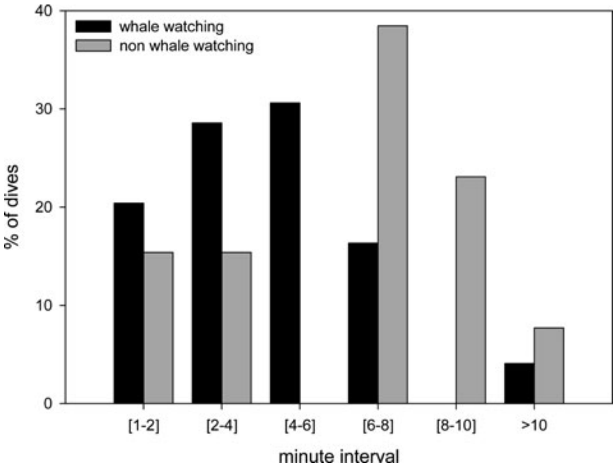


Fig. 6. The duration of long dives (defined as dives exceeding 60 seconds). The whales carry out longer long dives when no whale watching boats are present. $N_{\text{whale watching}} = 49$, $N_{\text{non whale watching}} = 13$.

Site fidelity across years

Of the 20 whales identified in Godthaabsfjord in 2007, 40% were resighted in the fjord in 2008. Furthermore, of the individuals identified from the ID-photos available from Godthaabsfjord in the time period from 1992 to 2008, we found a return rate of 30.2%. These high resight rates are despite the small sample size (Table 1) and effort over that entire period and the number thus represents the minimum rates of return during the 16 year period.

Few studies on humpback whales have looked at site fidelity on a regional scale. However, Clapham *et al.* (1993) addressed the issue and found a mean rate of return of 73.2% in individual humpback whales foraging in the Southern Gulf of Maine. Also, Weinrich (1998) did a study on small scale site fidelity in calves in the Gulf of Maine and found a strong degree of small scale site fidelity for calves (79.4%) returning to a regional area where they had been observed the year before. He argued that calves are introduced to the feeding areas during their year of maternal dependence and this introduction appears essential to their future choice of feeding ground on a regional scale. We also sighted young calves in the company of adult animals. It seems highly unlikely that the high rate of resightings found in both 2008 and in the period from 1992 to 2008 is a mere coincidence. First, the coast of West Greenland from Disko Bay to Arsuk, where foraging by humpback whales is known to take place, stretches more than 1000 km (Heide-Jørgensen & Laidre, 2007) and with a highly convoluted coastline with numerous fjords. Secondly, 3000 humpback whales are estimated to comprise the West Greenland feeding aggregation and could in theory enter the open fjord system. Therefore, the likelihood of at least 40% out of some 20 individuals from a 3000 animal population entering the fjord two years in a row by coincidence is very low. Thus, our findings here support the notion of small scale site fidelity reported by Weinrich (1998). Secondly we demonstrate that individual humpback whales not only return to the same general feeding areas within hundreds of kilometres but also within few kilometres, illustrating strong navigational skills, and long term memory of the spatial and temporal distribution of food resources, likely introduced to them by their mothers.

Small scale site fidelity has been documented in other migrating cetacean species as well. Ciano & Heule (2001) found individual sperm whales (*Physeter macrocephalus*)

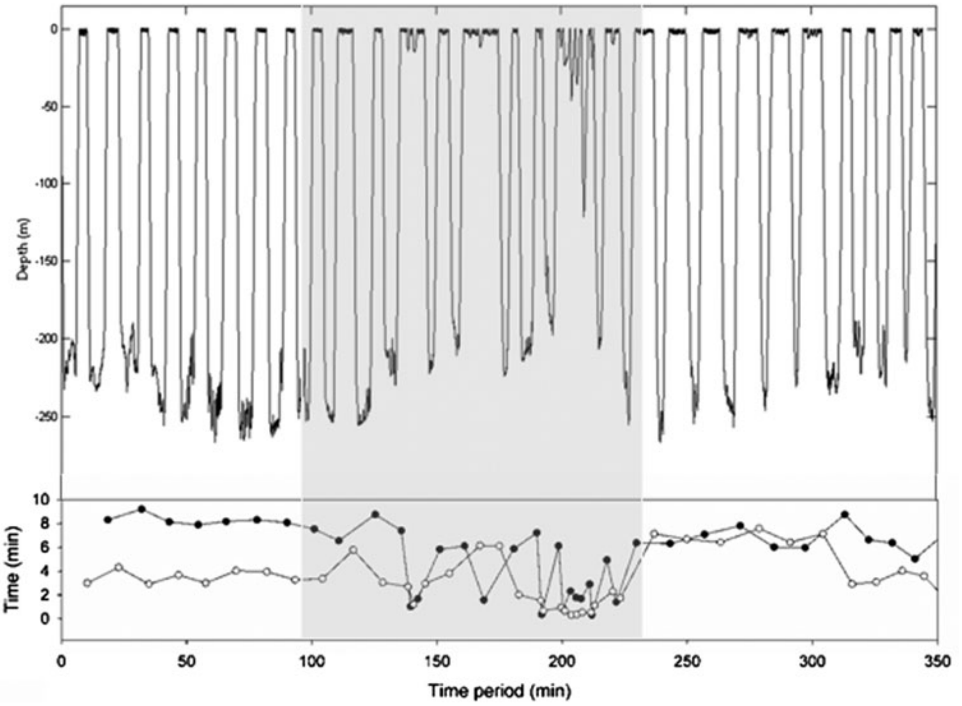


Fig. 7. Dive profile of humpback whale. The shadowed area illustrates the time period where the whale was exposed to whale watching and where high levels of engine noise were measured on and off. (Top) Illustrates the diving pattern of the whale over time; (Bottom) illustrates diving duration (•) and time combined spent at the surface (o) over time.

returning to Bleik Canyon, Norway, over years. One individual in their study was resighted during 10 consecutive years. We also confirmed an individual to return to Godthaabsfjord during at least 7 years in the period from 1992 to 2008. As the number of ID-photos covering this entire period is scarce, the resight rate of 7 years for this individual whale must be a minimum.

As the coloration patterns of humpback whale calves can change dramatically within the first two years (Carlson *et al.*, 1990; Blackmer *et al.*, 2000), there is a chance that some of the new identifications in 2008 are individuals identified in 2007 that have undergone large changes in fluke coloration, leading to an underestimation of the degree of small scale site fidelity. Collection of genetic samples can in the future establish if new individuals are offspring of the individual humpback whales that already show a strong degree of small scale site fidelity towards Godthaabsfjord.

Seasonal patterns and habitat use

As seen in Figure 3A the highest numbers of whales were observed from the land station in June. In July fewer whales were present during surveys but in August more whales were yet again spotted during the survey hours. This was the case in both 2007 and 2008 although more so in 2007. This pattern is consistent with the number of individuals identified during the field seasons with photo-id. In both years, we identified most whales in June but in July the number of new individuals seemed to level off. In August new individuals continued to be identified. This suggests that most whales are present in the early summer month but during mid-summer few new encounters are made indicating little new arrival. Also, the decrease in observations from the land station during July suggests that some individuals move elsewhere to feed. This notion is supported by a single id-photo taken by locals in Aasiaat (approximately 550 km north of Nuuk in Disko Bay) in July 2008 which we matched to an individual photographed in Godthaabsfjord in June the same year. Satellite data on humpack whales in West Greenland also support this notion (Heide-Jørgensen *et al.*, 2007).

The first whales arrive to Godthaabsfjord in May. In the same month capelin migrate from the depth of the banks and into the shallow waters of the fjord to spawn. Capelin spawning is separated temporally along the west coast of Greenland and begins in April at the southern tip of Greenland (Friis-Rødel & Kanneworf, 2002). Spawning starts in Godthaabsfjord in mid-May in the innermost part of the fjord and ends in June in the outermost parts (Hedeholm, personal communication). In the north from Disko Bay to Uummannaq spawning occurs from mid-June to mid-July. It seems likely that some whales time their arrival to coincide with capelin spawning in Godthaabsfjord. It is possible that some of them migrate northwards during the foraging season to benefit from the staggered spawning behaviour of capelin. Other whales may stay/arrive to take advantage of other food sources such as euphausiids. Upwelling during the winter forms the basis of a spring and a late summer bloom in Godthaabsfjord due to the highly nutrient water (Larsen & Hammond, 2004). This creates favourable conditions for the herbivorous euphausiids feeding on algae. Large amounts of euphausiids were caught during the 2008 'Dana' cruise in Godthaabsfjord in mid-August (Rysgaard, personal communication). Furthermore, in late May 2008 we observed humpback whales lunge feeding on the surface in areas with high densities of visual observable euphausiids, and on one occasion euphausiids were observed inside the mouth of a feeding whale in June. Hence, it appears that the variable residence time within our field seasons reflect that the humpback whales, influenced by small scale site fidelity, employ different regional migratory patterns to match the availability of different food sources during the foraging season.

In other areas humpback whales have been shown to alter their distribution regionally subsequent to changes in the distribution of their prey species between years (Payne *et al.*, 1990; Weinrich *et al.*, 1997). In this study a change in the distribution of humpback whales was also found between our consecutive field seasons as indicated in several ways. During the collection of ID-photos, whales where mostly present in the main course of the fjord from Saarloq to Kangeq in 2007. In 2008 the whales were more often spotted in the transversal waters running from Qorqut to south-west of Sermitsiaq (Figure 1). Consequently, during our land based surveys fewer observations of whales were made in 2008 compared to 2007. We do not have data on the distribution of humpback whale prey species in Godthaabsfjord in either field season and we are therefore not able to investigate if prey caused this difference in whale distribution or the shorter residence time of humpback whales in 2007.

The fact that more whales are seen moving than staying suggests that the survey area (i.e. between Nuuk and Nordland) is used for transit, rather than as a feeding area. This was especially true for 2008.

Management implications of small-scale site fidelity and low local-population size

When considering reopening a hunt on humpback whales in Greenland the small scale site fidelity displayed by the whales in this study along with the limited number of individuals identified in the fjord in both field seasons should be considered. The small scale site fidelity and the fact that only a small fraction of the West Greenland humpback whale population makes use of Godthaabsfjord imply that, if individuals are hunted within the fjord, the number of whales in the fjord may decrease in the years to follow. The whale watching boats in Nuuk depend on the whales that stay within the fjord as whale watching is only carried out in the vicinity of Nuuk city and not in Davis Strait. Thus, a debate on a quota on West Greenland humpback whales should consider the high site fidelity in the light of the economic interests in non-lethal exploitation through whale watching.

Whale watching in Godthaabsfjord

Whale watching worldwide was estimated to turn over 2.1 billion US$ in 2008 and attracting more than 13 million guests (O'Connor *et al.*, 2009). Several studies on whale watching have shown that disturbances from vessels or swimmers cause a significant change in behaviour in many cetacean species (e.g. Bejder *et al.*, 1999, 2006; Scheidat *et al.*, 2004; Lusseau *et al.*, 2006). From our results it is clear that the humpback whales in Godthaabsfjord can be disturbed by the sometimes aggressive and unregulated whale watching, as testified by a significant change in diving behaviour when foraging. Increased apparent median swimming speed in the presence of boats is a sign of avoidance along with the fact that the whales are surfacing fewer times before a long dive when boats are present (Scheidat *et al.*, 2004). The fewer surfacing periods apparently result in truncated long dives due to a decrease in the time to replenish oxygen stores when at the surface. Among the parameters measured, only the degree of change in directionality was not different between the two situations. A similar situation was observed by Williams *et al.* (2006), where killer whales approached by boats responded by decreasing their dive times and increasing the change in direction. Also, Scheidat *et al.* (2004) observed that humpback whales in Ecuador reacted to whale watching boats by significantly increasing their swimming speeds and through more erratic swimming paths. Because our data were homogenized to avoid problems of tracks of different length, our tracks may have become too short to be able to distinguish between whale watching and non-whale watching situations with respect to change of headings. Yet, our results could also reflect that humpback whales display different avoidance techniques in the presence of boats. The increase of the whale watching industry and the many private boats that exercise whale watching in Godthaabsfjord thus have the potential to cause significant disturbance of individual humpback whales in Godthaabsfjord. Animals with long residence times could be particularly exposed.

Whale watching in Greenland is not regulated and on most occasions we observed boats at high speeds within few metres of the whales. On several incidents more than one boat was present and we counted up to 15 boats on a single occasion. If the relatively small number of humpback whales, identified in this study, to some degree reflects the abundance in Godthaabsfjord, and given that they are not all present at the same time, it is likely that the same individuals are being repeatedly targeted by whale watching boats during their stay in the fjord.

As the summer season provides the only chance for the whales to restore their fat reserves, repeated disturbance may likely reduce the food intake over the season along with the additional energetic costs of avoidance. Figure 7 shows shorter dive duration when foraging, most likely as a result of the shorter time period spent at the surface before diving. The profile also indicates a post-exposure reaction as the whale spends additional time at the surface between long dives an hour after the boat had left. Thus the whales seem affected for an almost equally long period during exposure and post-exposure. This could indicate an oxygen debt incurred during the exposure and the need for additional ventilation due to increased speed and less time spent at the surface in the vicinity of the boat. However, more dive profiles of whales both exposed to whale watching and whales unexposed would be needed to make general conclusions.

In most countries with commercial whale watching, regulations and codes of conduct have been developed to mitigate negative effects on the targeted animals. In New Zealand the Marine Mammal Protection Regulations 1992 are established (MMPR; New Zealand Government, 2008) to provide guidelines on how to interact with whales in a least intrusive manner. A study by Lusseau (2003) in New Zealand showed that bottlenose dolphin, *Tursiops* spp., behaved differently according to boats either respecting or ignoring the MMPR guidelines. He found, that a research vessel, which in an 8 year period had respected the MMPR guidelines, did not seem to affect the behaviour of the dolphins. On the contrary, boats with an intrusive approach caused the dolphins to increase their dive intervals.

While limited whale watching, despite short term disturbance, may not have any long term effects on individual animals nor the part of the West Greenland population that use Godthaabsfjord, more intense whale watching could render such negative effects real. If the presently unregulated whale watching in Godthaabsfjord continues to grow, it may have an indirect effect on fitness of individual humpback whales as the energy needed, e.g. migration and calving is reduced if the food intake is reduced through vessel induced disturbances of normal foraging behaviour. For example, a reduction in food intake of 5% over the season may cause some whales to skip a breeding season, hereby avoiding migration due to insufficient energy reserves. This will result in fewer calves being born overall. Furthermore, intense whale watching could result in females having decreased energetic resources to produce or nurse their offspring which will have a direct effect on survival of the calves.

So while whale watching is often considered an economically important and non-invasive use of whales, our findings indicate that expanded and intensive, unregulated whale watching may cause fitness reductions for some individuals in the West Greenland stock, which calls for guidelines if such effects are to be mitigated.

CONCLUDING REMARKS

Although the humpback whales in Godthaabsfjord do not reside in this area for the entire foraging season but migrate between foraging areas, these whales display a strong degree of small scale site fidelity where the same limited number of individuals out of an estimated population of 3000 return to Godthaabsfjord between and within years. This demonstrates that individual, migrating humpback whales have navigational skills that allow them to find a fjord entrance that is less than 10 km wide. If humpback whales are hunted within the fjord it is questionable if such individuals will be replaced. This will affect the still growing whale watching industry in Nuuk which lies on the whales within the fjord system. Intense and unregulated whale watching can have more subtle negative effects on the humpback whales foraging in Godthaabsfjord, causing a change in both swimming and foraging behaviour. To ensure a sustainable whale watching industry we suggest that guidelines similar to the MMPR are enforced in Greenland.

ACKNOWLEDGEMENTS

We thank K. Clausen, R. Hedeholm, L. Heilmann, F. Heinrich, H. Bates and F. Ugarte for assistance in the field. We thank the locals in Nuuk, Tupilak Travel and the crew on IVIK for all their help in collecting ID-photos. Thanks to M. Weinrich, L. Bejder, J. Teilmann and F. Ugarte for comments on previous versions of the manuscript. The study was funded by the Oticon Foundation, KIIIN (Department of Culture, Education, Research and Church in Nuuk) and the Centre of Marine Ecology and Climate Effects, Greenland Institute of Natural Resources. P.T.M. was supported by the Danish Natural Science Research Council via a Steno and frame grants.

REFERENCES

Altmann J. (1974) Observational study of behaviour: sampling methods. *Behaviour* 49, 228–239.

Bejder L., Dawson S.M. and Harraway J.A. (1999) Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science* 15, 738–750.

Bejder L., Samuels A., Whitehead H., Gales N., Mann J., Connor R.C., Heithaus M.R., Watson-Capps J., Flaherty C. and Krützen M. (2006) Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology* 20, 1791–1798.

Blackmer A.L., Anderson S.K. and Weinrich M.T. (2000) Temporal variability in features used to photo-identify humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science* 16, 338–354.

Calambokidis J., Steiger G.H., Rasmussen K., Urbán J.R., Balcomb K.C., Geuvara P.L., Salinas M.Z., Jacobsen J.K., Baker S.C., Herman L.M., Cerchio S. and Darling J.D. (2000) Migratory destinations of humpback whales that feed off California, Oregon and Washington. *Marine Ecology Progress Series* 192, 295–304.

Carlson C.A., Mayo C.A. and Whitehead H. (1990) Changes in the ventral fluke pattern of the humpback whale (*Megaptera novaeangliae*), and its effect on matching; evaluation of its significance to photo-identification research. *Report of the International Whaling Commision* (Special Issue 12) SC/A88/ID35, 105–111.

Ciano J.N. and Heule R. (2001) Photo-identification of sperm whales at Bleik Canyon, Norway. *Marine Mammal Science* 17, 175–180.

Clapham P.J., Baraff L.S., Carlson C.A., Christian M.A., Mattila D.K, Mayo C.A., Murphy M.A., and Pittman S. (1993) Seasonal occurrence and annual return of humpback whales, *Megaptera novaeangliae*, in the southern Gulf of Maine. *Canadian Journal of Zoology* 71, 440–443.

Della Rosa L., Secchi E.R., Maia Y.G., Zerbini A.N. and Heide-Jørgensen M.P. (2008) Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. *Polar Biology* 31, 771–781.

Friis-Rødel E. and Kanneworf P. (2002) A review of capelin (*Mallotus villosus*) in Greenland waters. *ICES Journal of Marine Science* 59, 890–896.

Gailey G.A. and Ortega-Ortiz J.G. (2000) *User's manual 'Pythagoras' Version 1.0: Theodolite Cetacean Tracking.* Galvestone, TX: Texas A & M University.

Heide-Jørgensen M.P. and Laidre K.L. (2007) Autumn space-use patterns of humpback whales (*Megaptera noveangliae*) in West Greenland. *Journal of Cetacean Research and Management* 9, 121–126.

Heide-Jørgensen M.P., Simon M.J. and Laidre K.L. (2007) Estimates of large whale abundance in Greenlandic waters from a ship-based survey in 2005. *Journal of Cetacean Research and Management* 9, 95–104.

Heide-Jørgensen M.P., Laidre K.L., Hansen R.G., Rasmussen M., Burt M.L., Borchers D.L., Dietz R. and Teilmann J. (2008) Revised abundance estimates of humpback whales in West Greenland. *Report of the International Whaling Commission* SC/60/AWMP7, 1–35.

IWC (1986) Chairman's report of the thirty-seventh annual meeting. *Report of the International Whaling Commission* 36, 10–29.

IWC (2008) *Annual Report of the International Whaling Commission 2008*, Cambridge: International Wholing Commission.

Johnson M.P. and Tyack P.L. (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanographic Engineering* 28, 3–12.

Katona S.K., Baxter B., Brazier O., Kraus S., Perkins J. and Whitehead H. (1979) Identification of humpback whales by fluke photographs. The behavior of marine mammals. In Winn H.E. and Olla B.L. (eds) *Behavior of marine mammal science, Volume 3, Cetaceans.* New York: Plenum Press, pp. 33–44.

Larsen F. and Hammond P.S. (2004) Distribution and abundance of West Greenland humpback whales (*Megaptera novaeangliae*). *Journal of Zoology* 263, 343–358.

Lusseau D. (2003) Male and female bottlenose dolphins (*Tursiops* spp.) have different strategies to avoid interactions with tour boats in Doubtful sound, New Zealand. *Marine Ecology Progress Series* 257, 267–274.

Lusseau D., Slooten L. and Currey R.J.C. (2006) Unsustainable dolphin-watching tourism in Fiordland, New Zealand. *Tourism in Marine Environment* 3, 173–178.

Martin A.R., Katona S.K., Mattila D., Hembree D. and Waters T.D. (1984) Migration of humpback whales between the Caribbean and Iceland. *Journal of Mammalogy* 65, 330–333.

New Zealand Government (2008) *Marine mammal protection regulations, 1992 (SR 1992/322).* Reprint as at 11 September 2008.

O'Connor S., Campbell R., Cortez H. and Knowles T. (2009) *Whale watching worldwide: tourism numbers, expenditures and expanding economic benefits, a special report from the International Fund for Animal Welfare.*Yarmouth MA, USA, prepared by Economists at Large.

Palsbøll P.J., Allen J., Bérubé M., Clapham P.J., Feddersen T.P., Hammond P.S., Hudson R.R., Jørgensen H., Katona S., Larsen A.H., Larsen F., Lien J., Mattila D., Sigurjónsson J., Sears R., Smith T., Sponer R., Stevick P. and Øien N. (1997) Genetic tagging of humpback whales. *Nature* 388, 767–769.

Payne M.P., Wiley D.N., Young S.B., Pittman S., Clapham P.J. and Jossi J.W. (1990) Recent fluctuations in the abundance of baleen whales in the Southern Gulf of Maine in relation to changes in selected prey. *Fishery Bulletin* 88, 687–696.

Pomilla C. and Rosenbaum H.C. (2005) Against the current: an inter-oceanic whale migration event. *Biology Letters* 1, 476–479.

Scheidat M., Castro C., Gonzalez J. and Williams R. (2004) Behavioural responses of humpback Whales (*Megaptera novaeangliae*) to whale watching boats near Isla de la Plata, Machalilla National park, Ecuador. *Journal of Cetacean Research and Management* 6, 63–68.

Stevick P.T., Allen J., Clampham P.H., Friday N., Katona T.K, Larsen F., Lien J., Mattila D.K., Palsbøll P.J., Sigurjórnsson J., Smith T., Øien N. and Hammond P.S. (2003) North Atlantic humpback whale abundance and the rate of increase four decades after protection from whaling. *Marine Ecology Progress Series* 258, 263–273.

Stevick P.T., Allen J., Clapham P.H., Katona T.K., Larsen F., Lien J., Mattila D.K., Palsbøll P.J., Sears R., Sigurjórnsson J., Smith T.D., Vikingsson G., Øien N. and Hammond P.S. (2006) Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology* 270, 244–255.

Weinrich M., Martin M., Griffiths R., Bove J., and Schilling M. (1997) A shift in distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine. *Fishery Bulletin* 95, 826–836.

Weinrich M. (1998) Early experience in habitat choice by humpback whales (*Megaptera novaeangliae*). *Journal of Mammalogy* 79, 163–170.

Whitehead H., Kevin C., Perkins J., Bryant P. and Nichols G. (1983) Population size, stock identity, and distribution of the humpback whales off West Greenland—summer 1981. *Report of the International Whaling Commission* 33, 497–501.

Williams R., Trites A.W. and Bain D.E. (2002) Behavioral response of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *Journal of Zoology, London* 256, 255–270.

and

Williams R., Lusseau D. and Hammond P.S. (2006) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation* 133, 301–311.

Correspondence should be addressed to:
T.K. Boye
Zoophysiology, Department of Biological Sciences
University of Aarhus
C.F. Møllers Allé, Building 1131, 8000 Aarhus C, Denmark
email: tennaboye@hotmail.com

Large whale ship-based survey

Chapter 5

Paper IV:
Heide-Jørgensen MP, Simon MJ & Laidre KL. 2007

Estimates of large whale abundance in Greenland waters from a ship-based survey in 2005.
J Cetacean Res Manage 9(2): 95-104

Estimates of large whale abundance in Greenlandic waters from a ship-based survey in 2005

M.P. HEIDE-JØRGENSEN, M.J. SIMON AND K.L. LAIDRE

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

Contact e-mail: mhj@ghsdk.dk

ABSTRACT

A ship-based line transect survey of large whales in East and West Greenland was conducted in September 2005. The survey platform primarily targeted capelin, *Mallotus villosus*, using acoustic methods and systematically covered the east and west coasts of Greenland from the coast to the shelf break (approximately 200m). The surveyed area comprised 81,000km² in East Greenland and 225,000km² in West Greenland. A total of 194 sightings of 13 cetacean species were obtained and standard line transect methods were used to derive abundance estimates of the four most commonly encountered large cetaceans. Fin whales, *Balaenoptera physalus*, were most abundant in East Greenland (3,214, 95% CI=980-10,547) with lower abundances estimated for West Greenland (1,980, 95% CI=913-4,296). Sei whales, *B. borealis*, were frequently encountered in the same areas as fin whales, but the estimated abundance in East Greenland (763, 95% CI=236-2,465) was lower than in West Greenland (1,599, 95% CI=690-3,705). Humpback whales, *Megaptera novaeangliae*, were found both in offshore and coastal areas of West Greenland (1,306, 95% CI=570-2,989) and in low numbers in East Greenland (347, 95% CI=48-2,515). Finally, common minke whale, *B. acutorostrata*, abundance was estimated at 1,848 (95% CI=197-17,348) for East Greenland and 4,479 (95% CI=1,760-11,394) for West Greenland. Inclusion of sightings of unidentified large baleen whales in West Greenland distributed in proportion to species and strata increased abundance estimates for fin, sei, and humpback whales to 2,824 (95% CI=1,346-5,925), 2,009 (95% CI=948-4,260), and 1,514 (95% CI=560-4,089), respectively. Despite good conditions and considerable effort, few cetaceans were observed in the northernmost strata in West Greenland. This suggests that the southbound fall migration of large whales from North West Greenland had already started by the time the survey was initiated. The abundance estimates presented in this study are negatively biased. No corrections were applied for whales missed by observers or for whales submerged during the passage of the survey platform, which should cause a particularly large negative bias, for the estimates of common minke whale abundance.

KEYWORDS: FIN WHALE; COMMON MINKE WHALE; HUMPBACK WHALE; SEI WHALE; SURVEY-VESSEL; NORTHERN HEMISPHERE; ABUNDANCE ESTIMATE; *g*(0); DISTRIBUTION

INTRODUCTION

Information on the abundance of large whales in Greenland waters, including fin whales, *Balaenoptera physalus*, sei whales, *B. borealis*, humpback whales, *Megaptera novaeangliae*, and common minke whales, *B. acutorostrata*, is scarce and outdated. During 1982/83, the first ship-based cetacean sighting surveys were conducted in West Greenland by the Greenland Fisheries Research Institute (m/v *Regina Maris* and m/v *Kathleen*). Inclement weather conditions prevented the collection of sufficient sightings for abundance estimates from these surveys and no abundance estimates were calculated. After this, aerial surveys were used as the survey platform to increase coverage during the relatively small window of time when survey conditions are optimal in Greenlandic waters.

Between 1983 and 1993, visual aerial surveys of large cetaceans were conducted nine times in West Greenland. Only two times during this decade (cue-counting surveys in 1987/88 and again in 1993) did the surveys provide useful abundance estimates of large whales (Hiby and Hammond, 1989; Larsen, 1995; Larsen *et al.*, 1989). From these surveys, fin whale abundance was estimated at 1,096 (95% CI=520-2,100) in West Greenland in 1987/88 (IWC, 1992). In 1993, another estimate of approximately 200 fin whales was obtained, but was considered unrealistically low due to poor survey coverage (Larsen, 1995). In 2002 and 2004, visual aerial photographic surveys were conducted (Witting and Kingsley, 2005) and resulted in an estimated abundance of fin whales (980, 95% CI=402-2,392), similar to that obtained in 1987/88.

Abundance estimates of common minke whales were also obtained from the cue counting survey in 1993 and were estimated at 8,371 (95% CI=2,414-16,929) whales in West Greenland (Larsen, 1995). This estimate was larger (but not significantly different) than the estimate obtained on the 1987/88 survey (3,266 common minke whales, 95% CI=1,700-5,710) (IWC, 1990, p.43). The visual photographic surveys in 2002 and 2004 resulted in an abundance estimate of only 510 common minke whales (95% CI=138-1,889). This estimate was considered problematic for a number of reasons, including the fact that it seemed unrealistically low because the annual take in West Greenland (about 170 common minke whales) has remained relatively stable for the past 20 years (for a full discussion see 2006). Sei whale abundance has never been estimated in Greenland.

Humpback whale abundance has been estimated in Greenland based on visual and photographic surveys, as well as photo-identification (ID) techniques. Photo-ID surveys for humpback whale abundance were conducted off West Greenland in July and August 1988-93 (Larsen and Hammond, 2004). The surveys covered the coast between 62° and 66°N offshore to the 200m depth contour. A combined estimate over five years of surveys resulted in an estimate of 360 humpback whales (95% CI=314-413) in summer. Other estimates of humpback whale abundance in West Greenland include a line transect analysis of the visual aerial survey data from 1993 (Kingsley and Witting, 2001), which resulted in an uncorrected estimate of 599 (95% CI=237-1,512), as well as an estimate of 400 humpbacks based on sightings of 3 whales (CV=0.64) collected during aerial photographic surveys in 2002 and 2004 and the assumption that humpback whales spend a quarter of their time at the surface. However, no variance was associated with the coarse correction factor applied to these data (Witting and Kingsley, 2005).

It is important to notice that except for the photographic surveys in 2002-04, all previous surveys were conducted between mid July and late-August to cover the peak occurrence of common minke whales along the West Greenland coast. In particular common minke whales have shown affinity for southbound movements in September (Heide-Jørgensen *et al.*, 2001; Víkingsson and Heide-Jørgensen, 2005) and surveys conducted in September may not capture all of the whales found earlier in the summer.

In 2004, the Scientific Committee of the International Whaling Commission (IWC) had stated that it is difficult to provide satisfactory advice on sustainable takes from Greenlandic stocks without recent and robust abundance estimates (IWC, 2005). Available estimates of all large baleen whale abundance in West Greenland waters at that time were either outdated or unreliable. Thus, there was an urgent need for abundance estimates in Greenland given that common minke and fin whales are taken annually in Greenlandic waters, with removals in West Greenland between 1999-2004 averaging 172 common minke whales and 9 fin whales. Additionally, a total of 9 humpback whales were caught in 2004/05 as bycatch in pond nets and in a crab fishery that utilises bottom traps attached to surface buoys.

This manuscript reports on a ship-based survey of large cetaceans conducted in West and East Greenland in September 2005. Abundance estimates were developed for all large whale species where sufficient sightings were available. These provide updated abundance estimates for large cetaceans in Greenland waters as well as updating knowledge on distribution and numbers at both coasts. A simultaneous aerial survey provided additional information about abundance and distribution of large whales in West Greenland (Heide-Jørgensen *et al.*, 2007).

METHODS

Field methods

The Icelandic fisheries research vessel r/v *Bjarni Saemundsson* RE 30 (length 56m and height to upper deck 7m) was used as the platform for the sighting survey. The survey was conducted between 2 September and 3 October 2005 during a systematic acoustic survey targeting capelin, *Mallotus villosus*, on the West and East Greenland shelf.

Observations were made from a wooden box (length: 180cm, width: 226cm, height of walls: 145cm) built with an effective windshield on the roof of the bridge. Four cetacean observers scanned in pairs from the main platform, each covering 90 degrees in front of the vessel. Observers had an angle board mounted in front of them and a distance stick on a string around their neck. The length of the strings was such that one mm from the horizon corresponded to a declination angle of 0.1 degree, when measuring standing on the observation platform. The eye height of the observers was approximately 10.3m above sea level. When a whale or a cue of a whale was observed, the observer immediately measured the angle to the sighting with the angle board and the distance from the horizon to the sighting with the distance stick, which was later converted into distance from the boat to the whale. When the horizon was not visible or in the instances when a sighting was too brief for the observer to measure both angle and distance, the observer would estimate the distance by eye.

The observers were trained to estimate distances through distance estimation experiments, where a zodiac with a radar reflector was placed at distances between 100-1,600m to the boat (within the survey field). The observers estimated the distance by eye and then measured the distance using distance sticks. The real distance to the zodiac was measured with a laser rangefinder (Zeiss, Halem II) and the radar of the ship by the captain. Initially all observers' slightly underestimated distances exceeding 1,000m, both when estimated by eye and when measured with distance sticks. This underestimation was likely to have been reduced after the distance training, as the observers became aware of the bias. A second distance estimation experiment was scheduled to test this, but it could not be carried out due to low visibility and bad weather.

The observers only used binoculars for species identification after recording a whale sighting. On-effort observations were carried out during all hours of daylight and when weather conditions permitted (Beaufort sea state <6 and visibility >500m).

Measurements of angle and distance were noted in a sighting log together with date, time, position, group size and composition, swimming direction and surface behaviour. An effort log was kept every half hour or less if observation conditions changed. The effort log contained information about the date, time, location, bearing of the ship, weather and visibility. Positional information was obtained with a handheld Global Positioning System (GPS) or from instruments on the bridge.

The survey was designed to systematically cover the area between the coast of West Greenland and offshore (up to 100km) to the shelf break. Transect lines were placed in an east-west direction and the survey started at the northernmost lines. Some fjord areas including Vaigat, Disko Bay and Nuuk Fjord were also covered. Ferry time between Iceland and the surveyed area in West Greenland was used for whale sightings as weather permitted. Based on expected densities of whales the surveyed area was divided into 6 strata, with 1 stratum in East Greenland and 5 strata in West Greenland (Fig. 1). The Disko Bay area and the Nuuk Fjord were considered separate strata.

Analysis

Abundances of fin, sei, humpback and common minke whales were estimated using *Distance* 4.1 (Thomas *et al.*, 2001). Based on the minimum Akaike Information Criteria (AIC), the half-normal key, $k(y) = \exp(-y^2/(2\times A^2))$, with one cosine adjustment was chosen separately for each species for fitting the detection functions of grouped, perpendicular sighting distances. Effort (L) and sightings (n) during sea states of < Beaufort 6 were included for fin, sei and humpback whales abundance estimations following Buckland *et al.* (1992) and Víkingsson *et al.* (In Press). Only sightings and effort at sea states of < Beaufort 3 were included in the calculation of common minke whale abundance. Different right truncations were chosen for each species and common detection functions for all strata were derived. On-effort sightings in standard survey mode outside strata were included in the detection functions and in pod size estimates, but not in encounter rates (Table 1). Except for common minke whales, where all sightings were of individual whales, pod sizes combined for all strata were estimated by regression of *ln*(pod size) against the estimated probability of detection (Buckland *et al.*, 2001). Encounter rate, n/L, and the empirical variance was estimated and used to derive standard errors following Buckland *et al.* (2001). Confidence intervals were calculated following Burnham *et al.* (1987, p.212), assuming the abundance estimates had a log-normal distribution.

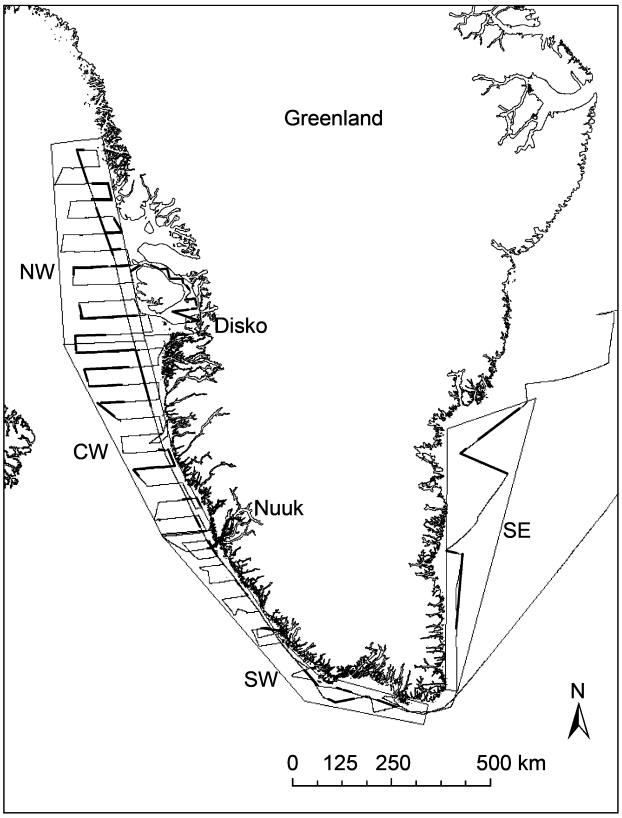


Fig. 1. Survey transect lines (thin lines), realised survey effort (thick lines) and delineation of strata for the ship-based survey of large cetaceans in Greenland in September 2005 in Beaufort sea states >6.

RESULTS

A total of 222 hours of on-effort observations were made where approximately 1,622 n.miles were covered in sea states < Beaufort 5 and 760 n.miles were covered in sea states of <3 (Fig. 1). During the survey, 194 sightings of 531 individual whales were made, including 13 different species (Table 1). The largest species diversity was observed in the Denmark Strait and off East Greenland's coast, where 11 of the 13 cetacean species were seen. No cetaceans were observed north of the Disko Bay in West Greenland (Fig. 1).

Distribution of whales

Six species of baleen whales were seen: blue whales (*Balaenoptera musculus*); fin whales; common minke whales; sei whales; humpback whales; and right whales (*Eubalaena glacialis*). Fin whales were most often found in dense aggregations in offshore areas, particularly along the East Greenland coast and southwest of Disko Bay. Sei whales did not extend as far north, but were otherwise found in the same areas as fin whales. Common minke whales were observed in the same areas as fin whales but in lower numbers. The humpback whale was the only species observed both offshore and inshore (Figs 2 and 3). One northern right whale and two blue whales were observed in East Greenland in the same area (65.1842°N 29.9558°W) on 3 September (Fig. 4).

Sightings of odontocetes included sperm whales, *Physeter macrocephalus*, pilot whales, *Globicephala melas*, white-sided dolphins, *Lagenorhynchus acutus*, white-beaked dolphins, *Lagenorhynchus albirostris*, killer whales, *Orcinus orca* and an unidentified beaked whale. Most odontocetes were seen in East Greenland (Fig. 5). White beaked dolphins were seen close to Cape Farewell and the one unidentified beaked whale, *Ziphiidae sp.*, was seen in a deep canyon between the coastal banks in South West Greenland. Sperm whales were observed off the east coast of Greenland and once in coastal waters on the west coast (Fig. 5).

Abundance estimates

Fin whales were detected at distances of up to 2km and sei whales at distances of up to 2.5km. Sightings were truncated at 1,800m to reduce the effect of measurement error on distant sightings. Both fin and sei whales had a high detection probability up to ~800m from the platform and there was a peak between 50 and 150m close to the trackline. The reason for this peak was not known. The detection function showed a satisfactory fit to the distribution of the 45 perpendicular distances of fin whale sightings (Fig. 6, χ^2 goodness-of-fit statistic not significant, p=0.53) and the effective search half-width (*esw*=944m) could be estimated with low variance (CV=0.12, Table 2). There were no sightings of fin whales in North West Greenland and in Disko Bay and the abundance was higher

Table 1

Sightings of different species of marine mammals during the survey. Observations are included from all Beaufort sea states and areas that are not included in the abundance estimation. In parenthesis are the unidentified sightings apportioned to species.

	Number of sightings				
Species	Total	Used in detection function	Used in abundance estimation	Outside survey region	Number of individuals
Blue whale	2	-	-	-	2
Fin whale	54	45 (57)	41 (53)	4 (4)	87
Sei whale	21	64 (81)	18 (23)	1 (1)	33
Humpback whale	30	26 (29)	21 (24)	5 (5)	46
Unidentified large cetacean	39	-	-	-	48
Northern right whale	1	-	-	-	1
Minke whale	14	12	10	2	14
Sperm whale	10	-	-	-	13
Beaked whale	1	-	-	-	1
Killer whale	2	-	-	-	8
Long-finned pilot whale	2	-	-	-	11
White-beaked dolphin	4	-	-	-	18
Atlantic white-sided dolphin	4	-	-	-	140
Unidentified dolphin	2	-	-	-	100
Harbour porpoise	2	-	-	-	3
Seal	14	-	-	-	79

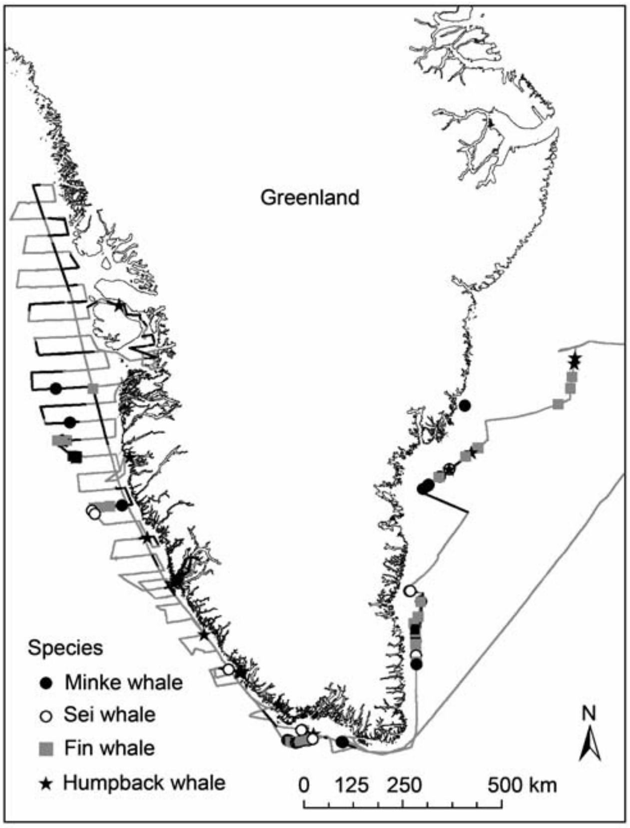


Fig. 2. Sightings of the four large cetaceans targeted in the ship based survey in Greenland September 2005. On-effort sections of transect lines (thick lines) are shown together with the sightings. [●]=common minke whales, [○]=sei whales, [▨]=fin whales and [★]=humpback whales.

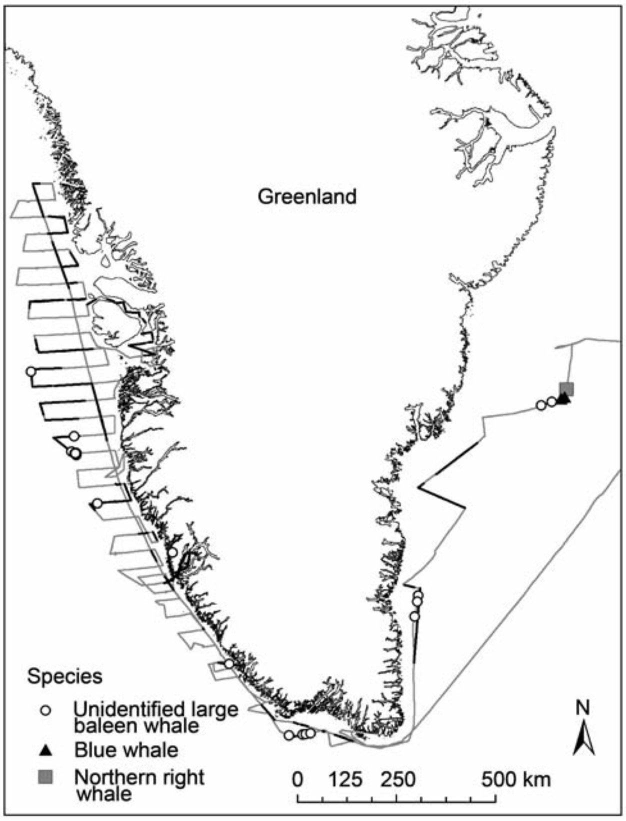


Fig. 4. Sightings of blue whales [▲], northern right whale [▨] and unidentified large baleen whales [○].

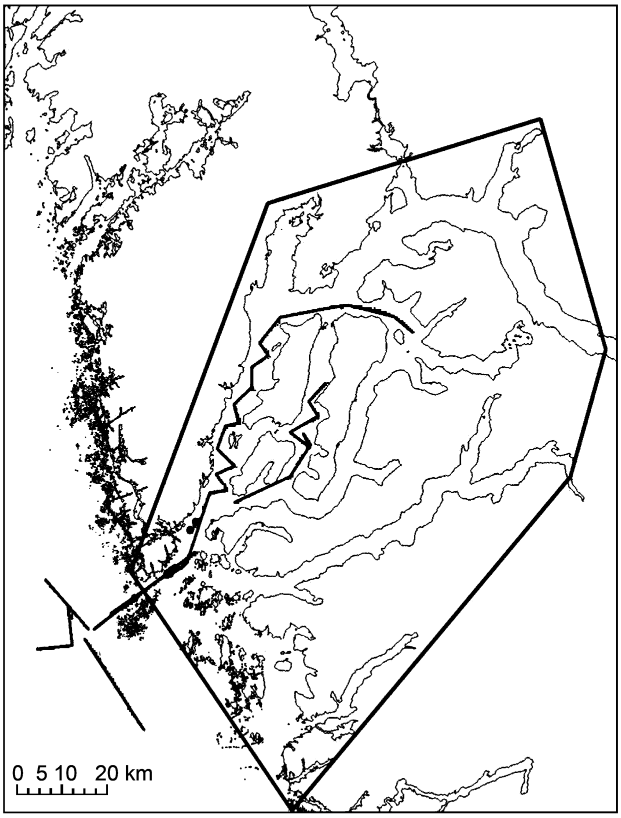


Fig. 3. Effort and sightings of humpback whales inside Nuuk Fjord. The polygon shows the stratum area used for extrapolating the density estimate.

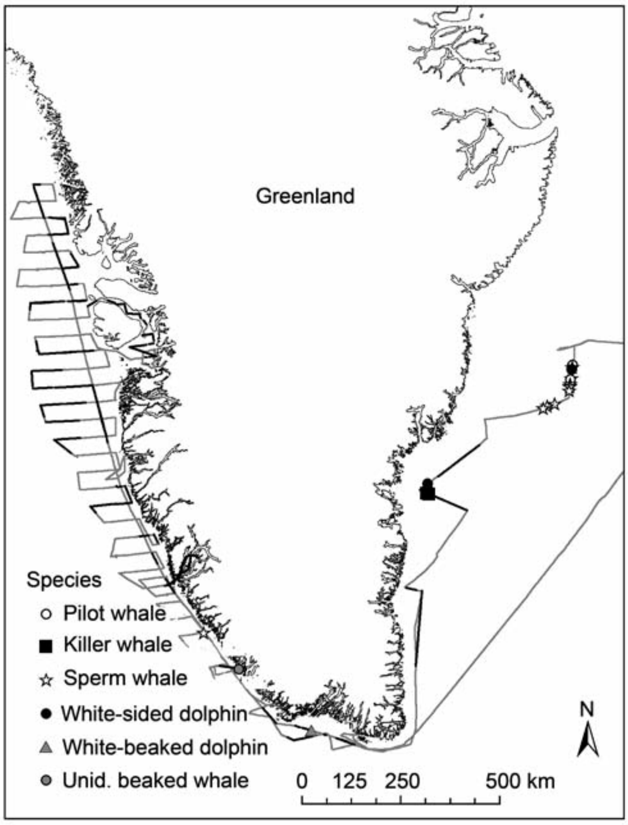


Fig. 5. Sightings of sperm whales [☆], pilot whales [○], white-sided dolphins [●], white-beaked dolphins [△], killer whales [■] and unidentified beaked whale [◉].

in East Greenland (*n*=3,214 fin whales, CV=0.48) than in South Greenland (i.e. Centralwest and Southwest, *n*=1,980 fin whales, CV=0.38).

The detection function for the 18 sei whales sightings alone (*esw*=978m) was very similar to the detection function of the combined sightings of fin whales and sei whales (*esw*=927m), except that the CV for the sei whales was twice (0.20) the CV for the combined data set (0.10). It was consequently decided to estimate the sei whale abundance utilising both fin and sei whale distance estimates for deriving a common detection function (Fig. 7 and Table 2, χ^2 goodness-of-fit statistic not significant, *p*=0.62). The largest abundance of sei whales was estimated in the southernmost part of West Greenland (*n*=1,599 sei whales, CV=0.42) and lower numbers were found in East Greenland (*n*=763 sei whales, CV=0.47).

Only 27 humpback whale sightings were available for estimating the detection function (Fig. 8) and the detection function provided an *esw* of 622m (CV=0.15, χ^2 goodness-of-fit statistic not significant, *p*=0.72). Humpback whales were seen in all strata except for North West Greenland and the largest numbers were found in South Greenland (*n*=944 humpback whales, CV=0.53) with lower numbers in East Greenland (*n*=347 humpback whales, CV=0.85, Table 2). A separate abundance estimate was developed for Nuuk Fjord based on 106 n.miles zig-zag coverage of 4.3% of the area of the fjord complex (Fig. 3) and 10 sightings of humpback whales which revealed an abundance of 145 whales (CV=0.38). However, all areas of the fjord were not evenly sampled and the abundance therefore should be used with caution (see Discussion).

Table 2A

Summary statistics for abundance estimates of fin whales and sei whales. For both species only effort during Beaufort sea states <6 was included.

	Fin whale					Sei whale				
Effective search half-width	944m					Fin and sei observations: 927m				
n	45 observations, right truncation >1,800					64 observations, right truncation >1,800				
CV	0.12					0.10				
Stratum	NW	DB	CW	SW	SE	NW	DB	CW	SW	SE
Area of stratum (km^2)	82,518	15,780	72,342	51,684	81,065	82,518	15,780	72,342	51,684	81,065
Sightings (*n*)	0	0	12	8	21	0	0	3	10	5
Effort (*L*) n.miles	449	163	475	177	252	449	163	475	177	252
Transects	18	16	20	15	5	18	16	20	15	5
Sighting rate (*n/L*)	0	0	0.03	0.05	0.08	0	0	0.01	0.06	0.02
CV			0.53	0.52	0.46			1.06	0.44	0.45
Density of pods	0	0	0.01	0.01	0.02	0	0	0.01	0.02	0.01
CV			0.54	0.53	0.48			1.06	0.45	0.46
Expected pod size	0	0	1.7	1.7	1.7	0	0	1.6	1.6	1.6
CV			0.08	0.08	0.08			0.06	0.06	0.06
Density of whales	0	0	0.01	0.02	0.04	0	0	0.01	0.03	0.01
CV			0.55	0.53	0.48			1.06	0.45	0.47
Abundance	0	0	871	1,109	3,214	0	0	217	1,382	726
CV			0.55	0.54	0.48			1.06	0.45	0.47
Total West Greenland	1,980 (CV=0.38, 95% CI=913-4,296)					1,599 (CV=0.42, 95% CI=690-3,705)				
Total East Greenland	3,214 (CV=0.48, 95% CI=980-10,547)					763 (CV=0.47, 95% CI=236-2,465)				

Table 2B

Summary statistics for abundance estimates of humpback whales and minke whales. For humpback whales only effort during Beaufort sea states <6 was included and for minke whales effort was restricted to sea states less than 3.

	Humpback whale						Minke whale				
Effective search half-width	622m						216m				
n	26, right truncation >1,600						12, right truncation >350m				
CV	0.15						0.25				
Stratum	NW	DB	CW	NF	SW	SE	NW	DB	CW	SW	SE
Area of stratum (km^2)	82,518	15,780	72,342	2,843	51,684	81,065	82,518	15,780	72,342	51,684	81,065
Sightings (*n*)	0	1	2	10	6	2	0	0	2	3	5
Effort (*L*)	449	163	475	106	177	252	217	60	149	60	274
Transects	18	16	20	31	15	5	12	8	9	7	8
Sighting rate (*n/L*)	0	0.01	0.01	0.10	0.03	0.01	0	0	0.01	0.05	0.02
CV		1.17	0.89	0.34	0.50	0.83			0.49	0.49	1.21
Density of pods	0	0.01	0.01	0.04	0.01	0.01	0	0	0.02	0.06	0.02
CV		1.18	0.89	0.37	0.52	0.84			0.55	0.55	1.24
Expected pod size	0	1.3	1.3	1.3	1.3	1.3	0	0	1	1	1
CV		0.09	0.09	0.09	0.09	0.09					
Density of whales	0	0.01	0.01	0.05	0.02	0.01	0	0	0.01	0.06	0.02
CV		1.18	0.90	0.38	0.53	0.85			0.55	0.55	1.24
Abundance	0	52	165	145	944	347	0	0	1,219	3,260	1,848
CV		1.18	0.90	0.38	0.53	0.85			0.55	0.55	1.24
Total West Greenland	1,306 (CV=0.42, 95% CI=570-2,989)						4479 (CV=0.46, 95% CI=1,760-11,394)				
Total East Greenland	347 (CV=0.85, 95% CI=48-2,515)						1848 (CV=1.24, 95% CI=197-17,348)				

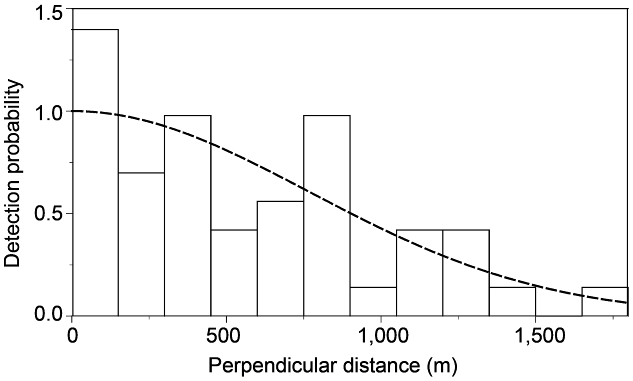


Fig. 6. Detection function for fin whales grouped in 150m intervals (n=45).

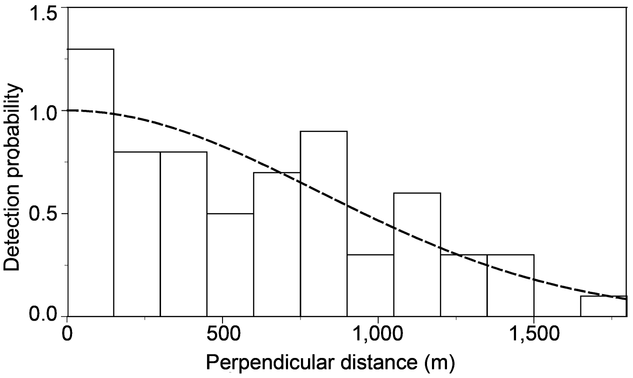


Fig. 7. Detection function for fin and sei whales combined grouped in 150m intervals (n=66).

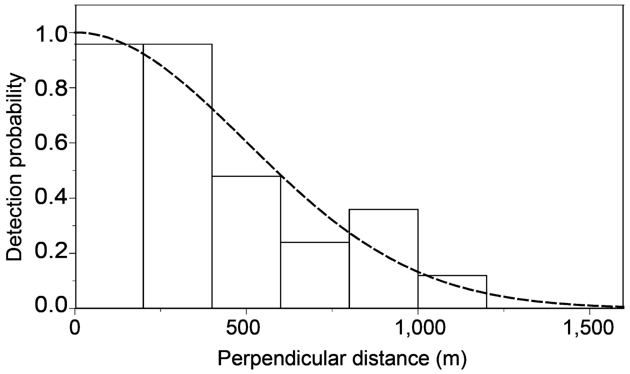


Fig. 8. Detection function for humpback whales grouped in 200m intervals (n=26).

Only 12 common minke whales were sighted, including sightings outside strata *en route* to and from Iceland. This low number does not provide sufficient data for a robust estimation of the detection function (Fig. 9). This is also reflected in the relatively large CV (0.25) for determination of the *esw* (216m, χ^2 goodness-of-fit statistic not significant, p=0.65). The low *esw* for common minke whales probably reflects the difficulty in detecting this species. Nevertheless estimates of common minke whale abundance were developed for the three areas where sightings occurred and with effort in sea states of < Beaufort 3 (Fig. 10). The largest numbers of common minke whales were in the southern part of West Greenland (4,479 common minke whales, CV=0.46) with fewer on the east coast (Table 2).

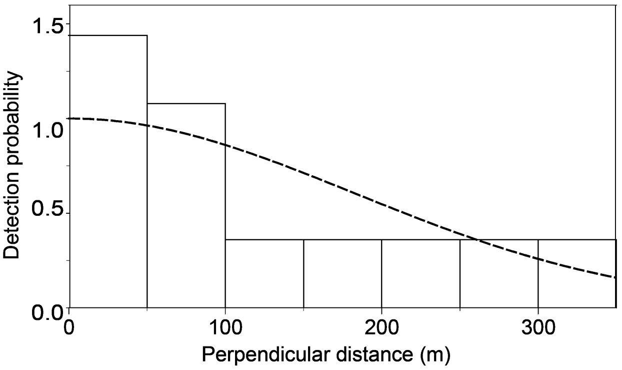


Fig. 9. Detection function for common minke whales grouped in 50m intervals (n=12).

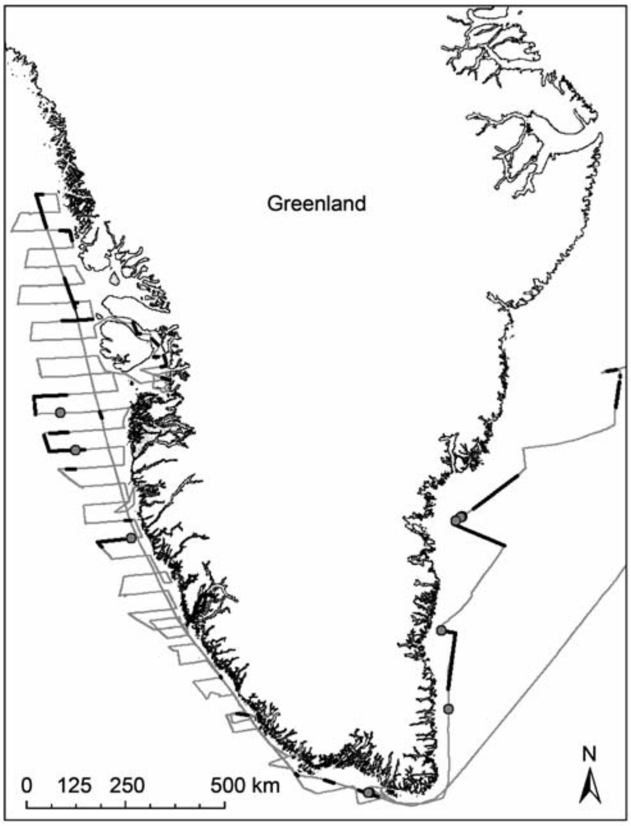


Fig. 10. Survey transect lines (thin lines), realized survey effort (thick lines) in Beaufort sea state <3 and common minke whale sightings.

A total of 35 sightings of blows of unidentified large baleen whales were recorded. In order to include these in more complete abundance estimates, the sightings were attributed to the three possible species (fin, humpback and sei whales, Table 3). The unidentified blows were apportioned to the six strata in proportion to the occurrence of each species in each stratum and the associated distance measurements were apportioned randomly to the three species. Thus, both new encounter rate estimates and new detection functions including variance estimates were derived. The inclusion of unidentified sightings resulted in a 43% increase in the abundance estimate for fin whales in West Greenland (raised to 2,824 fin whales, CV=0.38). The sei whale abundance increased by 26% with a slightly improved precision and the humpback whale abundance estimate increased in West Greenland (by 16%) with lower precision yet declined in East Greenland due to the change in *esw*.

Table 3

Summary statistics for abundance estimates of fin, sei, and humpback whales including unidentified sightings. For both species only effort during Beaufort sea states <6 was included.

	Fin whale			Sei whale			Humpback whale				
Effective search half-width	960m			Fin and sei observations: 982m			718m				
n	57 observ., right truncation >1,800			81 observ., right truncation >1,800			29, right truncation >1,600				
CV	0.11			0.09			0.14				
Stratum	CW	SW	SE	CW	SW	SE	DB	CW	NF	SW	SE
Area of stratum (km^2)	72,342	51,684	81,065	72,342	51,684	81,065	15,780	72,342	2,843	51,684	81,065
Sightings (*n*)	17	11	25	4	13	6	1	3	10	8	2
Effort (*L*) nmi	475	177	252	475	177	252	163	475	106	177	252
Transects	20	15	5	20	15	5	16	20	31	15	5
Sighting rate (*n/L*)	0.01	0.06	0.10	0.01	0.07	0.02	0.01	0.01	0.10	0.05	0.01
CV	0.52	0.50	0.48	0.87	0.39	0.39	1.17	0.89	0.34	0.62	0.83
Density of pods	0.10	0.02	0.03	0.01	0.02	0.01	0.01	0.01	0.03	0.02	0.01
CV	0.52	0.51	0.50	0.88	0.40	0.41	1.18	0.90	0.37	0.64	0.84
Expected pod size	1.7	1.7	1.7	1.6	1.6	1.6	1.3	1.3	1.3	1.3	1.3
CV	0.07	0.07	0.07	0.06	0.06	0.06	0.09	0.09	0.09	0.09	0.09
Density of whales	0.02	0.03	0.05	0.01	0.03	0.01	0.01	0.01	0.05	0.02	0.01
CV	0.52	0.51	0.50	0.88	0.41	0.41	1.18	0.90	0.38	0.64	0.85
Abundance	1,263	1,562	3,917	279 0.88	1,731	882	46	219	129	1,119	309
CV	0.52	0.51	0.50		0.41	0.41	1.18	0.90	0.38	0.64	0.85
Total West Greenland	2,824 (CV=0.38, 95% CI=1,346-5,925)			2,009 (CV=0.37, 95% CI=948-4,260)			1,514 (CV=0.51, 95% CI=560-4,089)				
Total East Greenland	3,917 (CV=0.50, 95% CI=1,122-13,672)			882 (CV=0.41, 95% CI=313-2,484)			309 (CV=0.85, 95% CI=43-2,240)				

DISCUSSION

Biases and problems with survey design

The sampling design used in this survey was not optimal for a cetacean survey and the realised survey effort was restricted by inclement weather conditions. It can specifically be argued that the South West strata in West Greenland had particularly uneven and poor coverage and that transect lines running parallel to the coast might follow density gradients of whales. One option is to eliminate the part of South West strata with poor coverage from the abundance estimates which reduces the abundance to about 2/3 for both estimates based on identified blows and those where unidentified blows were apportioned to species and strata (Table 4). This, however, leaves a large uncovered area in West Greenland where there are high densities of whales.

One option for eliminating the potential problem of transects running parallel to the coast is to include only east-west transects in the abundance estimates. However, this does not have a major impact on the abundance estimates, as a recalculation with only east-west transects only slightly changed the abundance estimates (Table 4). This is probably due to the fact that the bathymetry in West Greenland does not follow simple east-west gradients but is characterised by deep trenches with intersecting banks (Fig. 1). In addition, the distribution of whales is not a simple function of bathymetry in this region but rather is determined by complex oceanographic features, including areas of upwelling that potentially can be found in many areas across several strata.

The estimate of 145 humpback whales in the Nuuk Fjord alone initially seems high. Clearly the ship-based survey did not provide random or uniform coverage of the entire fjord

Table 4

Summary statistics for abundance estimates for fin, sei, humpback and minke whales under alternative assumptions for West Greenland. Approximately half of the South West Greenland stratum was removed when the area with poor coverage was removed from that stratum. CVs indicated in parenthesis.

Estimation options			Species			
Sightings	Transects	Coverage	Fin whale	Sei whale	Humpback whale	Minke whale
Identified blows	East-west going	Areas with poor coverage in SW Greenland and Nuuk Fjord eliminated	na	na	509 (0.49)	na
Identified blows	East-west going	Area with poor coverage in SW Greenland eliminated	1,317 (0.54)	1,031 (0.53)	663 (0.37)	4,068 (0.40)
Identified blows	East-west going	Continuous	1,777 (0.48)	1,604 (0.45)	1,141 (0.45)	5,307 (0.43)
Identified blows	All	Area with poor coverage in SW Greenland eliminated	1,520 (0.41)	1,026 (0.45)	829 (0.36)	3,239 (0.41)
Identified blows	All	Continuous	1,980 (0.38)	1,599 (0.42)	1,306 (0.42)	4,479 (0.46)
Unidentified blows apportioned to species and strata	All	Area with poor coverage in SW Greenland eliminated	2,115 (0.40)	1,291 (0.40)	926 (0.34)	na
Unidentified blows apportioned to species and strata	All	Continuous	2,824 (0.38)	2,009 (0.37)	1,514 (0.51)	na
Correction for perception bias *g*(0)=0.56, SE=0.07	All	Continuous	na	na	na	7,998 0.47

na = not applicable.

complex. Only about one fifth of the fjord was sampled and the density was extrapolated to other unsurveyed parts of the fjord under the unproven assumption of uniform density. If the estimated density is only applied to the sampled area then a conservative estimate of 29 whales, three times the number of sightings, is obtained. This however leaves 80% of the area without an abundance estimate. Satellite tracking studies and local observations demonstrate that humpback whales use the entire Nuuk Fjord as delineated by the stratum (Heide-Jørgensen and Laidre, 2007), (Fig. 3, GINR unpublished data), and therefore it is not unreasonable to extrapolate samples collected in the northern part of the mouth and in two fjord arms to the entire area shown in Fig. 3. In any case, the estimate from the Nuuk Fjord only contributes ~10% of the total abundance estimate for humpback whales in West Greenland.

Many sightings of large baleen whales could not be assigned to a species. If these 35 undetermined sightings were included in the abundance estimates in proportion to the correctly identified sightings of the four target species, then the abundance estimates increase as much as 43% for fin whales (resulting in a revised estimate of 2,824 fin whales, 95% CI=1,346-5,925). Similarly the abundance estimates for sei and humpback whales increase by 26% and 16%, respectively (Table 4).

All the abundance estimates presented in this manuscript are likely negatively biased for at least two reasons. First, no corrections have been made for whales submerged during the passage of the survey vessel or whales missed by the observers. This may be less of a problem for fin and sei whales, which can be seen at long distances from the vessel, but is certainly of concern for common minke whales, which are smaller and less conspicuous. Common minke whales in West Greenland are hunted intensively and considering the skittish behaviour of common minke whales in West Greenland, attraction to ships seems unlikely. The issue of ship avoidance (Palka and Hammond, 2001) was not addressed in this study. Secondly, the survey did not cover the entire stock area used by any of the whales in either East or West Greenland. The survey covered the banks of both areas, but whales were sighted at the borderlines of several strata indicating a connection to a larger unsurveyed area.

Abundance of fin whales

No fin whales were sighted in the northern survey strata (North West and in Disko Bay) despite good conditions and considerable effort. Fin whales have frequently been observed in these areas (Heide-Jørgensen *et al.*, 2003; Kapel, 1979;1984;1985; Kapel and Larsen, 1982;1983; Larsen, 1981) and the lack of sightings might be due to the late seasonal coverage. Fin whales were however estimated to occur in large numbers in Central West (1,263) and South West Greenland (1,562) as well as in East Greenland (3,917). The survey in East Greenland only covered parts of the distribution of fin whales between the coast and Iceland, where an estimated abundance of 24,000 fin whales was obtained in 2001 (Víkingsson *et al.*, In Press). The abundance of fin whales in West Greenland (1,980 95% CI=913-4,296) estimated by using only identified blows was larger, although not significantly higher, than the estimate from the aerial surveys in 1987 and 1988 (IWC, 1992) and lower than the estimate from the 2005 autumn aerial survey accepted by the IWC Scientific Committee (Heide-Jørgensen *et al.*, 2007; IWC, In press) of 3,200 (95% CI 1,400-7,200).

Abundance of sei whales

The high number of sightings and high abundance of sei whales in West Greenland was somewhat surprising. Sei whales are traditionally believed to occupy more southern areas of the North Atlantic (Cattanach *et al.*, 1993) and have not been found often in West Greenland. Kapel (1985) summarised observations and catches of sei whales in West Greenland waters in the 18th, 19th and 20th Centuries. The first confirmed sighting of a sei whale in Greenland was from Norwegian catches in 1924. During 1924-57, 18 sei whales were confirmed caught and a similar number of catches are unconfirmed, of which only four seem to be plausible sei whales. Kapel (1985) report that the erratic occurrence of sei whales in West Greenland waters may be related to the sea surface temperature, especially the influx of warm Irminger water to the southern part of Davis Strait. In 2005 the warmest sea surface temperatures were observed in West Greenland since 1876 (GINR unpublished data), and these warm temperatures may be related to the large abundance of sei whales in the area.

Abundance of humpback whales

An estimated abundance of 1,306 humpback whales (CV=0.42, 95% CI=570-2,989) from identified blows in West Greenland and 347 humpback whales in East Greenland (CV=0.85, 95% CI=48-2,515) is approximately three times larger than any previous estimates of this species in Greenland waters. Photo-ID surveys of humpback whales conducted off West Greenland during the 1990s resulted in an estimate of 360 humpback whales (CV=0.07) in West Greenland in summer (Larsen and Hammond, 2004). At that time three concentration areas were identified: an area off Nuuk, an area at approximately 63°30’N, and an area off Paamiut. This survey did not intensely cover any of these three areas, yet still resulted in a significantly larger abundance estimate than in the past, suggesting the present estimates may even be low. This survey covered a wider range of the humpback whale distribution in West Greenland than any previous surveys and thus has a more complete, although less intense, coverage of the humpback whale distribution in West Greenland. The long-distance movements and broad use of the West Greenland coast has recently been revealed by satellite tracking studies (Heide-Jørgensen and Laidre, 2007), suggesting humpback whales use a large area of West Greenland and have a broad distribution. Part of the difference in present and past abundances of humpback whales may be explained by a growth in the abundance of humpback whales in West Greenland, which is not unreasonable to assume given observations in other areas of the North Atlantic. Sigurjónsson and Gunnlaugsson (1990) observed an increase in humpback whale numbers around Iceland of 11.2% per annum between 1970 and 1988. Pike *et al.* (2005) observed an even higher growth rate for humpback whales around Iceland from the North Atlantic Sighting Surveys (NASS). Based on an assumed growth of 10% per year since 1990 and a presumed abundance of 500 humpback whales in West Greenland in 1990, a present-day (2005) abundance should be on the order of approximately 2,000 whales. This is within the confidence limits of the present abundance estimates.

Abundance of common minke whales

The relatively low number of sightings of common minke whales severely reduced the precision of the abundance estimates in this study. Estimation of a detection function was only possible through inclusion of sightings *en route* to and from Iceland. The variance on the common minke whale abundance estimates was very high, but it is important to note that correction for whales that were submerged during the passage of the survey platform and whales missed by the observers would raise the lower confidence limit of the estimate substantially.

One option for improving the accuracy of the common minke whale estimate is to use a correction factor for whales missed by the observer ($g(0)$) developed in a different survey. Øien (1990) used a double platform design to estimate $g(0)$ in an area west of Svalbard, where common minke whales occur in high densities. A large proportion of the common minke whale sightings were missed by the primary platform ($g(0)$=0.56, SE=0.07) and applying this correction factor gives a partially corrected abundance estimate for West Greenland of 7,998 common minke whale (CV=0.47, 95% CI=3,048-20,988). The $g(0)$ estimate was developed on a different survey platform with different observers and in an area with high densities of common minke whales where whale spotters presumably are more efficient (Øien, 1990). In addition, the correction does not include whales that were diving during the passage of the survey platform. In any case we believe that the corrected estimate probably provides an abundance estimate that is closer to the actual abundance of common minke whales in West Greenland in late autumn 2005. These estimates are not sufficiently different from the estimate accepted by the IWC Scientific Committee from an autumn 2005 aerial survey (Heide-Jørgensen *et al.*, 2007; IWC, In press) of 10,800 (95% CI 3,600-32,400).

Few sightings of common minke whales were made on the offshore banks of West Greenland, an area where they used to be frequently encountered (Kapel and Larsen, 1982). There has been no hunting of common minke whales in this offshore area since the ban on commercial whaling in 1985 and the lack of whales in this region cannot be attributed to harvest. It is well known that common minke whales travel extensively, and recent satellite tracking studies off Iceland show that this species can move 1,000km in just two months, reaching the Cape Verdes Isles from Icelandic waters in just 60 days. It is highly possible that common minke whales inhabiting Greenlandic waters are a temporary population that move in and out of important areas, as observed in Iceland (Heide-Jørgensen *et al.*, 2001; Víkingsson and Heide-Jørgensen, 2005). This makes it difficult to relate the present abundance estimate to any actual stock size.

Other species

Species diversity in cetacean sightings was much higher in East Greenland but abundance estimates could not be derived for all species. One northern right whale was sighted east of Greenland in an area slightly north and east of the whaling ground known by the whalers as the ‘Cape Farewell whaling ground’ used by American whalers during 1868-98 for finding right whales (Reeves and Mitchell, 1986). This is also the area where right whales have been sighted in recent years (Reeves *et al.*, 2004). Few odontocete whales were seen in West Greenland, these fish eaters seem to be sighted more typically in East Greenland in contrast to the many baleen whales sighted feeding on zooplankton in West Greenland.

CONCLUSIONS

The ship-based survey presented here provides a somewhat sporadic effort along East and especially South West Greenland. In some cases the patchy effort also leads to questionable extrapolations of densities to unsurveyed areas. The survey however provides insight into what can be accomplished by a ship-based cetacean survey effort in Greenland.

The abundance estimates for large cetaceans obtained during this survey are in some cases larger than expected and confirm that the waters of Greenland support large numbers of baleen whales during this season. The extensive ship survey coverage, coupled with the verification of high numbers of sightings and large group sizes by a concurrent aerial survey (Heide-Jørgensen *et al.*, 2007), suggest abundances are considerably larger than previously reported.

This survey was conducted late in the season. No whales were seen in the northernmost strata along West Greenland and only humpback whales were sighted in Disko Bay. Presumably most large whales were on their southbound exodus from Greenland by September (Heide-Jørgensen *et al.*, 2001; Víkingsson and Heide-Jørgensen, 2005) and this may have resulted in a reduced abundance relative to that which would have been estimated earlier in the summer.

ACKNOWLEDGEMENTS

We wish to thank Nina Eriksen, Anna-Sofie Stensgaard and Marianne H. Rasmussen for their enthusiastic participation in the survey. The skipper and the crew on r/v *Bjarni Saemundsson* is gratefully acknowledged for their navigation of the Greenlandic waters. We thank Gisli Vikingsson and Thorvaldur Gunnlaugsson, Marine Research Institute, Iceland, for providing materials for cetacean observations, such as binoculars, distance sticks and angle boards. Lars Witting and Fernando Ugarte kindly provided comments on this paper. This study was funded by the Greenland Institute of Natural Resources.

REFERENCES

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. vi+xv+432pp.

Buckland, S.T., Cattanach, K.L. and Gunnlaugsson, T. 1992. Fin whale abundance in the North Atlantic, estimated from Icelandic and Faroese NASS-87 and NASS-89 data. *Rep. int. Whal. Commn* 42: 645-51.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. and Pollock, K.H. 1987. *Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture*. No. 5 vols, *American Fisheries Society Monographs*. American Fisheries Society, Bethesda, Maryland. x+437pp.

Cattanach, K.L., Sigurjónsson, J., Buckland, S.T. and Gunnlaugsson, T. 1993. Sei whale abundance in the North Atlantic, estimated from NASS-87 and NASS-89 data. *Rep. int. Whal. Commn* 43: 315-21.

Heide-Jørgensen, M.P., Borchers, D., Witting, L., Simon, M., Laidre, K., Rosing-Asvid, A. and Pike, D.G. 2007. Final estimates of large whale abundance in West Greenland waters from an aerial survey in 2005. *J. Cetacean Res. Manage* Submitted.

Heide-Jørgensen, M.P. and Laidre, K. 2007. Autumn space-use-patterns of humpback whale (*Megaptera novaeangliae*) in West Greenland. *J. Cetacean Res. Manage.* Submitted.

Heide-Jørgensen, M.P., Nordoy, E.S., Øien, N., Folkow, L.P., Kleivane, L., Blix, A.S., Jensen, M.V. and Laidre, K.L. 2001. Satellite tracking of minke whales (*Balaenoptera acutorostrata*) off the coast of northern Norway. *J. Cetacean Res. Manage.* 3(2): 175-78.

Heide-Jørgensen, M.P., Witting, L. and Jensen, M.V. 2003. Inshore-offshore movements of two fin whales *Balaenoptera physalus* tracked by satellite off West Greenland. *J. Cetacean Res. Manage.* 5(3): 214-45.

Hiby, A.R. and Hammond, P.S. 1989. Survey techniques for estimating abundance of cetaceans. *Rep. int. Whal. Commn (special issue)* 11: 47-80.

International Whaling Commission. 1990. Report of the Scientific Committee. *Rep. int. Whal. Commn* 40:39-79.

International Whaling Commission. 1992. Report of the Comprehensive Assessment Special Meeting on North Atlantic Fin Whales, Reykjavík, 25 February-1 March 1991. *Rep. int. Whal. Commn* 42:595-644.

International Whaling Commission. 2005. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 7:1-62.

International Whaling Commission. 2006. Report of the Scientific Committee. Annex E. Report of the Standing Working Group (SWG) on the Development of an Aboriginal Whaling Management Procedure (AWMP). *J. Cetacean Res. Manage. (Suppl.)* 8:91-109.

International Whaling Commission. In press. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 10.

Kapel, F.O. 1979. Exploitation of large whales in West Greenland in the twentieth century. *Rep. int. Whal. Commn* 29: 197-214.

Kapel, F.O. 1984. Whale observations off West Greenland in June-September 1982. *Rep. int. Whal. Commn* 34: 621-27.

Kapel, F.O. 1985. On the occurrence of sei whales (*Balaenoptera borealis*) in West Greenland waters. *Rep. int. Whal. Commn* 35: 349-52.

Kapel, F.O. and Larsen, F. 1982. Whale sightings from a Norwegian small-type whaling vessel off West Greenland, June-August 1980. *Rep. int. Whal. Commn* 32: 521-30.

Kapel, F.O. and Larsen, F. 1983. Whale sightings off West Greenland in June-September 1981. *Rep. int. Whal. Commn* 33: 657-66.

Kingsley, M.C.S. and Witting, L. 2001. A preliminary analysis of aerial survey observations of humpback whales in Greenland waters. Paper SC/53/NAH23 presented to the IWC Scientific Committee, July 2001, London (unpublished). 51pp. [Paper available from the Office of this Journal].

Larsen, F. 1981. Observations of large whales off West Greenland, 1979. *Rep. int. Whal. Commn* 31: 617-23.

Larsen, F. 1995. Abundance of minke and fin whales off West Greenland, 1993. *Rep. int. Whal. Commn* 45: 365-70.

Larsen, F. and Hammond, P.S. 2004. Distribution and abundance of West Greenland humpback whales *Megaptera novaeangliae*. *J. Zool., London.* 263: 343-58.

Larsen, F., Martin, A.R. and Nielsen, P.B. 1989. North Atlantic Sightings Survey 1987: report of the West Greenland aerial survey. *Rep. int. Whal. Commn* 39: 443-46.

Øien, N. 1990. Estimates of *g*(0) for minke whales based on an independent observer experiment during the Norwegian sightings surveys in July 1988. *Rep. int. Whal. Commn* 40: 331-35.

Palka, D.L. and Hammond, P.S. 2001. Accounting for responsive movement in line transect estimates of abundance. *Can. J. Fish. Aquat. Sci.* 58: 777-87.

Pike, D.G., Paxton, C.G.M., Gunnlaugsson, T. and Víkingsson, G.A. 2005. Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters 1986-2001. *NAMMCO Sci. Pub.* 6. [Paper NAMMCO SC/12/11].

Reeves, R.R., Josephson, E. and Smith, T.D. 2004. Putative historical occurrence of North Atlantic right whales in mid-latitude offshore waters: ‘Maury’s Smear’ is likely apocryphal. *Marine Ecology. Progress Series* 282: 295-305.

Reeves, R.R. and Mitchell, E. 1986. American pelagic whaling for right whales in the North Atlantic. *Rep. int. Whal. Commn (special issue)* 10: 221-54.

Sigurjónsson, J. and Gunnlaugsson, T. 1990. Recent trends in abundance of blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) off west and southwest Iceland, with a note on occurrence of other cetacean species. *Rep. int. Whal. Commn* 40: 537-51.

Thomas, L., Strindberg, S., Marques, F.F.C., Borchers, D.L., Buckland, S.T., Anderson, D.R., Burnham, K.P., Hedley, S.L. and Pollard, J.H. 2001. Distance 4.0. Beta 4. Research Unit for Wildlife Population Assessment, University of St Andrews, UK. [Available at: *http://www.ruwpa.st-and.ac.uk/distance/*].

Víkingsson, G.A. and Heide-Jørgensen, M.P. 2005. A note on the movements of minke whales tracked by satellite in Icelandic waters in 2001-2004. Paper SC/57/O9 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea (unpublished). 3pp. [Paper available from the Office of this Journal].

Víkingsson, G.A., Pike, D.G., Desportes, G., Øien, N. and Gunnlaugson, T. In Press. Distribution and abundance of fin whales (*Balaenoptera physalus*) in the Northeast and Central Atlantic as inferred from the North Atlantic Sightings Surveys 1987-2001. *NAMMCO Sci. Publ.* 7.

Witting, L. and Kingsley, M. 2005. Abundance of marine mammals off West Greenland, 2002-2004. Paper SC/57/AWMP3 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea (unpublished). 13pp. [Paper available from the Office of this Journal].

Date received: January 2006
Date accepted: April 2007

Large whale aerial survey

Chapter 6

Paper V:
Heide-Jørgensen MP, Borchers DL, Witting L, Laidre KL, Simon MJ,
Rosing-Asvid A & Pike DG. 2008

Estimates of large whale abundance in West Greenland waters from an aerial survey in 2005.
J Cetacean Res Manage 10(2): 119-129-

Estimates of large whale abundance in West Greenland waters from an aerial survey in 2005

M.P. HEIDE-JØRGENSEN*, D.L. BORCHERS+, L. WITTING*, K.L. LAIDRE*, M.J. SIMON*, A. ROSING-ASVID* AND D.G. PIKE#

Contact e-mail: mhj@ghsdk.dk

ABSTRACT

An aerial line transect and cue counting survey of large whales in West Greenland was conducted in August and September 2005. The survey covered the area between Cape Farewell and Disko Island on the West Greenland coast out to the 200m depth contour. The surveyed area covered 163,574km^2 and a total of 246 sightings of 9 cetacean species were obtained. Abundance estimates were developed for humpback whales, *Megaptera novaeangliae* (21 sightings), fin whales, *Balaenoptera physalus* (78 sightings) and common minke whales, *B. acutorostrata* (42 sightings). The mean group size of humpback whales was 3.30 but groups as large as 95 animals were seen off effort. The mean group size of fin whales was 2.96 with groups as large as 50 seen. Common minke whale group size was 1.1 with only one sighting of a group of two whales. Humpback whales were found both in offshore and coastal areas of West Greenland with the exception of Store Hellefiske Bank and the Cape Farewell offshore area. The line transect abundance estimate of humpback whales was 1,218 (CV=0.56), uncorrected for submerged whales (availability bias) and whales that were available to be seen but were missed by the observers (perception bias). Fin whales were observed in all areas of the survey and the uncorrected line transect estimate was 1,660 (CV=0.38). When corrected for perception bias the estimates increases to 3,234 fin whales (CV=0.44). Common minke whales were found in almost equal densities in all strata except for the Cape Farewell offshore area, where none were seen. The cue-counting abundance estimate of common minke whales was 4,856 (CV=0.49) for West Greenland using a cue rate of 46.3 cues per hour (CV=0.11). If the estimate is corrected for perception bias the common minke whale abundance is estimated to be 10,792 whales (CV=0.59). Low coverage was attained in the northern area of West Greenland and this should cause an especially large negative bias for the estimates of fin whale and humpback whale abundance because this area is believed to have particularly large densities of these whales.

KEYWORDS: FIN WHALE; COMMON MINKE WHALE; HUMPBACK WHALE; SURVEY-AERIAL; SURVEY-VESSEL; NORTHERN HEMISPHERE; ABUNDANCE ESTIMATE; CUE COUNTING; DISTRIBUTION; *g*(0); SCHOOL SIZE

INTRODUCTION

Most estimates of abundance of large baleen whales, including common minke whales, *Balaenoptera acutorostrata*, fin whales, *B. physalus*, and humpback whales, *Megaptera novaeangliae*, in West Greenland waters are more than 10 years old. A series of aerial surveys of large baleen whales in West Greenland were conducted between 1983 and 1993 and abundance estimates were developed from cue counting techniques *(cf.* Hiby, 1985) in 1987/88 and in 1993 (Hiby *et al*., 1989; Larsen, 1995; Larsen *et al*., 1989). From these surveys, all conducted in July and August, fin whale abundance was estimated at 1,100 (95% confidence interval (CI) 520-2,100) in West Greenland in 1987/88 (IWC, 1992) and abundance of common minke whales was estimated at 3,266 in 1987/88 (95% CI 1,700-5,710 (IWC, 1990) and at 8,371 (95% CI 2,414-16,929) common minke whales in 1993 (Larsen, 1995).

Abundance of humpback whales in West Greenland was estimated from photo-ID surveys in July and August 1988-93, with a combined estimate over the five years of surveys of 360 humpback whales (95% CI 314-413) (Larsen and Hammond, 2004). A line transect analysis of the aerial survey in July and August 1993 resulted in an uncorrected estimate of 599 (95% CI 237-1,512) (Kingsley and Witting, 2001) and an aerial photographic survey in July through October 2002 and August through October 2004 provided an estimate of 400 humpback whales (CV=0.64) corrected for submergence about three quarter of the time.

In September 2005 a ship-based line transect survey was conducted in East and West Greenland covering the shelf areas out to the 200m depth contour (Heide-Jørgensen *et al*., 2007). Fin whales were most abundant in East Greenland with an estimate of 3,214 (95% CI 980-10,547) and a lower abundance of 1,980 (95% CI 913-4,296) was estimated for West Greenland. Humpback whales were found in both offshore and coastal areas of West Greenland and abundance was estimated at 1,306 (95% CI 570-2,989). They occurred in low numbers in East Greenland with abundance estimated at 347 (95% CI 48-2,515). Finally, common minke whale abundance was estimated at 1,848 (95% CI 197-17,348) for East Greenland and 4,479 (95% CI 1,760-11,394) for West Greenland. These abundance estimates are negatively biased due to incomplete survey coverage and lack of correction factors for availability and perception bias.

The lack of up-to-date information on the abundance of large cetaceans in West Greenland has made it difficult for the Scientific Committee of the International Whaling Committee (IWC) to provide advice on sustainable takes from especially common minke whales and fin whales in West Greenland (IWC, 2006). Given that the average annual removals during 1999-2004 of common minke whales and fin whales were 172 and 9, respectively, it seems prudent to update abundance estimates for these two species.

An aerial survey of large cetaceans was conducted in West Greenland in August-September 2005 and is reported on here. Abundance estimates were developed for fin whales, humpback whales and common minke whales and

---

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

+ *RUWPA, The Observatory, Buchanan Gardens, University of St Andrews, Fife, KY16 9LZ, Scotland.*

North Atlantic Marine Mammal Commission, Polar Environmental Centre, N-9296 Tromsø, Norway.

are presented here, with comparisons to the abundance estimates obtained during a ship based survey conducted simultaneously in 2005.

METHODS

Survey methods and design

The survey was conducted between 28 August and 23 September 2005. The survey platform was an Icelandic *Partenavia Observer P-68*, in which two observers were located in the rear seats each with bubble windows. An additional observer/flight leader was seated in the right front seat. Sightings and a log of the cruise track (recorded from the aircrafts GPS) were recorded on laptop computers. Declination angle to sightings was measured with Suunto inclinometers and lateral angle from the nose of the aircraft was estimated. No correction for the drift of the plane was applied. Sightings with time stamps were entered on dictaphones and on a computer-based voice recording system that also logged the positions of the plane. Target altitude and speed was 750 feet (229m) and 90kts (167km hr^{-1}), respectively. The survey was conducted in passing mode and large group sizes were only occasionally examined in closing mode. However, the initial group size was consistently used for the abundance estimations.

Cues were defined as the dorsal ridge breaking the surface for common minke whales and as a blow for fin and humpback whales. All cues were reported unless the group size was so large that reporting was impossible. Declination and lateral angles, as well as time for each cue, were recorded together with information on number of whales in the group and the visual cue of the sighting.

Survey conditions were recorded at the start of the transect lines and whenever a change in Beaufort sea state, horizontal visibility and glare occurred. The survey was designed to systematically cover the area between the coast of West Greenland and offshore (up to 100km) to the shelf break (i.e. the 200m depth contour). Transect lines were placed in an east-west direction except for south Greenland where they were placed in a north-south direction. The surveyed area was divided into six strata (Fig. 1) and southern strata were planned to be covered first.

Analytical methods

Humpback whales

Animal abundance was estimated by

$$\hat{N} = \frac{n}{2L}\hat{f}(0)\hat{E}[s]A$$

where n was the number of groups detected, L was the transect line length, $\hat{f}(0)$ was the intercept of the estimated probability density function of distances to detected groups, $\hat{E}[s]$ was estimated mean group size, and A was stratum area (see Buckland *et al*., 2001, for further details of estimation methods). Only effort and detections in sea states 4 and below were used in the analyses.

A regression of log group size against estimated detection probability was used to estimate mean group size and because of the small sample size, a single mean group size was estimated over all strata.

In addition alternative abundance estimates were calculated where small groups (<11 whales) were estimated using the above described line transect analysis and large groups (>10 whales) were estimated using a fixed strip width.

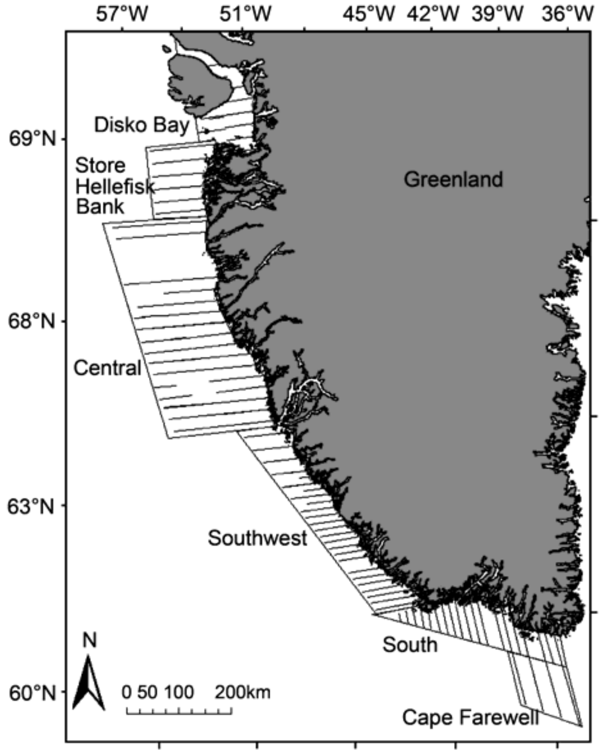


Fig. 1. Survey transect lines and delineation of strata for the aerial survey of large cetaceans in West Greenland in September 2005. The area of the strata was calculated as 12,312 km^2 for the Disko Bay strata, 15,669 km^2 for the Store Hellefiske Bank strata, 74,798km^2 for the central West Greenland strata, 29781 for the southwest Greenland strata, 11,523 km^2 for the Cape Farewell strata and 19,491km^2 for the South Greenland strata.

Fin whales

Fin whale abundance was also estimated using line transect methods. Only effort and detections in sea states 4 and below were used in the analyses. To reduce the influence of errors in the distance measurements the estimations were based on grouped distance data, using a regression of log school size on estimated detection probability to estimate mean group size. Because of small sample size, a single mean group size was estimated over all strata. Duplicates between right front and right rear observers of sightings were determined based on coincidence in timing, lateral angle and perpendicular distance.

Common minke whales

Standard cue-counting methods (assuming probability of detection at zero radial distance is 1) were used to estimate the abundance of common minke whales, as follows:

$$\hat{N} = \frac{n}{\varphi T\hat{\eta}}\hat{h}(0)\hat{E}[s]A$$

Here A is the survey area; n is the number of detected cues; T is the total time spent searching; $\varphi/(2\pi)$ is the fraction of a full circle searched (taken to be 0.5 here since the region ahead of abeam on both sides of the aircraft was searched); $\hat{h}(0)$ is the estimated slope of the probability density function of radial distances to detections, evaluated at distance zero; $\hat{\eta}$ is the estimated cue rate of animals (see Buckland *et al*., 2001, pp. 191-193 for further details). Only effort and detections in sea states 3 and below were used in the analysis.

Substantial random errors in measuring distance can lead to substantial positive bias (see Borchers *et al*., 2003), thus the data were examined for evidence of measurement error, and methods which take account of measurement errors were considered.

Although the sample size is small (only 4 duplicates from 32 sightings), the probability of detecting a cue at the closest distance was estimated and abundance was estimated using a 'point independence' method (Borchers *et al*., 2006) that does not assume certain detection at distance zero.

RESULTS

The survey covered the coast of West Greenland between northern Disko Island (70°45'N) south to Cape Farewell (60°N). Six strata were covered: Disko Bay, Store Hellefiske Bank, Central West Greenland, South West Greenland, South Greenland and an offshore Cape Farewell stratum (Fig. 1). All survey effort in Disko Bay and on Store Hellefiske Bank was completed before 12 September. After this, between 11 and 20 September, the survey was primarily concentrated in the southwest and south Greenland and after this effort was concentrated in the two strata in south Greenland. A total of 246 sightings were made during the survey. Species could not be determined for 54 sightings, but most of these were of unidentified dolphins (Table 1).

Distribution of sightings

Large baleen whale sightings were made in all strata (Figs 2a-d). Sightings of fin whales were heavily concentrated in the Central West Greenland strata in an offshore area at approximately 66°N 56°W, although additional sightings were made all along the West Greenland coast generally around the 200m depth contour (Fig. 2a). Sightings of humpback whales were also found at a high concentration off Central West Greenland, yet sightings of humpback whales in both the South West and South strata were made closer to the coast at depths of <100m (Fig. 2b). Common minke whale sightings were distributed along the entire coast and no apparent concentration areas were detected (Fig. 2c). Minke sightings were generally made at <200m depths. Sei whales were also mainly found in the same area where fin and humpback whales were found in large concentrations, although a few sei whales were seen outside of the high density region in Central West Greenland (Fig. 2d).

Large to medium sized toothed whales were also detected (Fig. 2d). Pilot whales (*Globicephala* spp.) were seen in all strata and sightings were generally far offshore beyond 400-600m depths. Two sightings of sperm whales occurred south of Cape Farewell in offshore waters. Several sightings of smaller toothed whales, particularly white-beaked dolphins (*Lagenorhynchus albirostris*) and Atlantic white-sided dolphins (*L. acutus*), were made. All sightings of these dolphins were concentrated in the South West and South strata and none were seen north of Nuuk (64°N). The many sightings of unidentified delphinoids (n=44) were in the same areas where the sightings of white-beaked dolphin and white-sided dolphins were made. Two unidentified small dolphins were seen in Disko Bay and these sightings were

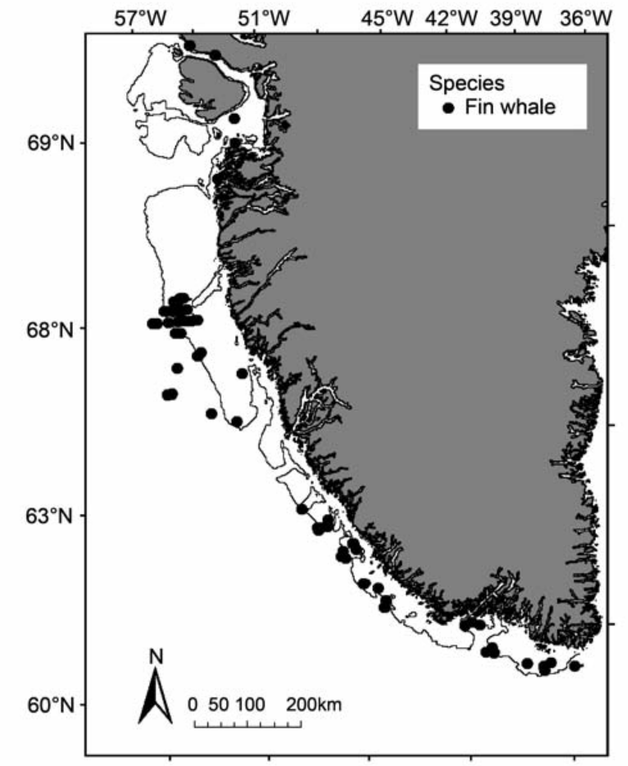


Fig. 2a. Sightings of fin whales during the aerial survey off West Greenland September 2005.

Table 1

The total numbers of observations of each of the different species of marine mammals observed during the survey. Observations are included from sea states and areas that are not included in the abundance estimations. Coefficients of variation are in brackets.

Species	Number of sightings	Number of individuals	Mean group size	Maximum group size	Minimum group size
Fin whale	78	231	2.96 (0.23)	50	1
Sei whale	4	13	3.30 (0.69)	10	1
Humpback whale	21	350	16.70 (0.35)	95	1
Sperm whale	2	2	1.00 (0)	1	1
Unidentified large whale	12	15	1.25 (0.14)	3	1
Minke whale	42	43	1.10 (0.02)	2	1
Pilot whale	10	181	18.20 (0.33)	50	1
Unidentified small whale	10	16	1.60 (0.27)	5	1
White-beaked dolphin	12	62	5.20 (0.25)	13	1
White-sided dolphin	3	27	9.00 (0.61)	20	3
Harbour porpoise	8	19	2.40 (0.26)	6	1
Unidentified dolphin	44	406	9.20 (0.15)	45	1

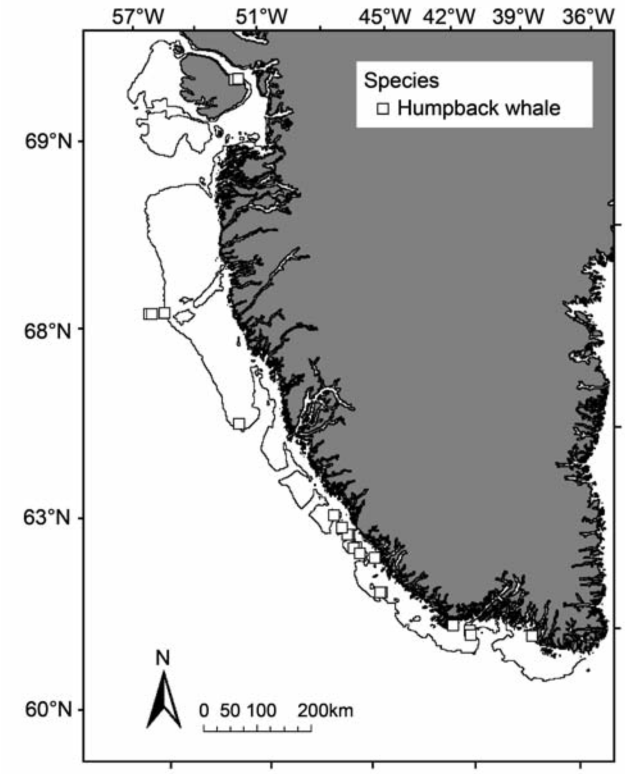


Fig. 2b. Sightings of humpback whales during the aerial survey off West Greenland September 2005.

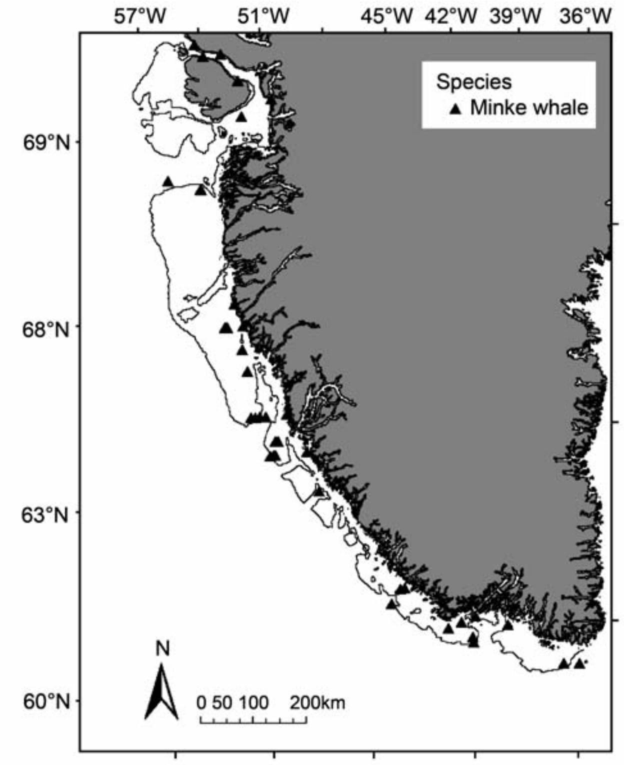


Fig. 2c. Sightings of common minke whales during the aerial survey off West Greenland September 2005.

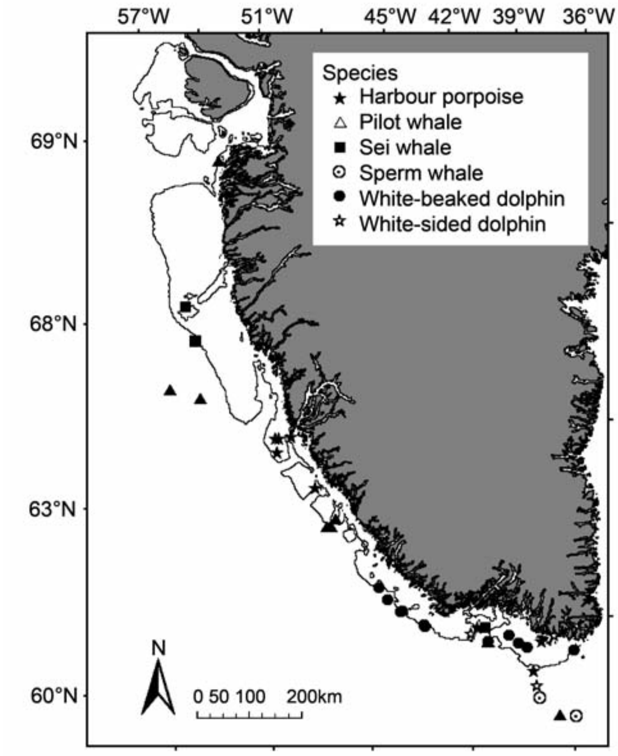


Fig. 2d. Sightings of sei whales, pilot whales, sperm whales, harbour porpoises, white-beaked and white-sided dolphin during the aerial survey off West Greenland September 2005.

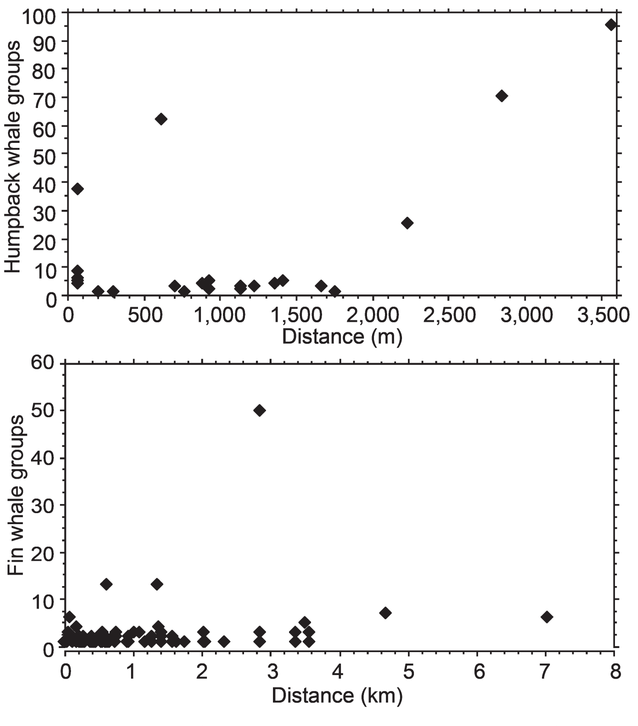


Fig. 3. Distribution of humpback whale (upper panel) and fin whale (lower panel) group sizes in relation to distance from trackline.

likely of harbour porpoises (*Phocoena phocoena*); additional sightings of this species were made south of Nuuk Fjord.

Humpback whale abundance estimates

Humpback whales were found predominantly in groups, and the size of the groups was often large; only 17% of detections were of single animals and 43% were of groups larger than five (Fig. 3). The frequent occurrence of humpback whales in large groups prevented the use of cue counting methods for abundance estimation, instead the abundance of humpback whales was analysed using standard line transect methods, assuming probability of detection on the line to be 1. There were no duplicate sightings of humpback whales so perception bias and measurement error could not be estimated.

Detection function and abundance estimates

Half-normal and hazard-rate detection functions were fitted to the grouped data. Sample size was lower than desirable for line transect surveys (only 22 groups out of 23 were within the truncation distance of 3km); this precluded stratifying for estimation of the detection function and $f(0)$ and it precluded use of covariates in this estimation. Based on Akaike's Information Criterion (AIC), a half-normal detection function model with no adjustment terms was chosen (Fig. 4). The associated χ^2 goodness-of-fit statistic was not significant ($p=0.63$), indicating an adequate fit to the data.

Estimates of the key components of the line transect estimator are shown in Table 2, together with summaries of stratum areas, effort and estimated density and abundance. Total abundance was estimate to be 1,218 humpback whales (CV=0.57) with log-based 95% confidence interval (423; 3,508) and log-based 90% confidence interval (501; 2,960).

One problem with the humpback whale abundance analysis was the combination of both solitary whales and whales in large groups (>10) that could bias both the estimates of mean group size and the detection function in line transect analysis (Fig. 3). An alternative approach was to estimate the abundance based on small groups (<11 whales) and using the same line transect technique described above with a right truncation at 2.0km. Abundance based on large groups (>10 whales) was then estimated separately using strip census analyses with a fixed strip width of 3.6km. The combined estimate of the line transect and strip census analyses was 1,158 (CV=0.35) humpback whales (Table 3) and was thus not different from the results obtained from the line transect analysis of all group sizes.

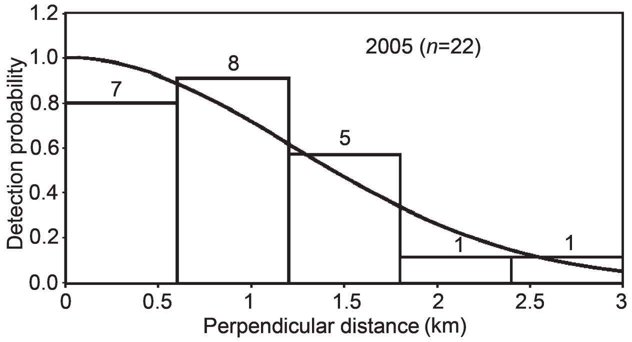


Fig. 4. Perpendicular distance histogram and fitted half-normal probability density function for humpback whale line transect data.

Fin whale abundance estimates

Fin whale group sizes were not as variable and large as for humpback whales; 61% of detections were of single whales, 17% were in groups of two and 9% were in groups of 5 or more (Fig. 3).

Measurement errors

Although the sample size was small, there appears to be little difference between the estimates of perpendicular distances from the two platforms at distances less than about 1.5km (Fig. 5). The level of distance 'binning' used in analysis (see Fig. 6) should make the line transect estimates of fin whale abundance insensitive to both the small errors at distances less than 1.5km and the more substantial errors at larger distances. The apparent lack of substantial errors at smaller distances (Figs 5 and 7) indicates that little, if anything, would be gained by incorporating a measurement error model in estimation. Estimating the measurement error process parameters from such a small sample size may add substantially to the variance of the resulting density and abundance estimates. Measurement errors were therefore dealt with only by using binned distance data in estimation.

Probability of detection at distance zero

Sightings from only the right side of the plane (where there were two independent observers) were used to estimate $g(0)$. Conditional detection functions for each observer

Table 2

Humpback whale data summary and estimates. K is number of transects; a is area (km^2); L is transect length (km); n is number of groups detected within 3km; n/L is encounter rate (groups per 1,000km); $\hat{f}(0)$ is the intercept of the probability density function; $\hat{E}[s]$ is estimated mean group size; $\hat{D}$ is estimated animal density (animals per 1,000 km^2); $\hat{N}$ is estimated animal abundance. Coefficients of variation are in brackets.

Stratum	Area (km^2)	K	L (km)	n	n/L	$\hat{f}(0)$	$\hat{E}[s]$	$\hat{D}$	$\hat{N}$
Cape Farewell	11,523	4	293	0	0.0			0	0
Central West	74,798	30	1,958	4	2.04 (0.91)			5.63 (1.00)	421 (1.00)
Disko Bay	12,312	12	556	1	1.80 (1.78)	0.664	8.3	4.95 (1.82)	61 (1.82)
South Greenland	19,491	19	1,106	4	3.62 (0.46)	(0.12)	(0.38)	9.97 (0.62)	194 (0.62)
Store Hellefiske Bank	15,669	7	577	0	0			0	0
South West	29,781	31	1,968	12	6.61 (0.42)			18.2 (0.60)	542 (0.60)
Total	**163,574**							**19.1 (0.57)**	**1,218 (0.57)**

Table 3

Estimates of humpback whale abundance based on line transect analyses of groups <10 and strip census estimates of groups >10.

	Right truncation	n	N	CV	Mean group size	Expected group size
Strip census estimate of groups >10	3.6km	5	647	0.48	57.8	
Line transect abundance of groups < 10	2.0km	18	511	0.53	3.39	4.06
			N (sum)	CV	lower 95% CI	upper 95% CI
Combined estimate			1,158	0.35	595	2,255

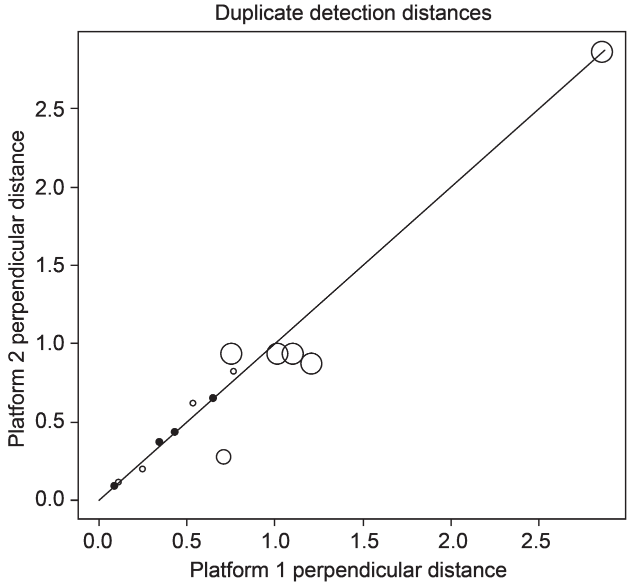


Fig. 5. Perpendicular distance estimates (in km) from duplicates (minke=solid dots, fin=circles; dots are proportional to group size (1, 2 or 3)). The line corresponds to platform 1 (front observer) and platform 2 (rear observer) estimated distances being equal.

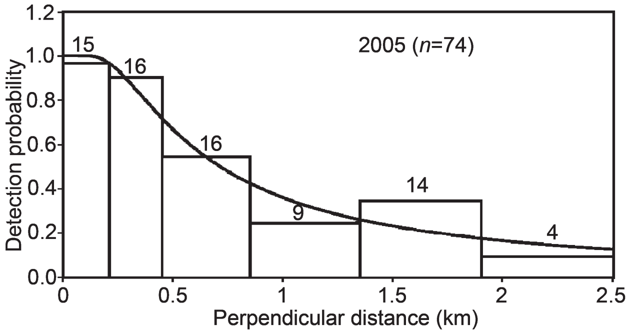


Fig. 6. Perpendicular distance histogram and fitted hazard rate probability density function for fin whale line transect data.

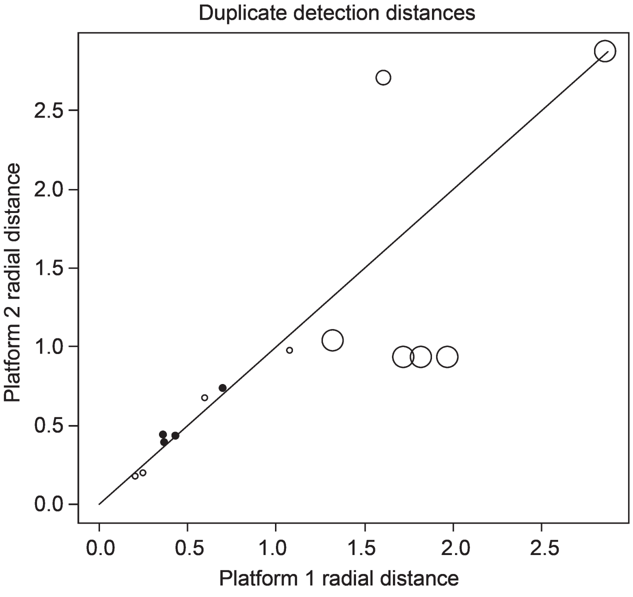


Fig. 7. Radial distance (in km) estimates from duplicates (minke=solid dots, fin=circles; dots are proportional to group size (1, 2 or 3)). The line corresponds to platform 1 (front observer) and platform 2 (rear observer) estimated distances being equal.

(conditional on detection by the other observer) were estimated using the iterative logistic regression, as implemented in *Distance* 5.0, release 2 (Thomas *et al.*, 2006). After truncating at 2.5km to remove an influential observation at 3km which led to conditional detection functions which increased slightly with distance, there remained 27 detections by the rear observer, 20 by the front observer and 6 duplicates. Fig. 8 shows the distribution of detections and duplicate proportions (proportion of each observer's detections which were seen by the other observer) as a function of distance, together with each observer's estimated conditional detection function (conditional on detection by the other observer). Models were selected using AIC and a model with radial distance and observer as explanatory variables was found to be best on this basis.

The probability of detecting a fin whale group on the trackline was estimated to be 0.34 (CV=0.29) for the rear observer, 0.26 (CV=0.32) for the front observer and 0.51 (CV=0.21) for both observers combined assuming that their probabilities are independent.

Detection function and abundance estimates

Truncation of perpendicular distances at 2.5km excluded 12% of detections (*n*= 84). Half-normal and hazard rate detection function forms were considered and a hazard rate function with no adjustment parameters was selected on the basis of AIC (Fig. 6). The associated χ^2 goodness-of-fit statistic was not significant (*p*=0.15), indicating an adequate fit to the data.

Estimates of the key components of the line transect estimator are shown in Table 4, together with summaries of stratum areas, effort and estimated density and abundance. Total fin whale abundance was estimated to be 1,660 animals (CV=0.38) and log-based 95% confidence interval (799; 3,450) and log-based 90% confidence interval (899; 3,066). The estimate corrected for $g(0)<1$, for both observers combined, was 3,234 animals (95% CI 1,412; 7,406, Table 4). This point estimate of abundance is likely negatively biased because $g(0)$ for the left side of the aircraft is likely to be lower than the combined $g(0)$ for the right side because the left side had only one observer.

An alternative approach that takes into account diving whales is the cue counting technique. Cue-counting methods were applied to estimate the abundance of solitary fin whales and to compare with line transect abundance of solitary fin whales. Using a cue rate of 50 cues per hour (Heide-Jørgensen and Simon, 2007), a cue counting abundance estimate of 8,889 (*n*=50, CV=0.68) solitary fin whales was achieved. This estimate is ~10 times bigger than a line transect estimate calculated solely for solitary fin whales (719, CV=0.40). The reason for this large difference is unclear; however, the detection function fitted to the observed radial distance distribution in the cue counting estimate showed a somewhat unrealistic rapid drop off close to the origin and cue counting estimates were not developed any further for fin whales.

Common minke whale abundance estimates

With the exception of one group of two whales, all common minke whale detections were of solitary animals and cue counting methods could be used for estimating abundance.

Measurement errors

The sample size of four common minke whale cues detected by both front and rear observers (minke duplicates) in the right side of plane was too small to estimate the distance

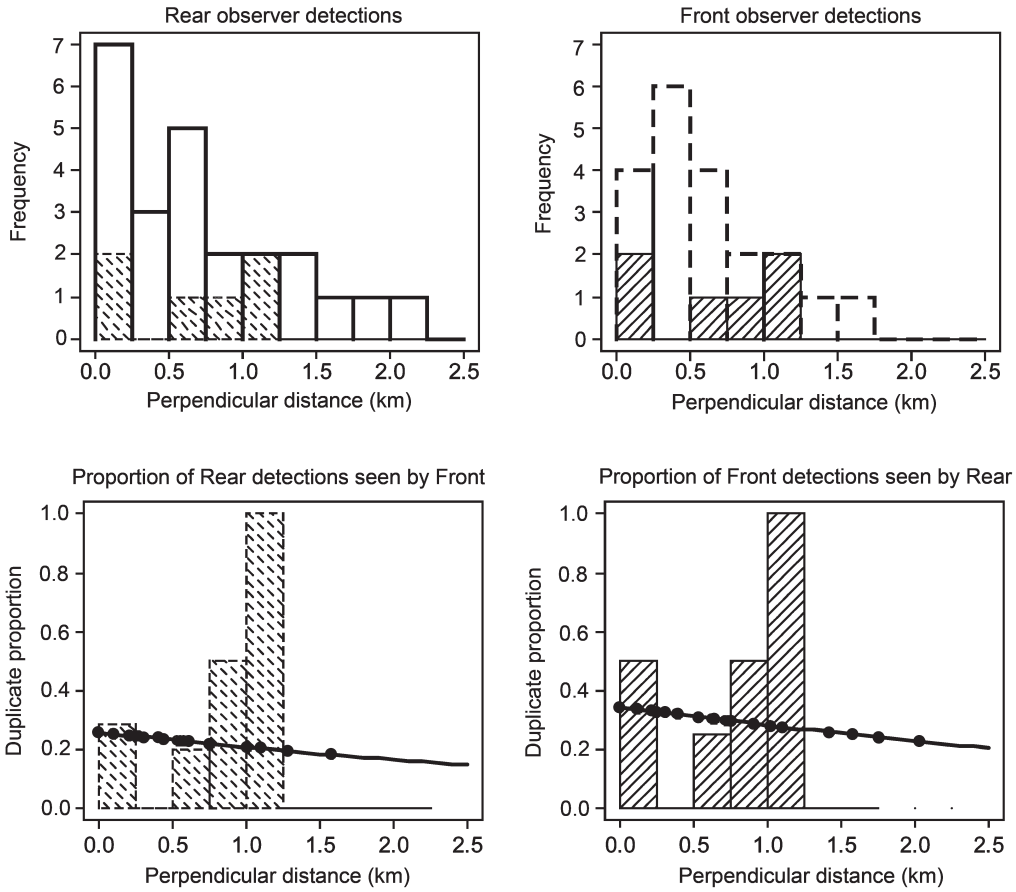


Fig. 8. Duplicate proportions and estimated conditional detection functions for fin whales. All data and estimates are for the right hand side of the aircraft only. The top row of plots shows the number of detections by each observer, with the numbers of these that were detected by the other observer (the duplicates) shaded. Bars with solid lines correspond to rear observer detections, bars with dashed lines correspond to front observer detections. The bottom row of plots shows the duplicate proportions, together with fitted detection function (smooth curve) and estimated detection probability for individual detections made by the observer in question.

Table 4

Fin whale data summary and estimates. K is number of transects; a is area (km^2); L is transect length (km); n is number of groups detected within 3km; n/L is encounter rate (groups per 1,000km); $\hat{f}(0)$ is the intercept of the probability density function; $\hat{E}[s]$ is estimated mean group size; $\hat{D}$ is estimated animal density (animals per 1,000 km^2); $\hat{N}$ is estimated animal abundance. Coefficients of variation are in brackets.

Stratum	Area (km^2)	K	L (km)	n	n/L	$\hat{f}(0)$	$\hat{E}[s]$	$\hat{D}$	$\hat{N}$
Cape Farewell	11,523	4	293	2	6.8 (2.09)	0.997 (0.22)	1.54 (0.12)	5.21 (2.10)	60 (2.10)
Central West	74,798	30	1,958	38	19.4 (0.41)			14.87 (0.47)	1,112 (0.47)
Disko Bay	12,312	12	556	1	1.80 (0.67)			1.38 (0.71)	17 (0.71)
South Greenland	19,491	19	1,106	17	15.4 (0.29)			11.78 (0.37)	230 (0.37)
Store Hellefiske Bank	15,669	6	577	6	10.4 (1.14)			7.96 (1.17)	125 (1.17)
Southwest Greenland	29,781	31	1,968	10	5.1 (0.28)			3.89 (0.37)	116 (0.37)
Total	163,574							10.15 (0.38)	1,660 (0.38)
Corrected for $g(0)<1$									3,234 (0.44)

measurement error process reliably. However, comparison of measurement of cues from both minke and fin whales suggest that the difference in measurement error between the two platforms within about 1.5km is negligible (Fig. 7) and no attempt was made to incorporate distance measurement error into the abundance estimation. It is not possible to estimate bias in estimating distance by either platform from these data.

Probability of detection at distance zero

Independent observer data were available only for the right side of the aircraft. These were used to estimate probability of detection at the closest radial distance used in analysis. As the front observer did not have a clear view of distance zero (because there was no bubble window in this position), and no detections were made within 0.2km of the aircraft, data were left-truncated at 0.2km before analysis. Fig. 9 shows

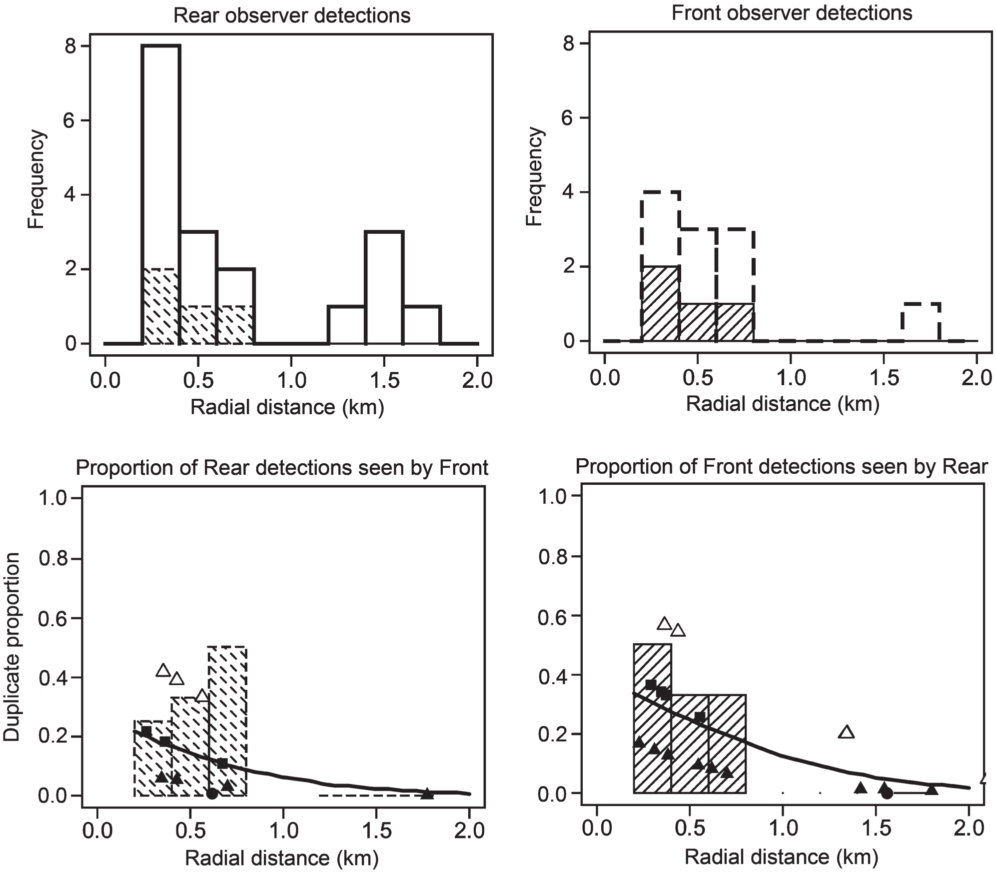


Fig. 9. Duplicate proportions and estimated conditional detection functions for common minke whales. All data and estimates are for the right hand side of the aircraft only. The top row of plots shows the number of detections by each observer, with the numbers of these that were detected by the other observer (the duplicates) shaded. Bars with solid lines correspond to rear observer detections, bars with dashed lines correspond to front observer detections. The bottom row of plots shows the duplicate proportions, together with fitted detection function (smooth curve) and estimated detection probability for individual detections made by the observer in question. Different Beaufort sea state for individual detections is indicated using different symbols: 0, 1, 2, and 3 are plotted using , , and respectively.

the duplicate proportions (proportion of each observer's detections which were seen by the other observer) as a function of distance, together with each observer's estimated conditional detection function (conditional on detection by the other observer). Conditional detection functions were estimated using the iterative logistic regression, as implemented in *Distance* 5.0, release 2 (Thomas *et al*., 2006). Models were selected using AIC and a model with radial distance, observer and Beaufort sea state as explanatory variables was found to be best on this basis.

The probability of detecting a cue at distance 0.2 km was estimated to be 0.36 (CV=0.39) for the rear observer, 0.22 (CV=0.42) for the front observer and 0.45 (CV=0.33) for both observers combined. As noted above, the sample size for this analysis was small (21 detections by the rear observer, 11 by the front observer, with 4 duplicates) and as a result, the reliability of these estimates is somewhat uncertain.

Detection function and abundance estimates

The slope of the probability density function $h(0)$ was estimated by fitting half-normal and hazard-rate functional forms to grouped radial distance data truncated at 1.6km. This led to seven detections (17% of the distances) being discarded. A hazard-rate detection function form with no adjustment terms was selected on the basis of AIC. The resulting detection function and fit of the pdf of radial distances to the observed radial distance distribution are shown in Figs 10 and 11. The associated χ^2 goodness-of-fit statistic was not significant (p=0.47), indicating an adequate fit to the data.

Estimates of the key components of the cue-counting estimator are shown in Table 5, together with summaries of stratum areas, effort and estimated density and abundance. Cue densities were converted to animal densities by dividing by an estimated cue rate of 46.3 cues per hour (CV=0.11) (Heide-Jørgensen and Simon, 2007). If detection

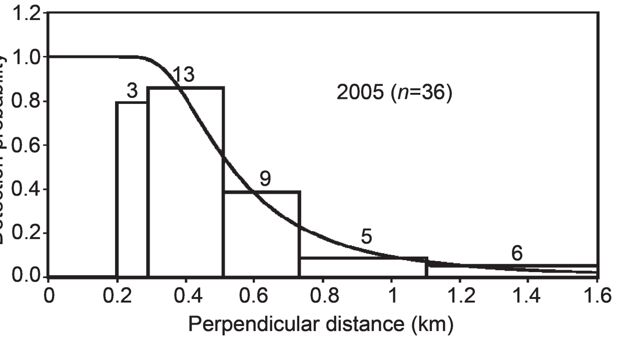


Fig. 10. Radial distance histogram and fitted hazard-rate detection function for common minke whale cue-counting data. (Note that the histogram bar heights have been scaled in inverse proportion to their mean radial distance, in order to place them on a comparable scale to the detection function curve.)

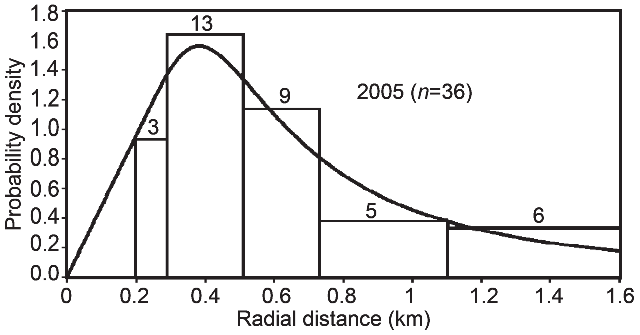


Fig. 11. Fit of the hazard-rate probability density function of radial distances to the observed radial distance distribution for common minke whale cue-counting data.

at distance 0.2km (called '$g(0)$' in the table) is assumed to be certain, total common minke whale abundance is estimated to be 4,856 animals (CV=0.49), log-based 95% CI=1,910-12,348 and log-based 90% CI=2,219-10,628. If detection at distance 0.2km is estimated as above, total common minke whale abundance is estimated to be 10,792 animals (CV=0.59), log-based 95% CI=3,594-32,407 and log-based 90% CI=4,289-27,156. In obtaining these estimates it is assumed that the observer on the left side of the aircraft has the same probability of detecting a cue at 0.2km as the two observers on the right side of the plane.

DISCUSSION

Due to inclement weather conditions the survey failed to cover areas west of Disko Island, the western part of the northern edge of Store Hellefiske Bank and a large part of the Central West Greenland strata. This lack of coverage, especially in the latter area, may cause a negative bias in the estimate of fin whale abundance in West Greenland, since large concentrations of fin whales are known to occur in this region. Supporting evidence for a negative bias is that the ship-based survey in September 2005 found large numbers of fin whales around 67°N, 57°W, the area not covered in the present survey. Furthermore locations from fin whales tracked by satellite as well as observations from Norwegian minke whalers indicate that fin whales occur in this area in conspicuous numbers (Heide-Jørgensen *et al*., 2007; Heide-Jørgensen *et al*., 2003). No survey coverage was attained in offshore areas (i.e. west of the 200m depth contour) south of 64°N and this may cause additional negative bias to the estimates of fin and common minke whale abundance in West Greenland.

The line transect estimate of humpback whale abundance in this study (1,218; 95% CI-423-3,508) was very similar to the estimate from a simultaneous ship-based survey (1,306; 95% CI-570-2,989) (Heide-Jørgensen *et al*., 2007). However, the estimate from the aerial survey is negatively biased because some animals will have been underwater and hence undetectable during passage of the plane and no corrections were made for whales missed by the observers. If estimates of the percentage of time humpback whales are visible from the air were available, this bias might be reduced substantially. Bannister and Hedley (2001) estimated the surface detection probabilities for aerial surveys of Southern Hemisphere humpback whales to range between 0.25 and 0.41. Satellite-linked time-depth recorders deployed on five humpback whales off Central West Greenland (Fyllas Bank) in June-July 2000 has shown that these whales spend between 29.7 and 43.6% of their time at the surface above 4m with an average of 36% (Dietz *et al*., 2002). If it is assumed that humpback whales can be seen at depths down to 4m the estimates will need to be multiplied by approximately three to account for the time the whales are visible (above a certain depth) to be seen by the observers. This would lead to a substantially larger abundance estimate of humpback whales in West Greenland.

Previously the abundance of humpback whales in West Greenland has been estimated to about 360 humpback whales (95% CI 314-413) for 1988-93 (Larsen and Hammond, 2004), 599 (95% CI=237-1,512) in 1993 (Kingsley and Witting, 2001) and 400 (CV=0.64) in 2002 and 2004 (Witting and Kingsley, 2005). The uncorrected aerial and the ship based surveys in 2005 both confirm that the current abundance of humpback whales in West Greenland is substantially larger than what was estimated in the surveys in the 1990s. This may be due to both a severe underestimation of abundance in previous surveys, growth in population size and/or increased affinity to the West Greenland feeding ground. The timing of the surveys in 2005 was one month later than the surveys conducted in the 1990s. Humpback whales arriving late on the West Greenland feeding ground could have contributed to the larger abundance estimates in 2005. The unprecedented observations of large groups of humpback whales (up to 95 individuals), often with a reddish defecation trailing behind, could be interpreted as an autumn feeding migration to West

Table 5

Minke whale data summary and estimates. K is number of transects; a is area (km^2); T is time spent searching (hours); n is number of cues detected within 1.6 km; n/T is encounter rate (cues per hour); $\hat{h}(0)$ is the slope of the density function; $\hat{D}$ is estimated animal density (animals per 10^6 km^2); $\hat{N}$ is estimated animal abundance. Coefficients of variation are in brackets. Estimated cue rate of $\hat{\eta}$ =46.3 cues per hour (CV=0.11) was used to convert cue density to whale density. Estimates in columns headed 'estimated $g(0)$' are those in columns headed '$g(0)$=1' divided by the estimated $g(0)$ of 0.45 (CV=0.33).

Stratum	Area (km^2)	K	T hour	n	n/T	$\hat{h}(0)$	$\hat{D}$	$\hat{N}$
Cape Farewell	11,523	3	1.26	0	0	4.77 (0.40)	0	0
Central West	74,798	27	11.47	12	1.047 (0.45)		34.35 (0.61)	2,569 (0.61)
Disko Bay	12,312	11	3.02	2	0.663 (0.45)		21.76 (0.61)	268 (0.61)
South Greenland	19,491	19	7.09	8	1.129 (0.38)		37.04 (0.56)	722 (0.56)
Store Hellefiske Bank	15,669	6	3.52	3	0.853 (0.55)		28.00 (0.69)	439 (0.69)
Southwest Greenland	29,781	29	11.38	10	0.879 (0.47)		28.84 (0.62)	859 (0.62)
Total	163,574						29.69 (0.49)	4,856 (0.49)
Corrected for $g(0)$<1							65.97 (0.59)	10,792 (0.59)

Greenland, but could also be the result of an aggregation of whales before the autumn migration out of Greenlandic waters.

Comparison of cue counting and line transect estimates for solitary fin whales resulted in a cue counting estimate that was ~10 times the line transect estimate. This suggests that the availability bias in line transect estimates may be large and that the fin whale abundance estimate presented here (based on a line transect analysis of all schools) may be substantially negatively biased. Circumstances made the cue counting estimate less attractive: the direction of the bias, if any, is unknown; the cue counting method can not deal with large group sizes; and the detection function showed an implausible drop near the origin.

The line transect estimate of fin whale abundance (1,660; 95% CI 799-3,450) was similar to the estimate obtained from a simultaneous ship-based survey (1,980; 95% CI 913-4,296). Both estimates are negatively biased to an unknown degree by incomplete coverage, lack of correction for submerged whales and especially for the aerial survey, by the lack of correction for whales missed by the observers. Correcting the aerial survey for perception bias increases the abundance estimate to 3,234 whales (95% CI 1,412-7,406). However, all three estimates confirm that the likely magnitude of the fin whale abundance off West Greenland in September is in the low thousands. The 1987/88 estimate of 1,100 (95% CI 520-2,100) fin whales in West Greenland (IWC, 1992) was a cue counting estimate and is therefore not directly comparable to the current abundance estimates. However, considering that the current but uncorrected estimates are larger than the earlier estimates corrected for availability bias (by the cue counting technique) it seems likely that the abundance of fin whales in West Greenland has increased. Additional evidence that fin whale abundance has increased in West Greenland comes from a simple comparison of encounter rates. About three times as many whales were seen (per unit effort) in the 2005 survey than in the 1987 survey. The later timing of the aerial survey in 2005 could be partially responsible by including fin whales arriving late on the West Greenland feeding ground. However, like humpback whales, fin whales were also seen in large groups of up to 50 whales. These group sizes were not seen on previous surveys, and could be interpreted as an autumn aggregation before the initiation of the southward migration.

The cue counting estimate of common minke whale abundance (4,856; 95% CI 1,910-12,348) was close to the estimate obtained from the simultaneous ship-based survey (4,479, 95% CI 1,760-11,394). The two estimates are however not directly comparable since the aerial survey estimate corrects for availability bias (cue counting technique) and the ship based survey estimate assumes that all common minke whales are at the surface to be seen during the passage of the survey platform. The cue counting common minke whale abundance estimate from this survey is also not significantly different from previous estimates from West Greenland, but when corrected for perception bias or $g(0)$ it is considerably larger than previous estimates, although not statistically different. The data that were used for estimating the perception bias were based on a small sample size from just one side of the plane and the estimate of $g(0)$ is similarly imprecise (CV=0.59). However, the few duplicate sightings between the front and rear observer indicate that a considerable number of common minke whales were not detected. In comparison with perception bias of other species of marine mammals in aerial surveys, common minke whales are clearly among the most difficult animals to detect and the low estimate of $g(0)$, i.e. the high estimated perception bias, determined in this study is not unexpected (Table 6). The $g(0)$ for the fin whales was unexpectedly low given their conspicuous large blows and body size. A possible explanation for the low fin whale detection is the fact that the survey was a multispecies survey where the detection might by negatively affected by the simultaneous recording of several species. Common minke whales are hard to detect because they are inconspicuous and spend a short time at the surface, but it could also be because of the rather demanding data collection from each cue of a whale. Finally the fact that the survey targets whales close to the plane (i.e. common minke whales) as well as those farther away (fin and humpback whales) might add to perception bias for common minke whales.

This study demonstrates the amount of data that can be obtained from an aerial survey effort of the shelf area off West Greenland in a year with reasonably good weather conditions. Other years in which surveys were attempted have had much more severe weather conditions and the timing of the present survey (late August and September) may have improved the likelihood of experiencing fair weather. The trade off is that the southward migration of baleen whales out of the Greenland shelf areas might already have started which also negatively affects the abundance estimates. Víkingsson and Heide-Jørgensen (2005) showed that some common minke whales tagged with satellite transmitters left the Icelandic shelf areas in mid September when they initiated their southbound migration.

This study has also brought to light the difficulties of applying the cue counting method to other species besides solitary common minke whales. Fin whales and humpback whales occur in groups and some of these groups are of up to 50 fin whales and 95 humpback whales. It is not a simple or practical task to count cues from tens of animals simultaneously and it becomes increasingly complicated with increasing whale pod size. Also, because there is a

Table 6

Estimates of fraction detected on the transect line for multispecies aerial surveys of marine mammals in West Greenland and characterization of the main features of the sighting process. GINR=Greenland Institute of Natural Resources.

Species	Survey platform	Mean pod size	Detection of cues	Perception bias	Estimation method	Ref.
Narwhal	Twin Otter	1.7	Dark but mostly in leads	0.86 (0.13)	Mark-recapture, full conditional independence	GINR
Beluga	Twin Otter	3.0	White moving groups	0.77 (0.10)	Mark-recapture, full conditional independence	GINR
Bowhead whale	Twin Otter	1	Big black body, blows, in leads	0.62 (0.19)	Mark-recapture, full conditional independence	GINR
Walrus	Twin Otter	1-2	Small brown body	0.51 (0.25)	Mark-recapture, full conditional independence	GINR
Fin whale	Partenavia	3.0	Large blows	0.51 (0.21)	Line transect, point conditional independence	This survey
Minke whale	Partenavia	1.1	Inconspicuous blows	0.45 (0.33)	Cue counting, point conditional independence	This survey

considerable range in fin whale group sizes, some of them large, the fin whale cue counting estimates will be fairly sensitive to whether or not animals in groups cue at the same rate as the observed individuals from which cue rate estimates were obtained.

The question remains if the cue counting method is the most efficient and accurate way to obtain abundance estimates of large cetaceans in West Greenland. Alternative methods include sight-resight methods applied to aerial line-transect survey (e.g. Innes *et al*., 2002) with correction for perception bias from double platform experiments and telemetry data on species specific surface times to correct for availability bias.

In summary, we believe that the abundance estimates presented in this study are definitely underestimates of the actual abundance of large whales in West Greenland because of incomplete coverage in presumed high density areas, no correction for perception bias in the case of humpback whales, lack of correction for availability bias for fin whales and humpback whales and sightings of unidentified large whales that were not included. Some whales may also have started their southbound autumn migration out of Greenland and were therefore not available to be counted during the survey.

ACKNOWLEDGEMENTS

We thank Njáll Sigurðsson and Gudmundur Thordarson for their steady observations, and Úlfar Henningsson for skilful flying. This study was funded by the Greenland Institute of Natural Resources.

REFERENCES

Bannister, J.L. and Hedley, S.L. 2001. Southern Hemisphere group IV humpback whales: their status from recent aerial survey. *Mem. Queensl. Mus*. 47(2): 587-98.

Borchers, D.L., Lake, J.L., Southwell, C. and Paxton, C.G.M. 2006. Accommodating unmodelled heterogeneity in double-observer distance sampling surveys. *Biometrics* 62: 372-78.

Borchers, D.L., Pike, D., Gunnlaugsson, T. and Víkingsson, G.A. 2003. Analyses of the NASS 1987 and 2001 minke whale cue counting surveys taking account of distance estimation errors. Paper SC/55/NAM3 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 33pp. [Paper available from the Office of this Journal].

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. vi+xv+432pp.

Dietz, R., Teilmann, J., Heide-Jørgensen, M.P. and Jensen, M.V. 2002. Satellite tracking of humpback whales in West Greenland. *NERI Technical Report* 411(2002): 1-40. [Published by National Environmental Research Institute, Ministry of the Environment, Denmark].

Heide-Jørgensen, M.P. and Simon, M. 2007. A note on cue rates for common minke, fin and humpback whales off West Greenland. *J. Cetacean Res. Manage*. 9(3): 211-14.

Heide-Jørgensen, M.P., Simon, M.J. and Laidre, K.L. 2007. Estimates of large whale abundance in Greenland waters from a ship-based survey in 2005. *J. Cetacean Res. Manage* 9(2): 95-104.

Heide-Jørgensen, M.P., Witting, L. and Jensen, M.V. 2003. Inshore-offshore movements of two fin whales *Balaenoptera physalus* tracked by satellite off West Greenland. *J. Cetacean Res. Manage*. 5(3): 214-45.

Hiby, A.R. 1985. An approach to estimating population densities of great whales from sighting surveys. *IMA (Inst. Math. Appl.) J. Math. Appl. Med. Biol*. 2: 201-20.

Hiby, A.R., Ward, A. and Lovell, P. 1989. Analysis of the North Atlantic Sightings Survey 1987: aerial survey results. *Rep. int. Whal. Commn* 39: 447-55.

Innes, S., Heide-Jørgensen, M.P., Laake, J., Laidre, K.L., Cleator, H., Richard, P. and Stewart, R.E.A. 2002. Surveys of belugas and narwhals in the Canadian high Arctic in 1996. *NAMMCO Sci. Publ*. 4: 169-90.

International Whaling Commission. 1990. Report of the Scientific Committee. *Rep. int. Whal. Commn* 40:39-79.

International Whaling Commission. 1992. Report of the Comprehensive Assessment Special Meeting on North Atlantic Fin Whales, Reykjavík, 25 February-1 March 1991. *Rep. int. Whal. Commn* 42:595-644.

International Whaling Commission. 2006. Report of the Scientific Committee. Annex E. Report of the Standing Working Group (SWG) on the Development of an Aboriginal Whaling Management Procedure (AWMP). *J. Cetacean Res. Manage. (Suppl.)* 8:91-109.

Kingsley, M.C.S. and Witting, L. 2001. A preliminary analysis of aerial survey observations of humpback whales in Greenland waters. Paper SC/53/NAH23 presented to the IWC Scientific Committee, July 2001, London (unpublished). 51pp. [Paper available from the Office of this Journal].

Larsen, F. 1995. Abundance of minke and fin whales off West Greenland, 1993. *Rep. int. Whal. Commn* 45: 365-70.

Larsen, F. and Hammond, P.S. 2004. Distribution and abundance of West Greenland humpback whales *Megaptera novaeangliae*. *J. Zool., London*. 263: 343-58.

Larsen, F., Martin, A.R. and Nielsen, P.B. 1989. North Atlantic Sightings Survey 1987: report of the West Greenland aerial survey. *Rep. int. Whal. Commn* 39: 443-46.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0. Release 1. Research Unit for Wildlife Population Assessment, University of St Andrews, UK. [Available from: *http://www.ruwpa.st-and.ac.uk/distance/*].

Víkingsson, G.A. and Heide-Jørgensen, M.P. 2005. A note on the movements of minke whales tracked by satellite in Icelandic waters in 2001-2004. Paper SC/57/O9 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea (unpublished). 3pp. [Paper available from the Office of this Journal].

Witting, L. and Kingsley, M. 2005. Abundance of marine mammals off West Greenland, 2002-2004. Paper SC/57/AWMP3 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea (unpublished). 13pp. [Paper available from the Office of this Journal].

Date received: September 2008
Date accepted: October 2008

Spatial distribution of large whales and their prey

Chapter 7

Paper VI:
Laidre KL, Heide-Jørgensen, MP, Heagerty P, Cossio A, Bergström B & Simon M. 2010

Spatial associations between large baleen whales and their prey in West Greenland.
Mar Ecol Prog Ser. 402: 269-284

Vol. 402: 269–284, 2010
doi: 10.3354/meps08423

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 8

Spatial associations between large baleen whales and their prey in West Greenland

Kristin L. Laidre[1, 2,]*, Mads Peter Heide-Jørgensen[2], Patrick Heagerty[3], Anthony Cossio[4], Bo Bergström[2], Malene Simon[2, 5]

[1]Polar Science Center, Applied Physics Laboratory, University of Washington, 1013 NE 40th Street, Seattle, Washington 98105, USA
[2]Greenland Institute of Natural Resources, Box 570, 3900 Nuuk, Greenland
[3]Department of Biostatistics, University of Washington, Seattle, Washington, USA
[4]Southwest Fisheries Science Center, 3333 North Torrey Pines Road, La Jolla, California, USA
[5]Department of Biological Sciences, University of Aarhus, C.F. Møllers Allé, 8000 Aarhus, Denmark

ABSTRACT: This study combined data on fin whale *Balaenoptera physalus*, humpback whale *Megaptera novaeangliae*, minke whale *B. acutorostrata*, and sei whale *B. borealis* sightings from large-scale visual aerial and ship-based surveys (248 and 157 sightings, respectively) with synoptic acoustic sampling of krill *Meganyctiphanes norvegica* and *Thysanoessa* sp. abundance in September 2005 in West Greenland to examine the relationships between whales and their prey. Krill densities were obtained by converting relationships of volume backscattering strengths at multiple frequencies to a numerical density using an estimate of krill target strength. Krill data were vertically integrated in 25 m depth bins between 0 and 300 m to obtain water column biomass (g m^{-2}) and translated to density surfaces using ordinary kriging. Standard regression models (Generalized Additive Modeling, GAM, and Generalized Linear Modeling, GLM) were developed to identify important explanatory variables relating the presence, absence, and density of large whales to the physical and biological environment and different survey platforms. Large baleen whales were concentrated in 3 focal areas: (1) the northern edge of Lille Hellefiske bank between 65 and 67° N, (2) north of Paamiut at 63° N, and (3) in South Greenland between 60 and 61° N. There was a bimodal pattern of mean krill density between depths, with one peak between 50 and 75 m (mean 0.75 g m^{-2}, SD 2.74) and another between 225 and 275 m (mean 1.2 to 1.3 g m^{-2}, SD 23 to19). Water column krill biomass was 3 times higher in South Greenland than at any other site along the coast. Total depth-integrated krill biomass was 1.3×10^9 (CV 0.11). Models indicated the most important parameter in predicting large baleen whale presence was integrated krill abundance, although this relationship was only significant for sightings obtained on the ship survey. This suggests that a high degree of spatio-temporal synchrony in observations is necessary for quantifying predator–prey relationships. Krill biomass was most predictive of whale presence at depths >150 m, suggesting a threshold depth below which it is energetically optimal for baleen whales to forage on krill in West Greenland.

KEY WORDS: Baleen whale · Capelin · Greenland · Krill · Nautical Area Scattering Coefficient · NASC · Optimal foraging · Survey

INTRODUCTION

The shelf ecosystems of the Arctic contain some of the most productive and tightly connected physical-biological systems in the marine environment. These relatively shallow domains play an important role in inflow and outflow from the Arctic Ocean, sea ice dynamics, and energy transfer through the ecosystem (Carmack & Wassmann 2006). Arctic continental shelves tend to accumulate large biomass concentrations either through seasonally restricted but intense production blooms or by local accumulation of biomass via advection.

---

*Email: klaidre@apl.washington.edu

The coastline of West Greenland is the longest continuous stretch of sub-Arctic to Arctic coastline in the world (Laidre et al. 2008). When the annual winter sea ice cover retreats, it triggers an enormous bloom of primary production on the shelf, attracting high densities of lower trophic level forage fish and zooplankton (Heide-Jørgensen et al. 2007a) ultimately culminating in large numbers of top marine predators. At least 10 species of cetaceans move in from the North Atlantic to take advantage of the explosion in production on the banks. Four of these, the fin whale *Balaenoptera physalus*, humpback whale *Megaptera novaeangliae*, minke whale *B. acutorostrata*, and sei whale *B. borealis* are the most abundant of the sub-Arctic baleen whales that migrate to the waters of West Greenland.

Optimal foraging theory suggests predators optimize their foraging behavior in patchy habitats to maximize fitness (Schoener 1971, Charnov 1976). Piatt & Methven (1992) examined this in baleen whales and suggested that a threshold prey density is required to facilitate foraging, and that seasonal and annual variations in prey densities play a role in the aggregation of whales and foraging profitability. In West Greenland, few data are available on the densities and spatial distribution of forage fish and zooplankton targeted by baleen whales (Kapel 1979) mostly because the area is vast and few large-scale prey surveys exist concurrent with cetacean sighting surveys. Based on stomach content analysis and visual observations (Kapel 1979), primary prey species for large whales are known to be krill, capelin *Mallotus villosus*, and to a lesser extent sandeel *Ammodytidae* spp., However, there is a limited understanding of how the distribution of whales in West Greenland is related to spatial and temporal variation in patchy resources (Heide-Jørgensen & Laidre 2007). These are important topics in light of changes in sea temperatures, sea currents, and biological production in the ecosystem due to climate warming (Myers et al. 2007). Furthermore, both fin and minke whales in West Greenland are subject to an annual subsistence harvest (Laidre et al. 2009), and understanding the dynamics of ecological relationships is critical.

The recent advancement of acoustic methods for assessing the abundance of prey species (Conti et al. 2005a,b, Conti & Demer 2006), combined with visual aerial survey techniques for estimating cetacean distribution and abundance, facilitate in-depth analyses of spatial relationships (Friedlaender et al. 2006). In this study, information from large-scale visual surveys of baleen whales and synoptic acoustic sampling of krill and capelin abundance in West Greenland were combined to examine quantitative spatial relationships between whales and their prey. We report on the distribution of the 4 whale species on the shelf of West Greenland and develop a series of statistical models relating whale occurrence to a suite of variables describing the physical environment and their prey. It was hypothesized that large whale occurrence and densities would be positively correlated with krill abundance over the survey area given the importance of the West Greenland shelf area for top predator feeding in summer.

MATERIALS AND METHODS

Ship survey data collection. Between 2 September and 3 October 2005 a systematic acoustic survey targeting capelin was conducted on the West Greenland shelf from the Icelandic fisheries research vessel RV 'Bjarni Saemundsson.' The survey was designed to cover the area between the coast and shelf break (up to 100 km offshore). Transect lines were placed in an east–west direction with 22 nautical mile (n mile) spacing and beginning approximately 3 n miles from the coast continuing west to the 400 m isobath. The survey began in the north and progressed south, including Vaigat, Disko Bay, and 5 fjords including Nuuk fjord (Fig. 1).

Acoustic data were collected continuously with a Simrad EK 60 echosounder at 38 and 120 kHz with 1 ms pulse duration and inter-pulse intervals of 1 s. Transducers were hull-mounted 5 m below the waterline. Echograms were used to estimate the abundance of capelin *Mallotus villosus* and krill *Meganyctiphanes norvegica* and *Thysanoessa* sp. Identification of observed sound-scattering organisms were groundtruthed by targeted pelagic trawl and plankton net hauls.

Simultaneous visual observations of large whales were conducted aboard the research vessel (Heide-Jørgensen et al. 2007b). Four cetacean observers scanned the water on either side of the vessel in pairs from an observation platform each covering 90 degrees in front of the vessel with an observer eye height of 10.3 m above sea level. The observers only used binoculars for species identification after recording a whale sighting. On-effort observations were carried out during all hours of daylight when weather conditions permitted (sea state less than 6 and visibility more than 500 m). Positional information was obtained with a handheld or onboard GPS. Sightings of whales from the ship-based survey were converted into abundance estimates using standard line transect techniques (see Heide-Jørgensen et al. 2007b for abundance estimates). The sea surface temperature was measured continuously along the ship track every minute.

Aerial survey data collection. A concurrent visual aerial survey for large whales was conducted between

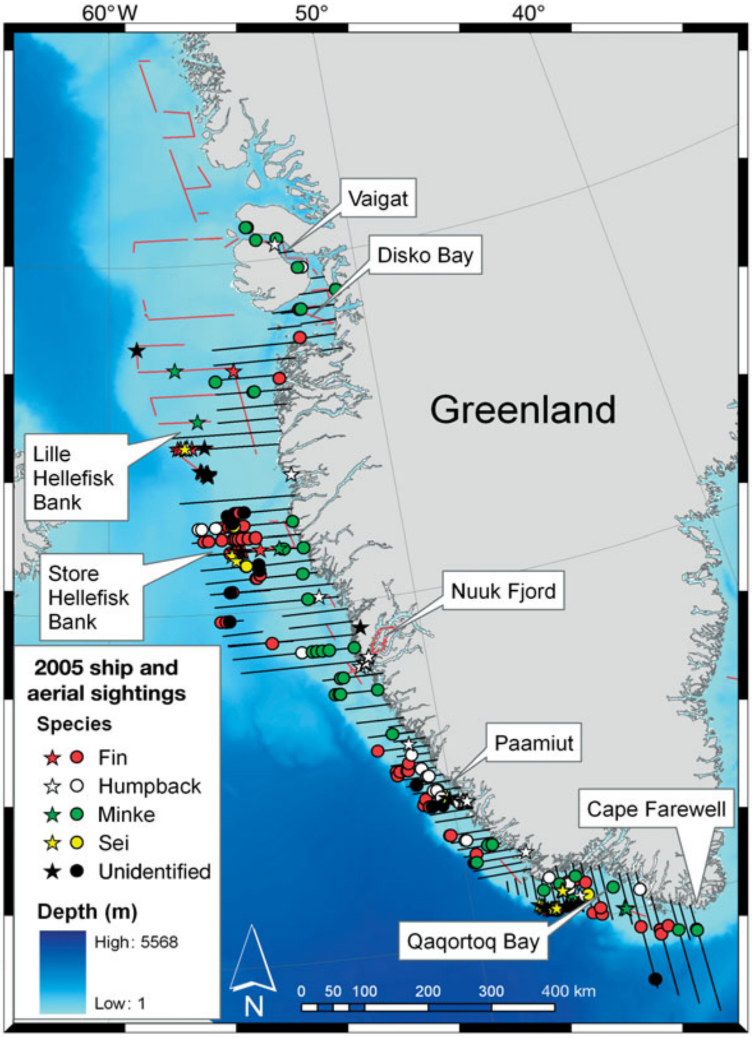


Fig. 1. Map of aerial and ship survey on-effort tracklines together with sightings of large baleen whale species in West Greenland. Ship survey effort is in red and aerial survey effort is in black. Note some survey lines overlap. Symbol colors represent different species sightings with ship survey sightings denoted by a star and aerial survey sightings denoted by a circle

28 August and 23 September 2005 (Heide-Jørgensen et al. 2008) in the same area. The survey platform was an Icelandic Partenavia Observer P-68 with 2 observers located in the rear seats each with bubble windows. An additional observer/cruise leader was seated in the right front seat. Declination angle to sightings was measured with Suunto inclinometers, and the lateral angle from the nose of the aircraft was estimated. Sightings were entered on dictaphones and on a computer-based voice recording system that also logged the position of the plane (from the aircraft GPS). Target altitude and speed was 750 feet (229 m) and 90 knots (167 km h^{-1}), respectively.

Survey conditions were recorded at the start of the transect lines and whenever a change in sea state, horizontal visibility, or glare occurred. The survey was designed to systematically cover the coast of West Greenland offshore to the shelf break (i.e. 200 m depth contour). Transect lines were placed perpendicular to the coast (i.e. in an east–west direction) except for South Greenland, where they were placed in a north–south direction (Fig. 1). Sightings of whales from the aerial survey were converted into abundance estimates using standard line transect and cue-counting techniques (see Heide-Jørgensen et al. 2008).

Acoustic analysis for krill abundance. Krill data were processed in 25 m depth bins at a spatial resolution of 1 n mile between daily sunrise and sunset. Data collected during nighttime or when the ship paused for CTD stations were excluded. Night data were excluded to minimize the bias of diel vertical migration of krill (Onsrud & Kaartvedt 1998) and data collected during CTD stations were excluded to reduce oversampling of krill at speeds under 2 knots. Relationships of volume backscattering strengths (S_v; dB re 1 m^{-1}) measured at multiple frequencies were used to apportion the integrated volume backscattering coefficients (Nautical Area Scattering Coefficient, NASC; m^2 n mile^{-2}) to krill versus other fish backscatter (see Hewitt et al. 2003, Riess et al. 2008), before converting NASC to a numerical density using an estimate of krill target strength (TS; dB re 1 m^2).

S_v at both frequencies was averaged over 25 m depth bins and 100 s. Background noise was subtracted and the S_v at 120 kHz ($S_{v\,120}$ kHz) was apportioned into regions of krill versus non-krill using a 2-frequency algorithm (see Madureria et al. 1993, Hewitt et al. 2003 for details). $S_{v\,120}$ kHz attributed to krill was integrated from 10 m below the surface (to exclude surface noise) to either a maximum of 500 m or approximately 5 m above the seafloor, resulting in NASC at 1 n mile increments. A ΔS_v range for 120 to 38 kHz of 4.6 to 11.1 dB was used for the delineation of krill from other backscatter based on length frequencies (CCAMLR 2005) for both *Euphausia superba* and *Meganyctiphanes norvegica* (Conti et al. 2005a,b).

The NASC were converted to biomass densities (g m^{-2}) using the simplified version of the Stochastic

Distorted Wave Born Approximation (SDWBA) model (Conti & Demer 2006). A normal distribution of orientations was used to derive the simplified SDWBA (θ = N[mean = 11°, SD = 4°]), estimated from an inversion of the SDWBA model using S_v measurements at multiple frequencies. The simplified SDWBA model required distributions of krill total lengths (TL or length-probability density functions [pdfs]) to derive weighted-mean backscattering cross-sectional areas per whale (= $4\pi 10^{TS/10}$; where TS is target strength, m^2 krill^{-1}; Demer & Hewitt 1995). Likewise, krill length-pdfs were needed to calculate weighted-mean masses per individual (W; g krill^{-1}) from appropriate mass-to-length relationships. This was based on net haul samples collected during the survey, calculated as:

$$W = 2.31 \times 10^{-2} \times TL^{2.6976} \quad (1)$$

Dividing NASC by σ ($\sigma = 4\pi r 10^{TS/10}$ where r is the reference range of 1 m) yields the number density (ρ; N n mile^{-2}) and multiplying ρ by W yields the biomass density (g m^{-2}). Krill biomass estimates were vertically integrated in 25 m incremental depth bins between 0 and 300 m (or 12 bins) to obtain water column krill biomass (g m^{-2}). Total integrated water column krill biomass (kg) in the study area was also estimated using a stratified sampling approach in the 5 geographic strata corresponding to whale abundance estimates from the ship-based survey reported in Heide-Jørgensen et al. (2007b).

Spatial data analysis. The Geographic Information System (GIS; ESRI Arc9) was used to make spatial associations between the location of cetacean sightings and a suite of environmental variables. The analysis was restricted to West Greenland waters and all data north of Cape Farwell (southern tip of Greenland located at 43.5° W longitude). The standard projection was Polar Stereographic (in m) with a central meridian of 55° W and reference latitude of 75° N. Coastline data for Greenland were obtained from the US Defense mapping agency as part of the World Vector Shoreline (WVS) at a scale of 1:250 000, referenced to mean high water in a datum of WGS84. Spatial bathymetric data were obtained from the International Bathymetry Chart of the Arctic Ocean (IBCAO, www.ibcao.org) (Jakobsson et al. 2008) with a 2 km resolution. This resolution was selected so that there was consistency in other remotely sensed and GIS covariates in the model. A categorical variable depth grid was also created with 3 depth categories: 0 to 500 m (shelf), 500 to 1500 m (slope), 1500 to 2300 m (deep). Sea-floor slope was calculated as integer value of the percent rise between adjacent bathymetry grid cells and classified into one of 4 categories, as follows: 0, 1 to 2, 3 to 4, and ≥5% rise. Point samples of sea surface temperature were used to create a continuous surface using a spherical ordinary kriging model based on a sub-sample of temperature values every 5 min (7160 data points) (temperature was collected every 1 min on the trackline). Kernel probability contours were calculated for each of the 4 baleen whale species sightings and for all species pooled together in 50, 75 and 95% probability contours.

Statistical analysis. Vertically integrated water column krill biomass (g m^{-2}) in 25 m depth increments and between 0 and 300 m was calculated every n mile. These point-based biomass estimates were translated to density surfaces for each depth increment using an ordinary kriging approach implemented in the ArcGIS Geostatistical Analyst extension. Kriging, a statistical approach suitable for representing interpolated surfaces for phenomena with strong random components (Pople et al. 2007), was best achieved with a spherical model fitted to the semi-variogram for each krill depth bin with no trend removal. A 45° search angle to the survey lines appeared to be optimal, capturing along- and between-survey line variability. Interpolated surfaces were restricted to the surveyed area (Fig. 1).

The spatial analysis examined the presence/absence or density of whales per unit (cell). The spatial analysis was conducted on a spatial resolution of 2 km. Four species were considered in the analysis: fin whales, sei whales, humpback whales, and minke whales. Sightings of large groups of humpbacks were truncated into categories of ≥30 animals and for fin whales ≥10 animals. We also included 3 species 'groups' in the models: all species pooled, all positively identified large baleen whales (fin, sei and humpback), and all unidentified large whales (excluding minkes).

The sightings and the effort from the ship and aerial surveys were combined into one model. We used all baleen whale sightings in sea states ≤6 on the ship survey, and ≤4 on the aerial survey. These criteria were modified slightly for the inclusion of minke whale sightings, where only sightings where sea state was ≤2 on the ship survey and ≤3 during the aerial survey were included. For the statistical modeling, it was necessary to obtain representative coverage of where whales were absent. We randomly sampled 5000 locations along both the ship and aerial trackline where no whale sightings were made. This represented over 20 times the number of whale sightings that occurred in the study area.

Input data for statistical models were whale sightings, randomly selected real absence locations, and GIS variables describing conditions hypothesized to determine whale presence/absence and density (group size). These included survey type (aerial vs.

ship), sea surface temperature (°C), latitude, longitude, krill water column biomass in (g m^{-2}) in 25 m depth increments and total integrated biomass, seafloor depth (m), and seafloor slope (% rise).

In order to evaluate whether data could be pooled from the 2 survey types (ship and aerial) we conducted both pooled and separate analyses on each data set and formally tested whether covariate effects differed by modality. We tested for significance of interactions by modality for each of the covariates.

Standard regression models were developed using the open-source statistical package R (R Development Core Team 2009). Models identified important explanatory variables relating the presence/absence and density of large whales to the physical and biological environment. We modeled the probability of whale occurrence as a function of environmental variables using Generalized Additive Modeling (GAM), where response variables were modeled as a smoothed function of all explanatory variables using nonparametric regression procedures. Standard GAM software was used descriptively to characterize trends. Inference about specific regression coefficients was made using a variation of Generalized Estimating Equations (GEE) and either logistic or Poisson regression while accounting for spatial autocorrelation (Heagerty & Lumley 2000). Due to colinearity between latitude and longitude, we transformed longitude to a new variable (res.long), which was the residual longitude after regression of longitude on latitude. This variable represented the east–west variation within the latitude. Based on covariate trends observed in the GAM analysis, all covariates were approximately linearly related to the outcome with the exception of latitude, which was modeled using both linear and quadratic terms. Significance was determined at the 0.05 level.

Depth-specific regressions were made on krill abundance at each depth interval to predict the probability (Pr) of a sighting using the following regression equation:

$$\text{Logit}(\Pr[y=1]) = b_0 + b_1(d) \times \log[\text{Abundance}(d)] + b_2 \times \text{Latitude} + b_3 \times \text{Latitude}^2 + b_4 \times \text{res.long} + b_5 \times \text{Depth} + b_6 \times \text{Temperature} + b_7 \times \text{Slope} \tag{2}$$

In this regression model the coefficient $b_1(d)$ represented the association between the likelihood of a sighting and the krill abundance measured at depth bin d. Since we considered depth bins ranging from 0 m up to 300 m at 25 m increments, we estimated 12 different depth-specific coefficients. Specifically, the slope coefficient $b_1(d)$ measured the increase in the risk of a sighting (log odds of any sighting) as the log[Abundance(d)] increased by 1 unit.

RESULTS

Baleen whale distribution

During the ship and aerial surveys 248 on-effort sightings of baleen whales were collected (Fig. 1). Search effort on both surveys was interrupted by nights and bad weather; however, 9266 km of survey effort was conducted during both surveys combined.

During the aerial portion, 157 sightings were made during 6458 km of on-effort searching. Of these, 78 were fin whales, 21 were humpback whales, 42 were minke whales, and 4 were sei whales. There were also 12 sightings of unidentified large baleen whales (Fig. 2, Table 1). During the ship portion, 91 sightings were made during 2808 km of on-effort. Of these, 30 sightings were from fin whales, 26 were humpback whales, 6 were minke whales, and 13 were sei whales. Additionally 16 sightings of unidentified large baleen whales were made (Fig. 2, Table 1). Group sizes were for the most part not larger than 10 with the exception of a few exceptionally large groups of fin and humpback whales on the aerial survey. This included groups as large as 95 humpback whales (Fig. 3) and 50 fin whales. Detailed documentation of sighting distribution and abundances of all species are reported in Heide-Jørgensen et al. (2007b, 2008).

Fin whales were the most common large whale sighted during both surveys (n = 108 sightings) and were found in high densities between the Store and Lille Hellefiske banks and off Paamiut. South Greenland was the area with the largest group sizes; 3 groups of 10 to 13 individual fin whales and one group of 50 individuals were observed at 60° N, 47° W (Fig. 2a). Humpback whale sightings (n = 47) were distributed along the coast with most sightings occurring nearshore and primarily in South Greenland. Five large groups of humpbacks (>25 individuals, with one group of > 95 individuals) were observed south of 62° N (Fig. 2b, Fig. 3). Minke whales (n = 48 sightings) were broadly distributed along the coast and had the least clumped distribution of the 4 species. There was a hiatus in distribution between SW (Southwest) Greenland and CW (Central West) Greenland (see Fig. 5 for area designation) with no sightings observed between 62° and 63° N (Fig. 2c). Several sightings of minke whales occurred in coastal waters of Vaigat and Disko Bay, areas with known high coastal capelin concentrations. Relatively few sightings of sei whales (n = 17) were made on both surveys. Of those, sei whales were found in 2 specific areas: on the banks at 66° N at Lille Hellefiske Bank and in South Greenland at 60° N, 47° W. Only one large group of 10 sei whales was seen (Fig. 2d).

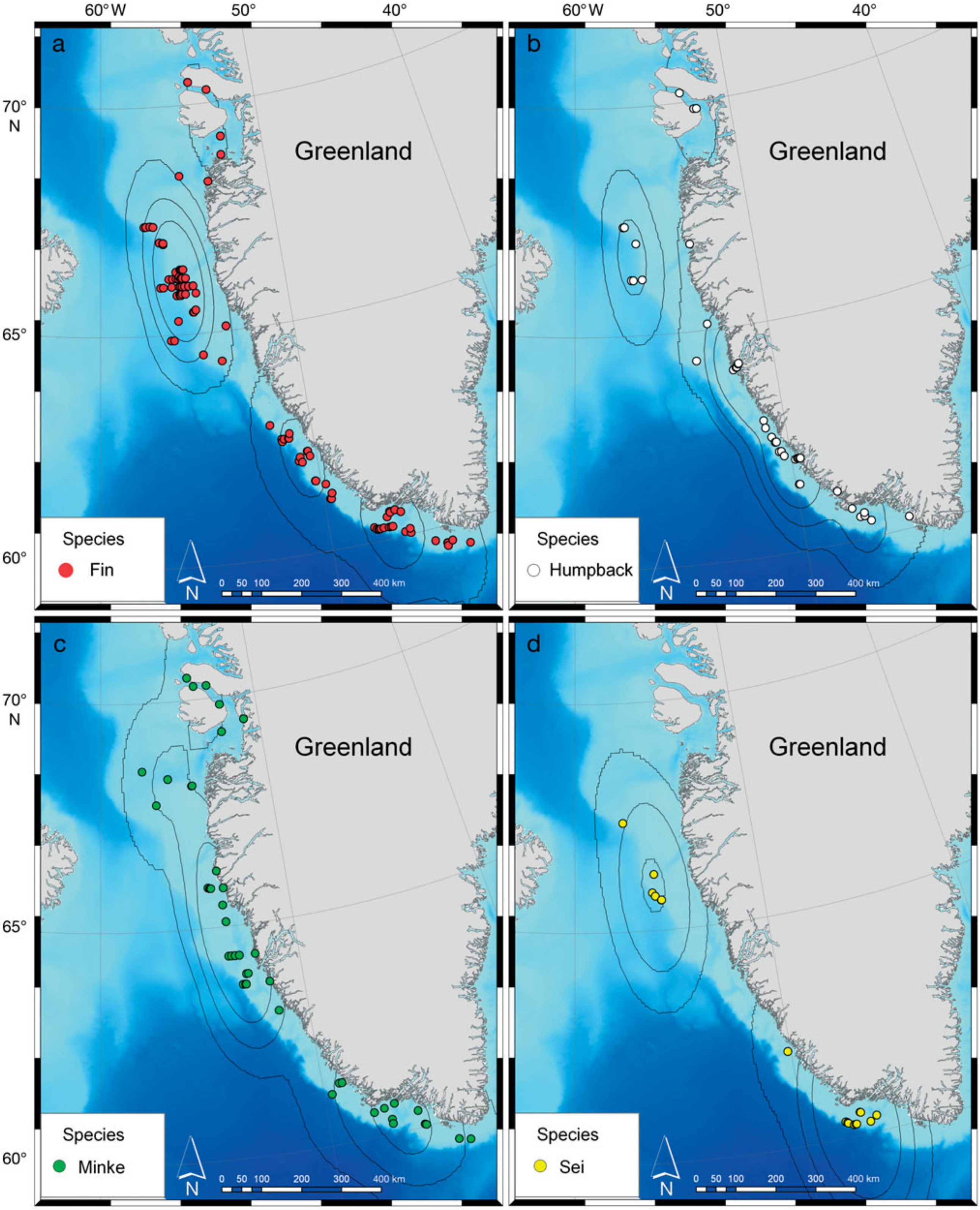


Fig. 2. *Balaenoptera physalus*, *Megaptera novaeangliae*, *B. acutorostrata*, and *B. borealis*. Distribution of sightings of 4 baleen whale species in West Greenland from ship and aerial surveys in 2005. Contour lines show approximate 50, 75 and 95% kernel contours

Table 1. Sightings and group sizes (ind.) of baleen whales on aerial and ship surveys in West Greenland 2005

Survey type	Species	Number of sightings	Average group size (range)
Aerial	Fin	78	3 (1–50)
	Humpback	21	17 (1–95)
	Minke	42	1 (1–1)
	Sei	4	3 (1–10)
	Unidentified	12	1 (1–3)
Ship	Fin	30	2 (1–5)
	Humpback	26	2 (1–5)
	Minke	6	1 (1–2)
	Sei	13	2 (1–5)
	Unidentified	16	1 (1–2)

Overall, large baleen whales were concentrated in 3 focal areas along the coast of West Greenland: (1) the northern edge of Lille Hellefiske bank between 65° and 67° N, (2) north of Paamiut at 63° N, and (3) in South Greenland between 60° and 61° N in Qaqortoq Bay. (Fig. 4). The area with the highest density of whales was between 65° and 67° N, and sightings of all 4 species were made in this area.

Capelin distribution

The target species during the acoustic survey was capelin, and continuous acoustic sampling along the cruise trackline for this species was conducted (Fig. 5). Capelin were virtually absent on the banks over the entire survey area. They were, however, present in large numbers in all coastal fjords and nearshore areas between 70° and 60° N. The capelin biomass in these fjords and near shore areas was previously estimated to be between 170 000 and 200 000 metric tonnes (Bergström & Vilhjalmarsson unpubl.). Capelin were excluded from the GAM analysis because of the highly discontinuous and coastal nature of their distribution, which made correlations with whale distribution on the offshore banks essentially impossible (Fig. 5).

Krill distribution

The mean density of krill (g m^{-2}) was examined in 25 m depth increments along the coast of West Greenland (Fig. 5). There was a weakly bimodal pattern in

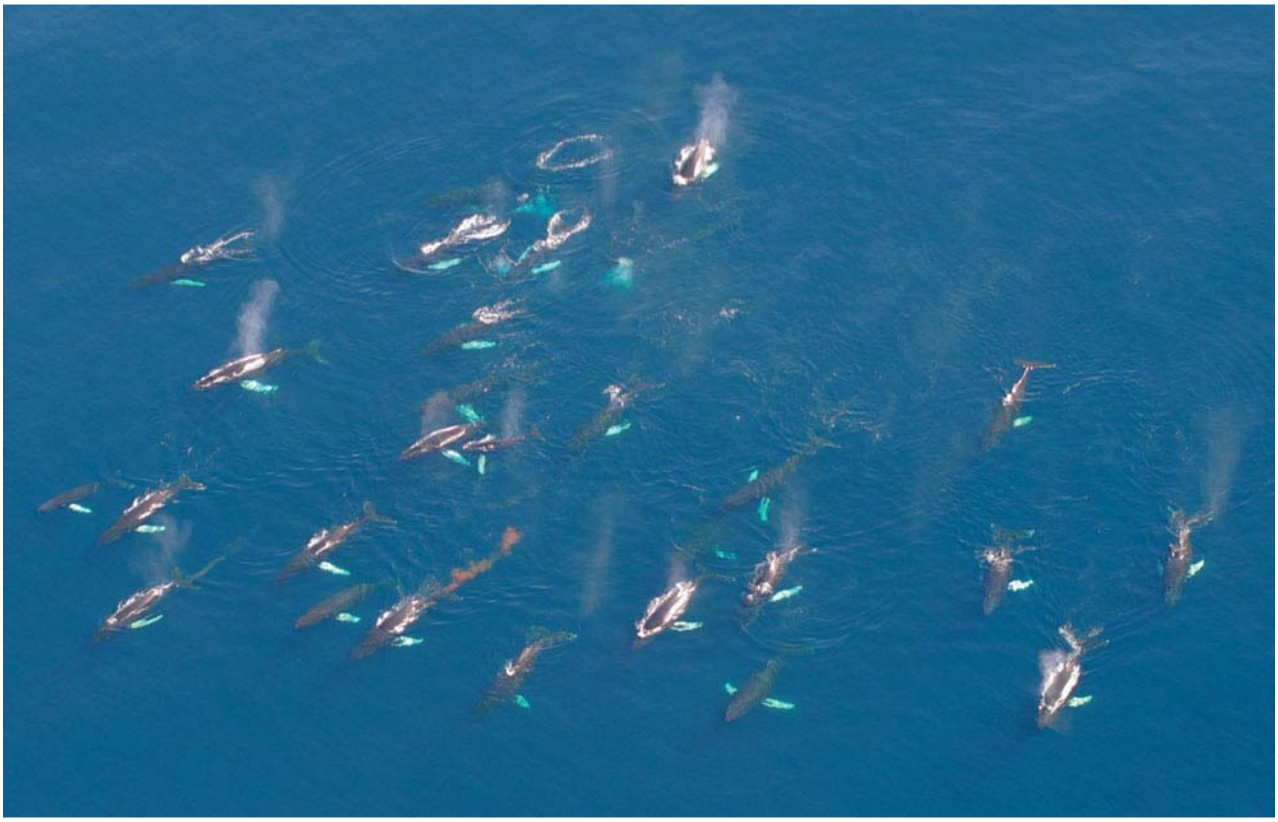


Fig. 3. *Megaptera novaeangliae*. Photo illustrating the exceptionally large group sizes of feeding humpback whales in West Greenland during the aerial survey conducted in 2005. Orange defecation is visible. Photos by Lars Witting

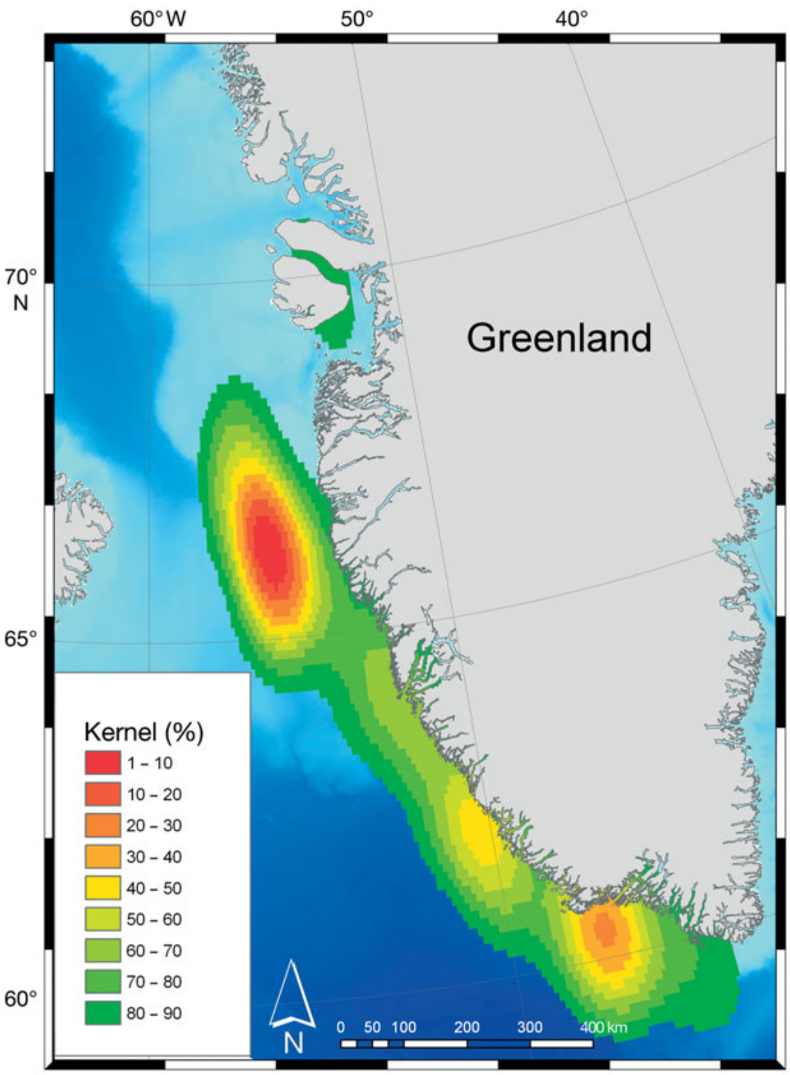


Fig. 4. *Balaenoptera physalus*, *Megaptera novaeangliae*, *B. acutorostrata*, and *B. borealis*. Kernel density estimation in 10% intervals for all sightings of large baleen whales from both ship and aerial surveys in 2005

mean krill density between 0 and 250 m. The first peak occurred between 50 and 75 m with mean values of 0.75 g m^{-2} (SD 2.74) and the second between 225 and 275 m with mean values of 1.2 to 1.3 g m^{-2} (SD 23 to 19). As depths increased past 250 m, mean krill density declined and was negligible by 500 m (Fig. 6). A striking pattern was the large aggregations of krill between 175 and 275 m (Fig. 6).

There was no correlation between mean krill density and latitude; however, density was 3 times higher at 60° N in South Greenland than at any other site along the coast (3.5 g m^{-2} SD 32). Mean krill density was <0.5 g m^{-2} at all latitudes with the exception of 2 small peaks at 63° and 66° N (<1.5 g m^{-2}). This was also the latitude where large outliers in krill density were found (>500 g m^{-2}) (Fig. 7), several orders of magnitude higher than all other measurements collected during the survey. This included 5 measurements of krill densities between 468 and 929 g m^{-2} (150 and 300 m), suggesting very dense but patchy aggregations. Large but less extreme values of krill density (160 to 165 g m^{-2}) were also detected at 66° N, suggesting dense aggregations at these latitudes.

Integrated water column biomass of krill was estimated for each of 5 strata on the ship survey (Fig. 5). Highest densities of krill were found in the southwest strata (12.29 g m^{-2}, SD 0.16) and in Nuuk fjord (11.13 g m^{-2}, SD 0.4) (Fig. 5), consistent with the high densities of whales in South Greenland. Total biomass in the whole survey area was estimated as 1.3 × 10^{9} kg of krill (CV 0.11), with the highest strata biomass found in SW Greenland (Table 2).

Spatial analysis

The complete model for large baleen whale presence on the West Greenland shelf included survey type and an interaction between integrated krill abundance and survey type (Table 3). This model suggested an observer was less likely to make a whale sighting on the ship. However, the interaction between survey platform and log of krill abundance was highly significant ($p < 0.001$). In separate models for each survey platform, the ship sighting data were strongly and positively correlated with the log of krill abundance ($b_1 = 0.64$, SE 0.12, $p < 0.001$) while no relationship was present for the aerial sighting survey ($b_1 = -0.08$, SE 0.12, $p = 0.5$). The relationship between whale density (given presence) and log krill abundance was weaker than that for presence and not significant in the full model (Table 4). However, in the ship-only model whale density was significantly explained by the log krill abundance ($p = 0.03$).

Other than krill, the models for both survey platforms exhibited significant responses to the same variables. This included longitude, slope, and sea surface temperature. Depth was not an important variable in models explaining either presence or density of large whales on the shelf of West Greenland. The consis-

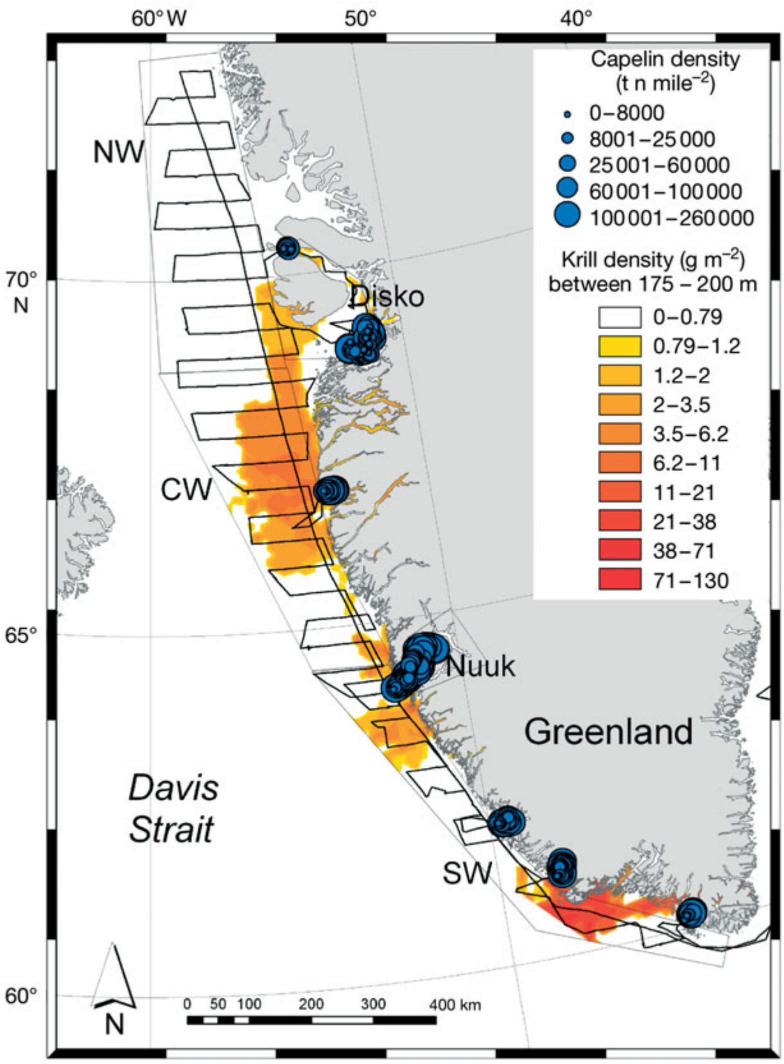


Fig. 5. *Mallotus villosus, Meganyctiphanes norvegica* and *Thysanoessa* sp. Trackline of continuous ship acoustic effort together with detections of capelin and concentrations of krill >0.8 g m^{-2} (kriged density between 175 and 200 m). Strata for total krill biomass calculations are labeled NW (Northwest), CW (Central West), SW (Southwest), Disko and Nuuk

tency between the significance of all other ecological variables across the 2 surveys suggested that the krill covariate was significant for the ship platform due to temporal continuity with whale sightings and acoustic data collection (used to determine krill biomass).

Response curves for all species combined demonstrate a nearly linear relationship between the presence of one or more whales at a given location and the biomass of krill in the area (Fig. 8). Response curves also suggested whale presence was inversely correlated to latitude and longitude, i.e. more whales were sighted in South Greenland (lower latitudes) and farther from shore (larger longitudes) (Fig. 8). In the model for whale density (given presence) there was a positive relationship to longitude, where larger groups were located farther east (or closer to the coast) (Fig. 9). Models were also developed independently for each species. Associations with log krill abundance were consistent across species despite much smaller sample sizes. However, the low number of sightings for each species when factoring in survey platform limited statistically robust conclusions.

The log odds-ratio plot for the presence of whales in West Greenland with respect to depth specific water column biomass of krill (g m^{-2}) demonstrated that krill water column biomass at depths of 150 to 175 m were most predictive of whale presence based on data from the ship survey (Fig. 10). The relationship was similar for group size. Depths below 150 m continued to be predictive of whale presence on the ship up to 300 m. Krill water column daytime biomass at depths above 100 m had no significant correlation to whale presence.

DISCUSSION

Data, covariates, and modeling

Our results suggest the most important variable for determining the presence of large baleen whales on the West Greenland summer feeding ground is krill biomass. This relationship, however, was only significant when there was close spatio-temporal proximity in whale sightings and measurements of krill. This is very likely due to the dynamic nature of krill on the shelf, where even a short temporal lag (on the order of days) weakens the association. This provides indirect evidence that the time-scale of cohesion for a krill patch is no greater than the several day asynchrony between the aerial and ship surveys. These results also imply that caution should be used in quantifying relationships between marine predators and their dynamic or ephemeral prey when observations on both are not synchronous.

There was a common effect of other covariates across survey types (slope, sea surface temperature), suggesting that other, less dynamic ecological correlates such as slope or longitude (distance from the coast) are similarly good in explaining whale presence

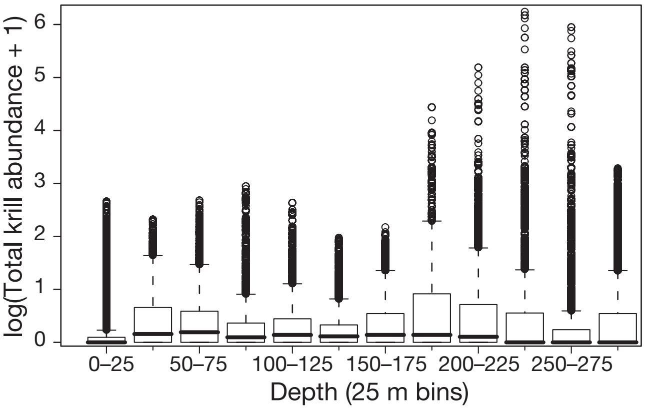


Fig. 6. *Meganyctiphanes norvegica* and *Thysanoessa* sp. Box plot of log krill water column biomass by depth bin in West Greenland from ship survey. Horizontal line indicates median response; bottom and top of box show 25 and 75 percentiles respectively. Open circles beyond interquartile range (dashed line with horizontal bars) are outliers

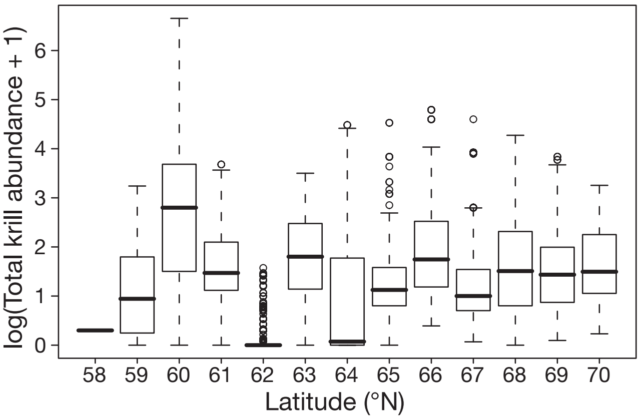


Fig. 7. *Meganyctiphanes norvegica* and *Thysanoessa* sp. Box plot of log krill water column biomass by latitude in West Greenland from the ship survey, where all measurements for a given degree of latitude were pooled. See Fig. 6 for explanation of box plots

regardless of a ship or plane survey platform. It is also important to consider the effect of kriging prey abundance. Kriging introduces measurement error and fills in space where the covariate was not measured directly, as is often the case with measures of prey density or biomass. Kriging is best performed if the spatial interpolation occurs at a smaller scale than the spatial extent of the prey patch.

Although models strongly indicated that large baleen whales are located in areas with high water column biomass concentrations of krill, models of density (or group size) did not. This may be due to the fact most group sizes were between 1 and 3 individuals. The distribution of values was therefore very narrow and it was difficult to identify significant relationships with density. The GAM functions used in the present study

Table 2. Total integrated water column krill biomass (kg) in 5 strata based on Heide-Jørgensen et al. (2007b). NW: Northwest; CW: Central West; SW: Southwest. See Fig. 5 for strata

Strata	Strata area (km^2)	Biomass of krill (kg)	CV
NW	82518	2.1×10^8	0.11
CW	72342	3.5×10^8	0.13
SW	51684	6.4×10^8	0.22
Disko	15780	1.2×10^8	0.12
Nuuk	2843	3.2×10^7	0.24
Total	225167	1.3×10^9	0.11

Table 3. Table of parameter estimates for a logistic regression of whale presence with respect to a suite of variables. The log.abundance variable represents the integrated krill abundance from 0 to 300 m. Res.long: residual longitude after regression of longitude on latitude; Depth: depth in m; SST: sea surface temperature in °C; Slope: seafloor slope in percent rise

	Estimate	SE	*Z*-statistic	p-value
Intercept	9.40	7.11	1.74	0.1865
Latitude	−0.17	0.12	2.15	0.1422
Latitude^2	0.06	0.03	4.95	0.0262
Res.long	−0.46	0.09	24.86	<0.001
Depth	−0.001	0.00	4.54	0.0330
Log. abundance	0.003	0.12	0.00	0.9788
SST	−0.49	0.16	9.71	0.001
Slope	0.14	0.03	26.51	<0.001
Factor(Survey Type)ship	−2.15	0.50	18.68	<0.001
Log. abundance: factor(Survey Type)ship	0.59	0.16	13.92	<0.001

Table 4. Table of parameter estimates for a Poisson regression of whale group size given presence with respect to a suite of variables. The log.abundance variable represents the integrated krill abundance from 0 to 300 m. See Table 3 for other definitions

	Estimate	SE	*Z*-statistic	p-value
Intercept	13.20	5.35	6.09	0.014
Latitude	−0.18	0.10	3.65	0.056
Res.long	−0.07	0.14	0.28	0.594
Depth	0.00	0.00	0.54	0.464
Log.abundance	0.00	0.20	0.00	0.991
SST	−0.03	0.39	0.01	0.937
Slope	−0.03	0.03	0.73	0.393
Factor(Survey Type)ship	−1.26	0.70	3.27	0.071
Log. abundance: factor(Survey Type)ship	0.08	0.29	0.08	0.778

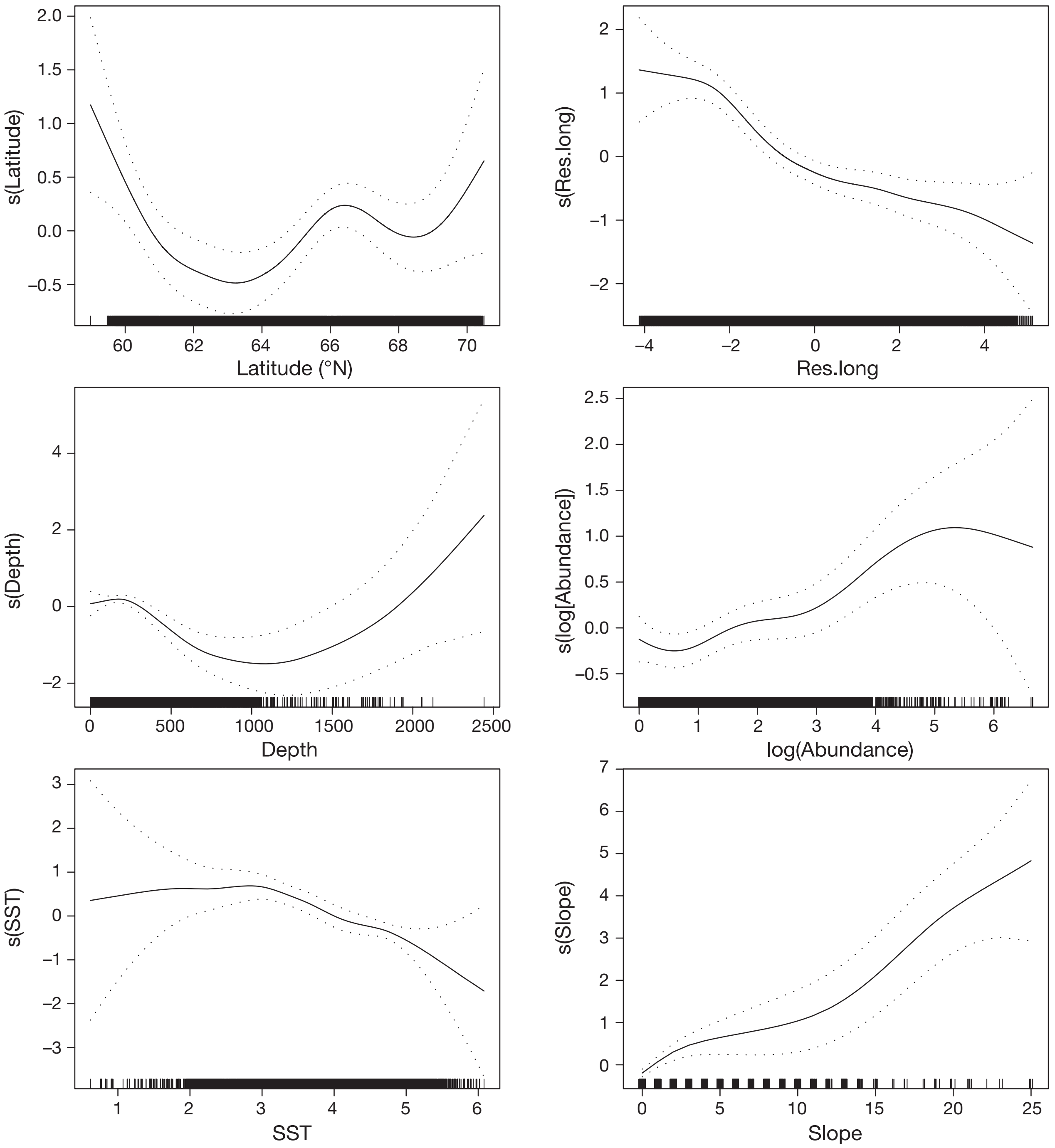


Fig. 8. *Balaenoptera physalus*, *Megaptera novaeangliae*, *B. acutorostrata*, and *B. borealis*. Generalized Additive Model (GAM) response curves for whale presence/absence and physical–biological variables using 2 km survey transects made during 2005 in West Greenland. These partial plots control for other predictions in the relationships shown. They are the result of back-fitting the algorithm used by the R-function GAM to calculate the additive contribution of each variable using nonparametric smoothing methods. Dashed lines represent 95 % confidence intervals for the fitted relationship

do not carry unrealistic assumptions of a normal distribution of errors or linear response shapes and are therefore appropriate for the wide range of continuous and categorical covariates used in this study. This approach is used widely for species distribution models and has proven to be robust to understanding species presence and absence patterns (Elith et al. 2006, Ferguson et al. 2006, Redfern et al. 2006, Wisz et al. 2008).

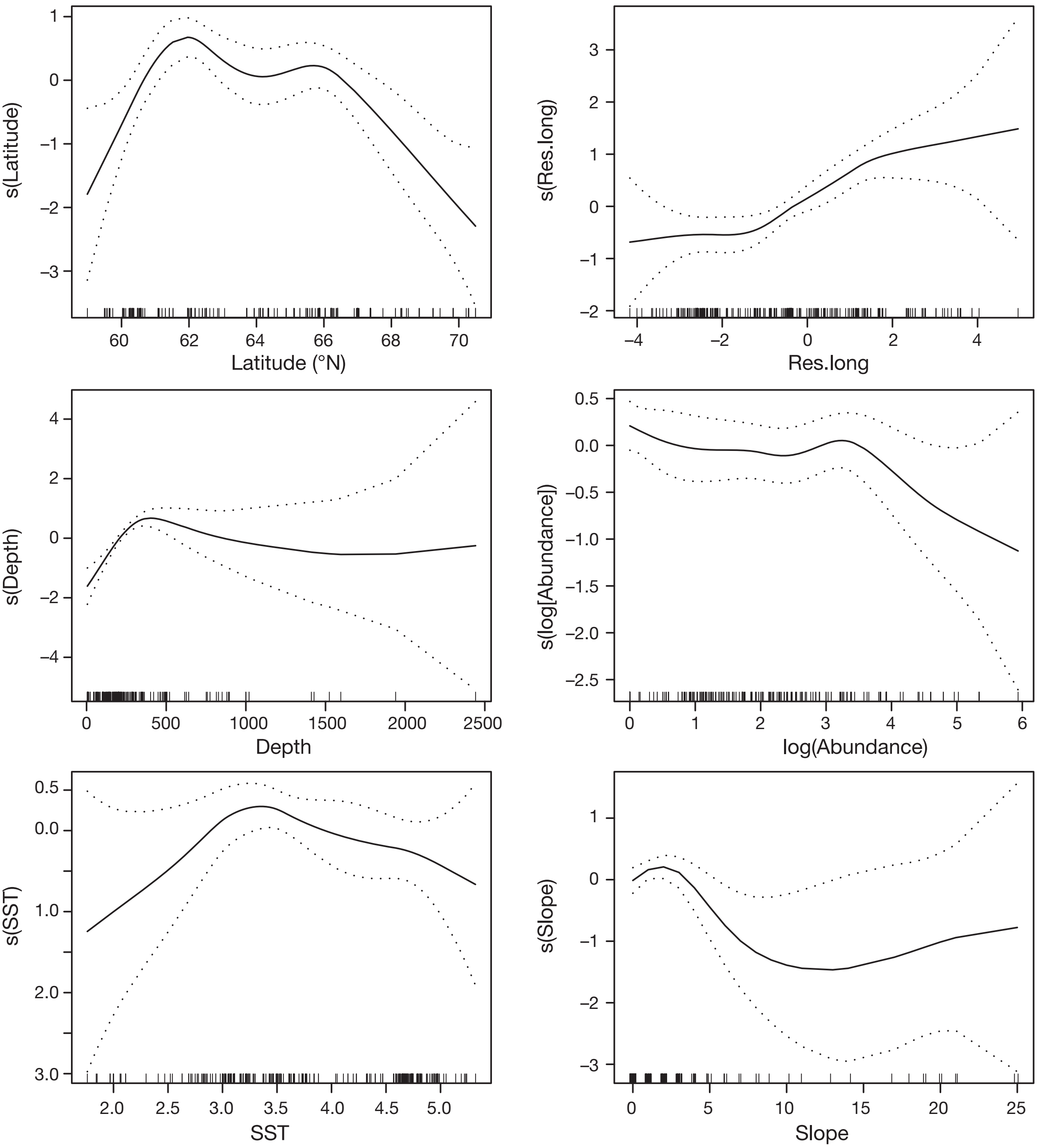


Fig. 9. *Balaenoptera physalus*, *Megaptera novaeangliae*, *B. acutorostrata*, and *B. borealis*. Generalized Additive Model (GAM) response curves for whale density given presence and physical–biological variables using 2 km survey transects made during 2005 in West Greenland

Relationships between krill and baleen whales

A striking relationship was apparent between the depth-specific krill water column biomass and the presence of whales in the ship survey data on the shelf. The biomass of krill at a given depth became highly predictive of whale presence at depths of 150 m or greater (and most predictive at 150 to 175 m), as demonstrated by the large log-odds ratio (Fig. 10). There was no relationship between the presence of whales and the abundance of krill in shallow depths <100 m, suggesting surface aggregations of krill do not

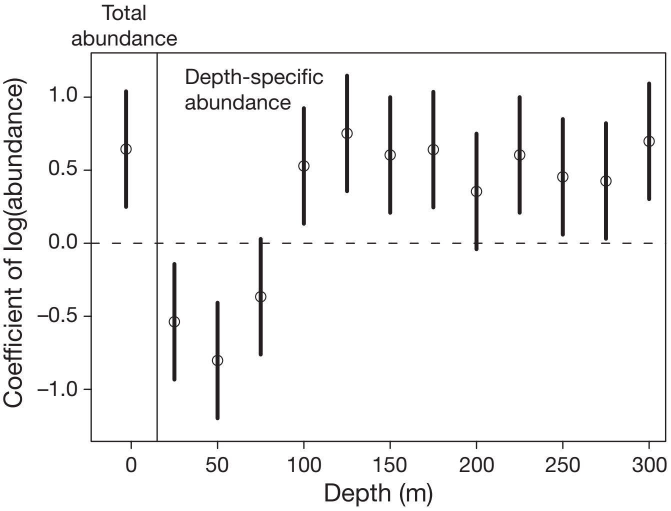


Fig. 10. *Balaenoptera physalus*, *Megaptera novaeangliae*, *B. acutorostrata*, *B. borealis*. Log odds-ratio coefficient with respect to depth for the probability of sighting a whale on the ship survey in West Greenland with respect to depth-specific water column biomass of krill *Meganyctiphanes norvegica* and *Thysanoessa* sp. (g m^{-2}). The ratio for total water column biomass of krill is shown on the left

determine where whales forage offshore on the West Greenlandic shelf. This follows well with the general patterns of krill density, where the largest aggregations of biomass appear below 175 m. It is interesting that the most predictive depth was not the peak in mean krill water column biomass (225 to 250 m). Krill in West Greenland likely make diurnal migrations similar to other Arctic zooplankton (Berge et al. 2009), and the depth at which baleen whales can reliably find large patches of krill likely varies depending on the time of day.

These results suggest there is a threshold depth at or below which it is energetically optimal for baleen whales to forage on krill. This appears to be >150 m in West Greenland and follows well with other studies that have suggested thresholds for optimal foraging in baleen whales (Piatt & Methven 1992). Extensive associations have been made between top marine predators and krill in other ecosystems (Ainley et al. 2006, Nicol et al. 2008, Ribic et al. 2008, Friedlaender et al. 2008). It has been shown that humpback whales target krill in the upper 100 m of the water column in the Antarctic (Fig. 8, Friedlaender et al. 2006, 2008). It is possible that whales in West Greenland target krill in shallower depths during nighttime.

The clear peak in krill density in South Greenland at 60° to 61° N is likely the reason for the high rates of occurrence of large whales in this area (Fig. 3, 4 & 5). This region was associated with large outliers in krill density that were orders of magnitude larger than the mean (several measures of krill over 500 g m^{-2}). Another focal area used by whales farther north, at approximately 66° N, was also associated with elevated mean densities of krill (Fig. 5); however, these krill densities were not as extreme as those in South Greenland. The aggregations of whales found in this area were primarily fin whales.

It is plausible that feeding conditions set up by physical variables in 2005 influenced the distribution and abundance of baleen whales on the West Greenland banks. June 2005 had some of the warmest temperatures (and highest salinities) measured in West Greenland during the past 50 yr, and an attractive hypothesis is that krill were advected to West Greenland with warmer water originating in the North Atlantic in 2005. What remains to be understood is whether the occurrence of krill in West Greenland in 2005 was part of an unusual large-scale advection event driven by specific oceanographic conditions or if krill are found regularly on the West Greenland banks in similar densities.

The models suggest that the relationship between whales and krill is significant when there is a very precise temporal match between data sets, and it would be useful to document how dynamic krill abundance is on the shelf of West Greenland. Unfortunately, there is little historical information available. Significant krill concentrations were detected on surveys in 1963 and 1964 in West Greenland (Smidt 1971); however, methods and coverage are not comparable to our study. Pedersen & Smidt (2000) presented a time series from standardized net hauls on Fyllas Bank between 1950 and 1984 but failed to detect any trends in krill abundance.

Unusually large group sizes of fin and humpback (Fig. 3) whales were found in the present study. This was surprising because surveys conducted regularly between 1983 and 2008 in West Greenland have shown that these whales occur in small groups of less than 5 individuals (Larsen & Hammond 2004, Witting & Kingsley 2005, Heide-Jørgensen et al. 2008). However, in the present study and consequent surveys in 2007 for fin whales (Greenland Institute of Natural Resources unpubl. data) these species were detected in unprecedented large groups of >50. It is possible these large group sizes are associated with unusually high abundances of krill in West Greenland. Sei whales feed almost exclusively on krill and have been infrequent visitors on the West Greenland banks for the past several decades (Kapel 1979) yet were detected frequently in our study (n = 17 sightings).

The estimates of krill biomass in this study should be considered indices rather than absolute estimates due to the potential for the signal-to-noise ratio (SNR) to wane at deeper depths. This was not measured and it is possible that krill abundance is underestimated at deeper depths. This would, however, not have any impact on the results presented here both because krill biomass is already shown to be higher at deeper depths and because foraging dives of large baleen whales are costly and generally limited to the depths (<300 m) investigated in our models.

Other potential prey species

Capelin are also an important and predicable prey resource for baleen whales in Greenland. Capelin occupy a central position in the trophic web of cold water ecosystems in the Atlantic and have attracted substantial scientific interest both due to their ecological importance and to their substantial value for both large-scale commercial fisheries and small-scale traditional use in Inuit culture (Rose 2005). This survey was conducted late in the summer when capelin were absent on the banks, having moved offshore with the exception of the highly dense coastal spawning aggregations. Capelin were excluded from the GAM analysis because of the highly discontinuous and coastal nature of their distribution (Fig. 5).

Spawning capelin are frequently targeted by minke and humpback whales in coastal regions like Disko Bay and Vaigat. Visual observations of feeding whales along the coast together with satellite tracking studies demonstrate that these aggregations are important during summer (Heide-Jørgensen & Laidre 2007); however, they are generally only targeted by a low number of individuals. Recent abundance estimates suggest approximately 1200 humpback whales occupy West Greenland in summer (Heide-Jørgensen et al. 2008) and most of these individuals are found outside of the coastal fjords on the offshore banks. Thus, it is expected feeding conditions out to the 200 m depth contour, such as krill densities, are more important on a population level than coastal capelin resources.

Species-specific foraging patterns

Large whales that arrive in West Greenland from wintering grounds in the Atlantic Ocean have species-specific feeding strategies during summer. In some cases, species have adopted multiple strategies for obtaining resources in West Greenland. Among those is the humpback whale. Low numbers of humpback whales (single individuals or groups of 2 to 3) are frequently and predictably found inshore feeding on capelin in Disko Bay, Vaigat, and Nuuk fjord in waters <25 m deep and <50 m from the shore. Humpback whales clearly rely on capelin resources; however, densities are low and the resource is patchy. Consequently, the majority of humpback whales foraging in West Greenland target offshore concentrations of prey such as krill or sandeels. Although krill are spread out over a much larger geographic area, the dense patches and high biomass can support a large biomass of foraging whales provided high density patches can be located. Locating dense aggregations of krill may require a higher degree of cooperation among whales, possibly explaining larger offshore aggregations.

Fin whales, like humpback whales, have a duel strategy of feeding on coastal capelin concentrations and offshore krill patches (Kapel 1979). Fin whales have been shown to utilize an energetically expensive strategy of lunge feeding at depth (see Croll et al. 2001, 2005, Simard et al. 2002) upon encounters with suitable densities of prey (Acevedo-Gutierrez et al. 2002, Goldbogen et al. 2006, 2007). In the present study, fin whales were primarily found in the area between the Store and Lille Hellefiske Banks and on the western edge of Store Hellefiske Bank. These are the most productive sites on the banks of West Greenland (Storr-Paulsen et al. 2004, Pedersen et al. 2005, Heide-Jørgensen et al. 2007a). Observations of fin whales in these areas together with high prey densities support conclusions from previous satellite tracking studies that fin whales move into these areas to feed (Heide-Jørgensen et al. 2003).

Minke whale distribution was the most irregular in this study (Fig. 2c). Sightings were made along the entire coast with few detectable patterns other than a slightly higher density in South Greenland. This region is known to be an important area for the species (Laidre et al. 2009). Minke whales are the most icthyophagous of the Balaenoptera and target primarily capelin and sandeels, reported both in studies of stomach contents of harvested whales caught in Greenland (Kapel 1979) and in other areas of the Atlantic (Macleod et al. 2004). They do, however, occasionally feed on krill in West Greenland, yet the importance of krill in their diet is unknown.

Sei whales occurred in low abundance on both the aerial and ship surveys. They have been proposed to occur in West Greenland during periods with an influx of warm water (Kapel 1979, Neve 2000). This species feeds almost exclusively on krill (Kapel 1979). Although sample sizes were too small to make conclusive associations between sei whale distribution and krill densities, the focal area of sightings corresponded well to the areas with the highest densities of krill and where the peak aggregations occurred (Fig. 2).

CONCLUSIONS

On multiple spatial scales, all foraging top predators must investigate and exploit a network of feeding sites in order to meet energetic demands (Stevick et al. 2008). In a highly variable environment such as West Greenland, this requires adopting different foraging strategies, exploiting diverse prey resources, and likely utilizing different levels of cooperation (or isolation) between individuals to succeed. All of these may be functions of mobility, the cost of transport, and the foraging success resulting from different strategies.

In summary, large whales in West Greenland clearly aggregate in areas with high concentrations of krill. This is necessary to meet energetic demands during the summer feeding period. West Greenland is a dynamic ecosystem, and the availability of prey is patchy and variable with transitory optimal physical conditions that set up the oceanographic and biological conditions necessary for recruitment of forage. Given the importance of Arctic shelf regions to predators seeking abundant resources in summer, there is potential for dramatic ecosystem shifts given the observed reductions in sea ice cover, ice thickness, extent, and duration, changes in current patterns and temperatures in these areas due to climate change (Carmack & Wassmann 2006).

Acknowledgements. The surveys were funded by the Greenland Institute of Natural Resources and the Greenland Home Rule government. Thanks to the many observers who collected data on both survey platforms. Four anonymous reviewers and comments from D. Demer, S. T. Jonsson, and E. Gurarie improved the manuscript.

LITERATURE CITED

Acevedo-Gutierrez A, Croll DA, Tershy BR (2002) High feeding costs limit dive time in the largest whales. J Exp Biol 205:1747–1753

Ainley DG, Ballard G, Dugger KM (2006) Competition among penguins and cetaceans reveal trophic cascades in the Western Ross Sea, Antarctica. Ecology 87:2080–2093

Berge J, Cottier F, Last KS, Varpe Ø and others (2009) Diel vertical migration of Arctic zooplankton during the polar night. Biol Lett 5:69–72

Carmack E, Wassmann P (2006) Food webs and physical-biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. Prog Oceanogr 71:446–477

CCAMLR (2005) Report of the first meeting of the subgroup on acoustic survey and analysis methods. SC-CAMLR-XXIV/BG/3. CCAMLR, Hobart

Charnov EL (1976) Optimal foraging, the marginal value theorem. Theor Popul Biol 9:129–136

Conti SG, Demer DA (2006) Improved parameterization of the SDWBA for estimating krill target strength. ICES J Mar Sci 63:928–935

Conti SG, Demer DA, Soule MA, Conti JHE (2005a) An improved multiple-frequency method for measuring in situ target strengths. ICES J Mar Sci 62:1636–1646

Conti SG, Demer DA, Brierley AS (2005b) Broad-bandwith, sound scattering, and absorption from krill (*Meganyctiphanes norvegica*), mysids (*Praunus flexuosus* and *Neomysis integer*), and shrimp (*Crangon crangon*). ICES J Mar Sci 62:956–965

Croll DA, Acevedo-Gutierrez A, Tershy BR, Urban-Ramirez J (2001) The diving behavior of blue and fin whales: Is dive duration shorter than expected based on oxygen stores? Comp Biochem Physiol 129A:797–809

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. Mar Ecol Prog Ser 289:117–130

Demer DA, Hewitt RP (1995) Bias in acoustic biomass estimates of *Euphausia superba* due to diel vertical migration. Deep-Sea Res I 42:455–475

Elith J, Graham CH, Anderson RP, Dudik M and others (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Ferguson MC, Barlow J, Fiedler P, Reilly SB, Gerrodette T (2006) Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecol Model 193:645–662

Friedlaender AS, Halpin PH, Qian SS, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in the Western Antarctic Peninsula shelf waters. Mar Ecol Prog Ser 317:297–310

Friedlaender AS, Fraser WR, Patterson D, Qian SS, Halpin PN (2008) The effects of prey demography on humpback whale (*Megaptera novaengliae*) abundance around Anvers Island, Antarctica. Polar Biol 31:1217–1224

Goldbogen JA, Calambokidis J, Shadwick RE, Oleson EM, McDonald MA, Hildebrand JA (2006) Kinematics of foraging dives and lunge-feeding in fin whales. J Exp Biol 209:1231–1244

Goldbogen JA, Pyenson ND, Shadwick RE (2007) Big gulps require high drag for fin whale lunge feeding. Mar Ecol Prog Ser 349:289–301

Heagerty PJ, Lumley T (2000) Window subsampling of estimating functions with application to regression models. J Am Stat Assoc 95:197–211

Heide-Jørgensen MP, Laidre KL (2007) Autumn space-use patterns of humpback whales (*Megaptera novaeangliae*) in West Greenland. J Cetacean Res Manag 9:121–126

Heide-Jørgensen MP, Witting L, Jensen MV (2003) Inshore-offshore movements of two satellite-tagged fin whales (*Balaenoptera physalus*) off West Greenland. J Cetacean Res Manag 5:241–245

Heide-Jørgensen MP, Laidre KL, Logsdon ML, Nielsen TG (2007a) Springtime coupling between phytoplankton, sea ice and sea temperature in Disko Bay, West Greenland. Prog Oceanogr 73:79–95

Heide-Jørgensen MP, Simon MJ, Laidre KL (2007b) Estimates of large whale abundance in Greenland in September 2005. J Cetacean Res Manag 9:95–104

Heide-Jørgensen MP, Borchers DL, Witting L, Simon MJ, Laidre KL, Rosing-Asvid A, Pike D (2008) Estimates of large whale abundance in West Greenland waters from an aerial survey in 2005. J Cetacean Res Manag 10:119–129

Hewitt RP, Demer DA, Emery JH (2003) An eight year cycle in krill biomass density inferred from acoustic surveys conducted in the vicinity of the South Shetland Islands during the austral summers of 1991/1992 through 2001–2002. Aquat Living Resour 16:205–213

Jakobsson M, Macnab R, Mayer M, Anderson R and others (2008) An improved bathymetric portrayal of the Arctic Ocean: implications for ocean modeling and geological, geophysical and oceanographic analyses. Geophys Res Lett 35:L07602, doi:10.1029/2008GL033520

Kapel FO (1979) Exploitation of large whales in West Greenland in the twentieth century. Rep Int Whaling Comm 29: 197–214

Laidre KL, Heide-Jørgensen MP, Nyland J, Mosbech A, Boertmann D (2008) Latitudinal gradients in sea ice and primary production determine Arctic seabird colony size in Greenland. Proc Biol Sci 275:2695–2702

Laidre KL, Heagerty P, Heide-Jørgensen MP, Witting L, Simon M (2009) Sexual segregation of common minke whales (*Balaenoptera acutorostrata*) and sex ratio of catches in Greenland. ICES J Mar Sci 66:2253–2266

Larsen F, Hammond PS (2004) Distribution and abundance of West Greenland humpback whales (*Megaptera novaeangliae*). J Zool 263:343–358

Macleod K, Fairbairns R, Gill A, Fairbairns B, Gordon J, Blair-Myers C, Parsons ECM (2004) Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography and prey off the Isle of Mull, Scotland. Mar Ecol Prog Ser 277:263–274

Madureira LSP, Ward P, Atkinson A (1993) Differences in backscattering strength determined at 120 and 38kHz for three species of Antarctic macroplankton. Mar Ecol Prog Ser 93:17–24

Myers PG, Kulan N, Ribergaard MH (2007) Irminger water variability in the West Greenland Current. Geophys Res Lett 34:L17601, doi:10.1029/2007GL030419

Neve PB (2000) The diet of the minke whale in Greenland – a short review. NAMMCO Sci Publ 2:92–96

Nicol S, Clarke J, Romaine SJ, Kawaguchi S, Williams G, Hosie GW (2008) Krill (*Euphausia superba*) abundance and Adélie penguin (*Pygoscelis adeliae*) breeding performance in the waters off the Béchervaise Island colony, East Antarctica in 2 years with contrasting ecological conditions. Deep-Sea Res II 55:540–557

Onsrud MSR, Kaartvedt S (1998) Diel vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. Mar Ecol Prog Ser 171: 209–219

Pedersen SA, Smidt ELB (2000) Zooplankton distribution and abundance in West Greenland waters, 1950–1984. J Northwest Atl Fish Sci 26:45–102

Pedersen SA, Ribergaard MH, Simonsen CS (2005) Micro- and mesozooplankton in Southwest Greenland waters in relation to environmental factors. J Mar Syst 56:85–112

Piatt JF, Methven DA (1992) Threshold foraging behavior of baleen whales. Mar Ecol Prog Ser 84:205–210 s

Pople AR, Phinn SR, Menke N, Grigg GC, Possingham HP, McAlpine C (2007) Spatial patterns of kangaroo density across the South Australian pastoral zone over 26 years: aggregation during drought and suggestions of long distance movement. J Appl Ecol 44:1068–1079

R Development Core Team (2009). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna; www.R-project.org.

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD and others (2006) Techniques for cetacean-habitat modeling. Mar Ecol Prog Ser 310:271–295

Reiss CS, Cossio AM, Loeb V, Demer DA (2008) Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. ICES J Mar Sci 65:497–508

Ribic CA, Chapman E, Fraser WR, Lawson GL, Wiebe PH (2008) Top predators in relation to bathymetry, ice and krill during austral winter in Marguerite Bay, Antarctica. Deep-Sea Res II 55:485–499

Rose GA (2005) Capelin (*Mallotus villosus*) distribution and climate: a sea 'canary' for marine ecosystem change. ICES J Mar Sci 62:1524–1530

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404

Simard Y, Lavoie D, Saucier FJ (2002) Channel head dynamics: capelin (*Mallotus villosus*) aggregation in the tidally driven upwelling system of the Saguenay St. Lawrence Marine Park's whale feeding ground. Can J Fish Aquat Sci 59:197–210

Smidt ELB (1971) Summary report of the ICNAF NORWESTLANT surveys, 1963. Int Comm Northwest Atl Fish Redb Part III:275–295

Stevick PT, Incze LS, Kraus SD, Rosen S, Wolff N, Baukus A (2008) Trophic relationships and oceanography on and around a small offshore bank. Mar Ecol Prog Ser 363:15–28

Storr-Paulsen M, Wieland K, Hovgård H, Rätz HJ (2004) Stock structure of Atlantic cod (*Gadus morhua*) in West Greenland waters: implications of transport and origin. ICES J Mar Sci 61:972–982

Wisz MS, Tamstorf MP, Madsen J, Jespersen M (2008) Where might the western Svalbard tundra be vulnerable to pink-footed goose (*Anser brachyrhynchus*) population expansion? Clues from species distribution models. Divers Distrib 14:26–37

Witting L, Kingsley M (2005) Abundance of marine mammals off West Greenland, 2002–2004. International Whaling Commission Scientific Committee Meeting document SC/57/AWMP3. Available from www.iwcoffice.org

Editorial responsibility: Hans Heinrich Janssen,
Oldendorf/Luhe, Germany

Submitted: February 2, 2009; Accepted: November 16, 2009
Proofs received from author(s): February 16, 2010

Acoustic monitoring of fin whales in Davis Strait

Chapter 8

Paper VII:
Simon M, Stafford KM, Beedholm K, Lee CM, Madsen PT. 2010

Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging.
J Acoust Soc Am. 128(5): 3200-3210

Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging

Malene Simon
Department of Birds and Mammals, Greenland Institute of Natural Resources, P.O. boks 570, Kivioq 2, 3900 Nuuk, Greenland;
Department of Biological Sciences, Zoophysiology, Aarhus University, C. F. Møllers Allé 3, Building 1131, 8000 Århus C, Denmark

Kathleen M. Stafford
Ocean Acoustics Department, Applied Physics Laboratory, University of Washington, 1013 NE 40th Street, Seattle, WA 98105–6698

Kristian Beedholm
Department of Biological Sciences, Zoophysiology, Aarhus University, C. F. Møllers Allé 3, Building 1131, 8000 Århus C, Denmark

Craig M. Lee
Ocean Physics Department, Applied Physics Laboratory, University of Washington, 1013 NE 40th Street, Seattle, WA 98105–6698

Peter T. Madsen
Department of Biological Sciences, Zoophysiology, Aarhus University, C. F. Møllers Allé 3, Building 1131, 8000 Århus C, Denmark

(Received 11 May 2010; revised 8 September 2010; accepted 13 September 2010)

Most baleen whales undertake migrations between low-latitude breeding grounds and high-latitude feeding grounds. Though little is known about the timing of their migration from the Arctic, fin whales are assumed to undertake a similar migratory pattern. To address questions about habitat use and migrations, the acoustic activity of fin whales in Davis Strait, between Greenland and Canada, was monitored continuously for two years using three bottom-moored acoustic recorders. The acoustic power in the fin whale call frequencies peaked in November–December, showing that fin whales are present in Davis Strait much later in the year than previously expected. The closely timed peaks in song activity and conception time imply that not all fin whales migrate south to mate, but rather start mating at high latitudes rather than or before migrating. Singing activity was strongly linked to daylight hours, suggesting that fin whales might feed during the few daylight hours of the late fall and early Arctic winter. A negative correlation between the advancing sea ice front and power in fin whale frequencies indicates that future changes in sea ice conditions from global warming might change the distribution and migratory patterns of fin whales near the poles.
© *2010 Acoustical Society of America.* [DOI: 10.1121/1.3495946]

PACS number(s): 43.80.Ka, 43.80.Lb [WWA] Pages: 3200–3210

I. INTRODUCTION

Long-range migratory behavior is found in a number of animal species including fish (Jakobsson and Østvedt, 1999), insects (Urquhart and Urquhart, 1977), mammals (Strelkov, 1969) and birds (Salomonsen, 1967). Though many ecological factors influence migratory behavior, seasonal variation in resources is often a major driving force for long distance migrations (Alerstam *et al.*, 2003). That is also believed to be the case for most baleen whale species who undertake long migrations between high latitude, productive feeding grounds during summer and warmer oligotrophic mating/breeding grounds in the tropics during winter (Kellogg, 1929; Norris, 1967).

Long migratory routes have been mapped for humpback (*Megaptera novaeangliae*), right (*Eubalaena australis* and *E. glacialis*) and gray whales (*Eschrichtius robustus*) with identified high-latitude feeding and low-latitude breeding grounds (e.g., Bannister *et al.*, 1999; Clapham, 1996; Kraus *et al.*, 1986; Pike, 1962). Discovery tag returns from commercial whaling suggest that blue whales (*Balaenoptera musculus*) and fin whales (*B. physalus*) may undertake similar migrations: feeding at high latitudes during summer and moving to lower latitudes for mating during winter (Kellogg, 1929; Norris, 1967; Mizroch *et al.*, 2009). That notion is supported by acoustic data for fin whales from the Pacific (Stafford *et al.*, 1999), and likely also Antarctica, showing a negative correlation between calling rate and increasing sea ice concentration (Širović *et al.*, 2004, 2009). Although no clear fin whale migratory routes have been identified, a number of studies suggest that most populations migrate between high and low latitudes while a few populations seemingly reside in the same area year-round (Lockyer, 1984; Mizroch *et al.*, 2009).

Fin whales are one of the most abundant cetaceans in the Davis Strait off Western Greenland, where they likely play an important role in an ecosystem that experiences large temporal and spatial fluctuations in primary and secondary production over the year (Laidre *et al.*, 2010). Though the Davis Strait is a fin whale summer feeding ground, little is known about how long and with what purposes other than feeding fin whales use the Davis Strait over the year. This lack of data on fin whales partly stems from difficulties in studying them over sufficiently large temporal and spatial scales. For high latitude populations in particular, harsh weather conditions make it challenging to study habitat use during the autumn and winter, as traditional sighting surveys are not feasible due to low light conditions, sea ice and heavy seas, underlining the need for other experimental methods.

Passive acoustic monitoring (PAM) is increasingly used as a tool to study the presence, relative abundance, migratory movements and behavior of large baleen whales (e.g., Moore *et al.*, 2006; Mellinger *et al.*, 2007). Singing fin whales lend themselves to PAM by producing repetitive, powerful low frequency (LF) 20-Hz pulses. The dominating LF part of the song consists of stereotyped ~1 s long down-sweeps centered at 20 Hz (Watkins *et al.*, 1987) that appear in bouts of either single calls or call doublets, repeated for up to many hours at a time with a regular inter-pulse-interval that varies among fin whale stocks (Thompson *et al.*, 1992; Watkins *et al.*, 1987; Clark *et al.*, 2002; Delarue *et al.*, 2009). Other than the LF pulse, the call often also contains a simultaneous high frequency (HF) component. The HF component may vary between populations of fin whales; Eastern Antarctic fin whales have a center frequency of 99 Hz while those near the Western Antarctic Peninsula and the Scotia Sea have a center frequency of 89 Hz (Širović *et al.*, 2004, 2009).

With an estimated source level of 170–190 dB re 1 μPa and call production in all the world's ocean basins, the song is believed to serve in long range acoustic communication (Payne and Webb, 1971; Charif *et al.*, 2002; Širović *et al.*, 2007; Thomson and Richardson, 1995). The occurrence of a peak in fin whale song just before the estimated peak conception time (Lockyer, 1984) and the identification of males as singers (Croll *et al.*, 2002), have led to the hypothesis that the song is part of a male mating display (Watkins *et al.*, 1987; Croll *et al.*, 2002).

Diel variation in baleen whale calling rates has been reported from several species and a correlation between feeding, sunlight and calling activity has been proposed (Stafford *et al.*, 2005; Baumgartner and Fratantoni, 2008) although such evidence for fin whales is relatively weak (Watkins *et al.*, 1984, 1987). Blue whales seem to have a clear diel variation in their acoustic activity by producing most B-calls during night and dusk, when prey may be less available to them and using D-calls during day time foraging (Stafford *et al.*, 2005; Wiggins *et al.*, 2005; Oleson *et al.*, 2007). Fin whale calls from Bermuda showed only slight, inconsistent differences in calling rates between day and night (Watkins *et al.*, 1987). However, radio tracking observations suggested that their behavioral states changed between these two light regimes (Watkins *et al.*, 1984).

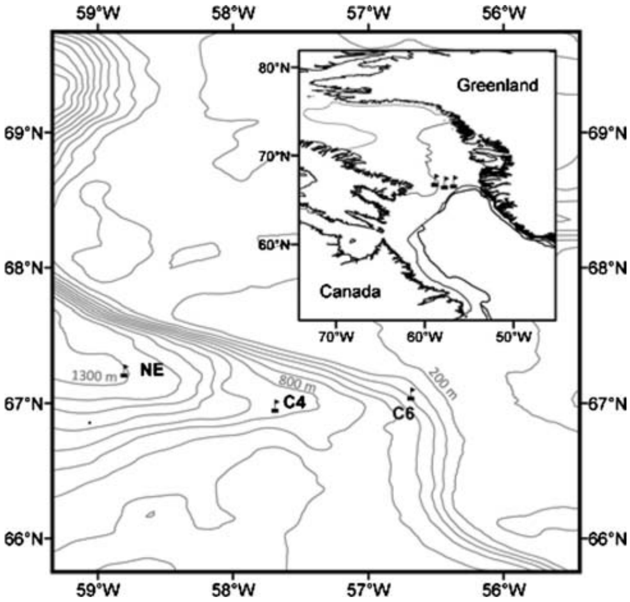


FIG. 1. Locations of the three instruments deployed at 300 m depth in the Davis Strait. The monthly extension of the sea ice edge from November 2006 to March 2007 is shown as lines in the inset map.

Very little is known about how fin whales use Arctic high latitude habitats from October to May and specifically if and why they migrate south. Using continuous passive acoustic monitoring in the Davis Strait from October 2006 to September 2008 we set out to investigate the temporal and spatial patterns of fin whale singing and address implications for fin whale migration, feeding and mating behavior. Here we use patterns in the power of fin whale frequency bands to address questions about how fin whale presence may be influenced by sea ice conditions, and we present the first measurements of fin whale song from the Davis Strait and estimate the difference in the active space of HF and the LF song components. The analysis of long term recordings in a very hostile environment show that singing fin whales are present in the Davis Strait in large numbers until the end of December demonstrating that at least part of the population does not move south in the early fall as expected. Rather they stay in the Davis Strait to use this Arctic habitat as a feeding and/or mating ground even when the dark winter has arrived, and they do not seem to start migrating before the sea ice forms from the north.

II. METHODS

Continuous acoustic recordings were made in the Davis Strait with three autonomous recording devices (HARU-Phone III) from 23 October 2006 to 5 October 2007 (Fig. 1). One of them (C6) was redeployed until 4 September 2008. There was a distance of 45–85 km between the instrument moorings. Each recorder consists of a 16 bit analog to digital converter stored in a 6.5 in. pressure housing (Fox *et al.*, 2001). They were all deployed at 300 m depth as part of a moored oceanographic array in areas with seafloor depths of 400 m (C6), 870 m (C4) and 1300 m (NE) (Fig. 1). All three instruments had a recording sensitivity of −160 dB re 1 V/μPa. They sampled continuously at 2000 Hz with band pass filtering between 0.1 and 970 Hz. The recordings were saved in 6-h *.dat files and time-marked with an internal clock. Files were converted from the stored big-endian 16 bit binary data to standard *.wav files in Matlab 7.5 (*MathWorks*) for further analysis.

A. Calibration

On-mooring RAFOS sound sources (40 s 5 Hz up-sweep between 777.5 Hz and 782.5 Hz) produced on and received by the NE and C4 moorings were used for calibration. The mean relative received level of sync pulses from mooring NE and recorded on instrument C4 was −52.8 dB re clipping (rms) (sd=2.5) and the mean received level of sweeps played by mooring C4 and recorded by instrument NE was −56.4 dB re clipping (rms) (sd=2.3).

B. Acoustic analysis of individual calls

Fin whale song in the Davis Strait consists of two elements. A frequency down-sweep centered around 20 Hz (LF) and a higher frequency pulse centered near 130 Hz (HF) [Fig. 2(A)]. From recordings on instrument C6, we selected calls with a signal to noise ratio of >10 dB, and clear HF and LF pulses for further analysis. We measured the interpulse-interval (IPI), peak frequency (fp), −10 dB bandwidth (−10 BW) and frequency centroid (fc, defined as the frequency dividing the spectra in two halves of equal energy) of the two call components. The recordings were down sampled with a factor 5 and the analysis was done with bin widths of 0.8 Hz for the HF component (FFT=512) and bin width 0.4 Hz for the LF component (FFT=1024). To estimate the difference in detection range between the HF and LF pulse, the energy flux density levels were computed for both pulses within the same call after band pass filtering (LF: 15–35 Hz and HF: 110–160 Hz with a 2-pole Butterworth filter) in Matlab.

C. Fin whale call detection

The fin whale "20-Hz" call is a commonly recorded animal sound in the North Atlantic (Clark, 1995) and during some months of the year it is so abundant that the calls form a continuous band around 20 Hz in spectrogram displays [Fig. 2(B)], rendering automatic kernel detections futile. Following Širović *et al.* (2004, 2009), we therefore quantified fin whale calls as the power in the frequency band around the fin whale calls relative to surrounding noise bands. Širović *et al.* (2009) made a power analysis on the HF pulse components in the fin whale calls. The LF down-sweep has a fairly constant frequency signature across different geographical areas but the frequency of the HF element clearly varies (Širović *et al.*, 2009). Also, the HF component was often not detectable in our recordings. We therefore opted for a power analysis on the primary pulse, using a frequency band that covered the LF pulse (F_{fin}, 19–28 Hz). To ensure that the power contribution of fin whale calls was measured and not background noise in the F_{fin} frequency band, the summed powers in surrounding frequency bands of 13–17 Hz and 33–37 Hz were also computed, assuming white noise characteristics of the ambient noise from 13 to 37 kHz. The fin whale call power was subsequently computed as the power level of the fin whale frequency band in 1 s blocks with a 50% overlap (Hann window). The noise power and fin whale signal power was referenced to the grand average of the noise frequency band power (F_{noise}). We chose not to reference the instantaneous F_{fin} to the instantaneous F_{noise}, because it would then not have been possible to discern for instance if an increase in the F_{fin} power relative to F_{noise} power ratio was caused by a decrease in the F_{noise} power or an increase in F_{fin} power. To aid interpretation the power in both the F_{fin} and the F_{noise} frequency bands are displayed in the figures.

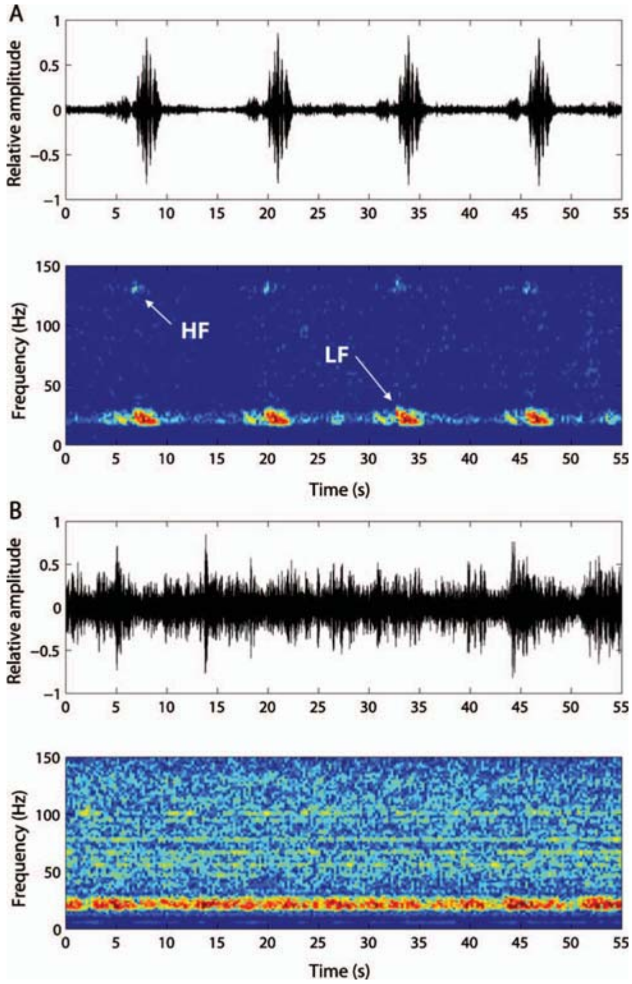


FIG. 2. (A) Time series and spectrogram of fin whale song with clearly separated calls consisting of high frequency (HF) and low frequency (LF) components. The pulses are recorded on top of a band of fin whale songs in the background. (B) Example of a band of LF fin whale signals too closely spaced in time to identify single pulses. FFT size: 2048, 50% overlap, window: 512.

D. Sea ice

The daily minimum distance from the mooring position to the sea ice edge was obtained from the National Ice Center, NOAA (http://www.natice.noaa.gov). In order to compare the ice data to the calling activity of the fin whales, we first averaged the acoustic power data to a per-day level and then determined the centralized rms-bandwidth of this reduced data set. The critical sampling period, which is the reciprocal of twice the bandwidth of the time series, was determined to be 5 days. Sea ice data F_{fin} power and F_{noise} power were all averaged into 5 day bins. Using this information, binary data sets were then generated of "fin whales present" and "sea ice present" time bins. A "fin whale present" period was defined as one where F_{fin} power exceeded F_{noise} power in the same time bin. The "sea ice present" data was set to one when the sea ice edge was south of the mooring. When the sea ice edge was north of the mooring position, the sea ice data was set to zero. We then tested the probability of observing the counted number (or less) of coincidences between sea ice and fin whale bins, using a binominal distribution. Also a Pearson's coefficient of correlation was calculated between distance to the sea ice edge and power in the fin whale frequency band and noise frequency band, respectively (all data sampled in bins of 5 days). As it might well have been the same whale recorded on several recorders we only tested the recording made on mooring C6 where we had data for both 2006 and 2007.

E. Diel variation

To visualize the daily pattern in fin whale calls, the summed power for both frequency bands, F_{fin} and F_{noise}, within 30-min time bins were arranged into a matrix, so that each column represented a single day and each row the individual half hours of the day. The matrices were then displayed as an image with signal power color-coded for comparison with the data for sunrise and sunset for the period in question. The time of sunrise and sunset at the mooring positions were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil/index.php).

The bandwidth of the F_{fin} power data averaged into half-hour bins was determined, and the critical period was in this case determined to be 6 h. However, to have a bin centered on noon, an odd number is called for, and we therefore used three 8-h bins instead. The average F_{fin} power per hour bin was calculated for the peak calling period, 12 November—22 December. A Jarque-Bera two-sided goodness-of-fit test was used to test the hypothesis that the data were not normally distributed, and in one case H_0 was accepted ($P<0.05$) for the F_{noise} band, therefore a nonparametric analysis of medians was adopted for all data sets. A two-tailed Mann-Whitney U-test on the power data (expressed in dB) was used to test the null-hypothesis that the intensity of the F_{fin} frequency band was the same during the light (bin 2) and dark periods (bin 1 combined with bin 3) of the day. For each station, two control data sets were also created for a similar period delayed by 80 days. These control data sets were treated the same way as the sets recorded during the peak period of intense singing. As the same whale calls might have been recorded on several recorders we only tested the recording made on mooring C6, which had the most powerful F_{fin} signal.

III. RESULTS

A. Fin whale call parameters

Frequency characteristics were measured on a total of 539 fin whale calls recorded in the Davis Strait in ten different days between 23 October and 17 November 2006. The LF pulse of the calls (Fig. 3) consists of a 1 s long downsweep, with a frequency centroid of 22.1 ± 0.63 Hz (mean ± std), peak frequency of 21.6 ± 1.38 Hz and a -10 dB bandwidth of 6.5 ± 1.28 Hz. The HF component (Fig. 3) consists of a ca. 0.3 s pulse with a frequency centroid of 131.9 ± 1.15 Hz, peak frequency of 132.2 ± 1.38 Hz and a -10 dB bandwidth of 14.8 ± 13.70 Hz. The mean interpulse interval (IPI) was 13.5 ± 2.44 s. There was a large (24.5 ± 2.60 dB) difference in the received energy flux density level between the HF and LF pulses within the same call, with the LF pulse having some 280 times more energy on average.

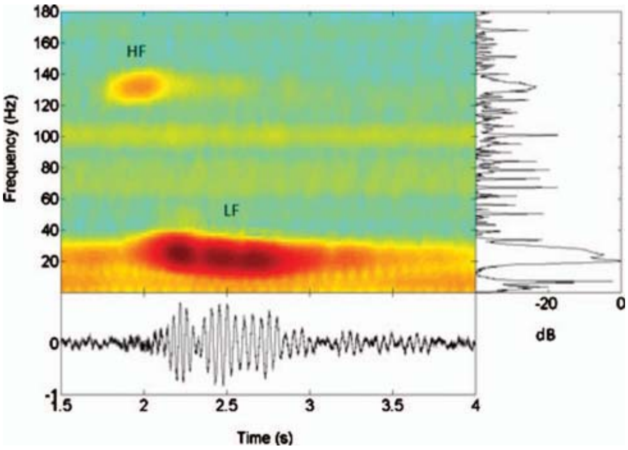


FIG. 3. Spectrogram, waveform and power spectrum of the time aligned average of 50 typical fin whale calls, showing the low frequency downsweep (LF) and the secondary, lower amplitude high frequency pulse (HF). FFT size: 1024, 94% overlap, Hann window.

B. Call detections in Davis Strait

Fin whale calls were detected from June to January, but there was a clear seasonal peak in the frequency band of fin whale calls from November to the end of December [Figs. 4(A)–4(D)]. The F_{fin} peak was especially strong at instrument C6 [Fig. 4(A)], where it formed a peak rising more than 15 dB above the average ambient noise level (F_{noise}) during both years of monitoring. The seasonal peak was also clear at C4, though 5 dB lower than C6 [Fig. 4(B)]. Instruments C4 and C6 were deployed at similar latitudes, but C4 was 45 km further west in water that was 869 m deep (v. 390 m for C6). The seasonal peak in the power of the fin whale song frequency band was present, but weak on instrument NE [Fig. 4(C)]. Instrument NE was deployed about 85 km further north (water depth 1267 m) than C6 and C4 (Fig. 1).

C. Sea ice

The fin whale power peaks in November–December followed by an abrupt decline in December just as the sea ice edge cover the mooring site in both years of the deployment [Fig. 5(A)]. The distance to sea ice edge and the occurrence of fin whale song had a 0.002% probability of not depending on one another (binominal distribution $P=0.00002$). There

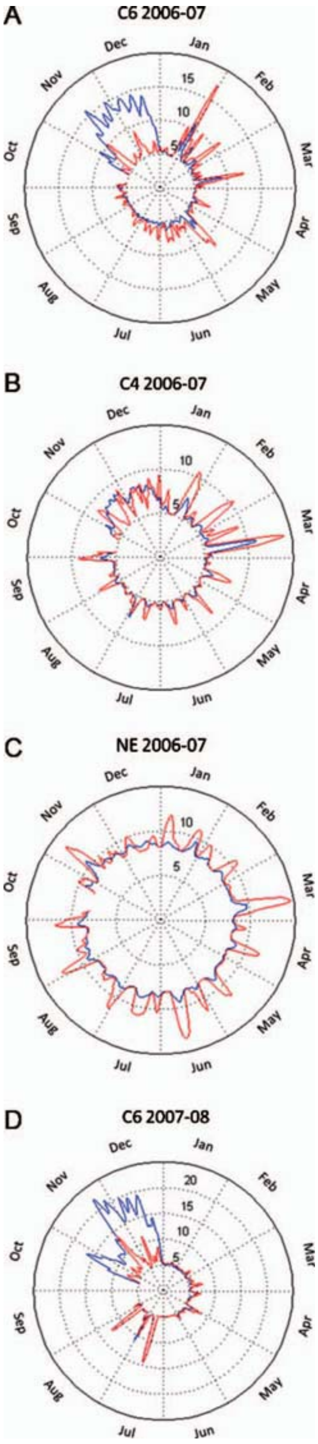


FIG. 4. Power analysis showing the seasonal output of the power in the fin whale frequency band, F_{fin} (blue) and the surrounding noise bands, F_{noise} (red). The power in both are bands expressed relative the yearly grand average of the background noise power.

was no significant correlation between the power in the noise frequency band and the distance to ice edge (Pearson's coefficient of correlation, N=124, P>0.4) indicating that the correlation between sea ice and fin whale song is not an artifact from noise correlating with formation or advance of sea ice [Figs. 5(A) and 5(B)].

D. Diel variation

During the peak singing period from November to December, all instruments showed a diel pattern in the F_{fin} power [Figs. 6(A)–6(D), upper panel]. At the onset of the song period (early November) the whales started singing at about 1400 (all times in local time calculated at the position of each recorder). They continued singing all night and stopped at about 0700 (Fig. 6). A similar pattern was observed throughout the peak singing period, with singing starting progressively earlier and ending later. By the end of the singing period, the singing started at about 1200 and stopped at about 0800.

The diel pattern to the fin whale singing activity in the period 12 November—22 December on mooring C6 in 2006 was significant (Mann-Whitney U-test, P<1e-9). The same was true for C6 in 2007 (Mann-Whitney U-test, P<0.001) and for mooring C4 (Mann-Whitney U-test, P<0.0001), but not for NE (Mann-Whitney U-test, P>0.3) where the F_{fin} signal was by far the weakest (Figs. 5 and 6). However, the diel pattern was still visually discernible in the recordings of NE [Fig. 6(C)]. In no cases did we see a lower F_{noise} acoustic power in bin 2 (noon) compared with bin 1 and bin 3 combined. The reduced F_{fin} energy during the hours surrounding noon, is not a pause, but merely a reduction in calling activity: the difference in median is only around 3 dB when it is most pronounced in location C6 in 2006.

The power of the F_{noise} did not show a similar diel pattern, confirming that the diel pattern observed in F_{fin} was not an artifact from ambient noise fluctuations [Figs. 6(A)–6(D), lower panels]. The oblique high-intensity lines seen in all these plots are most likely due to broadband low frequency strumming noise from tidal movements around the moorings [Figs. 6(A)–6(D), low panels].

IV. DISCUSSION

A. Spectral signatures of fin whale calls in the Davis Strait

We recorded very large numbers of LF pulses in the Davis Strait with spectral properties similar to those described from other areas (Thomson and Richardson, 1995; Širović *et al.*, 2004). The HF component of fin whales in the Davis Strait had a much higher frequency (131 Hz) compared to those reported from Antarctica (89 and 99 Hz). It is unknown if the production and pitch of the HF component in fin whale song are under control of the singing animal or if they are an anatomically induced by-product from making the 20 Hz pulse. Larger animals generally produce sound at lower frequencies compared to smaller animals (Fletcher, 2004). However, the mean size difference of ~2 m (some 10%) between southern and northern hemisphere fin whales (Brodie, 1975) is unlikely to generate the more than 30% increase in frequency observed in the Davis Strait fin whales. Rather, the difference in frequency of the HF pulse supports the notion put forward by Širović *et al.* (2009), that different populations of fin whales have different HF song components. If so, the center frequency of the secondary peak might be an acoustic indicator of fin whale population structures, and possibly serve a communicative function along

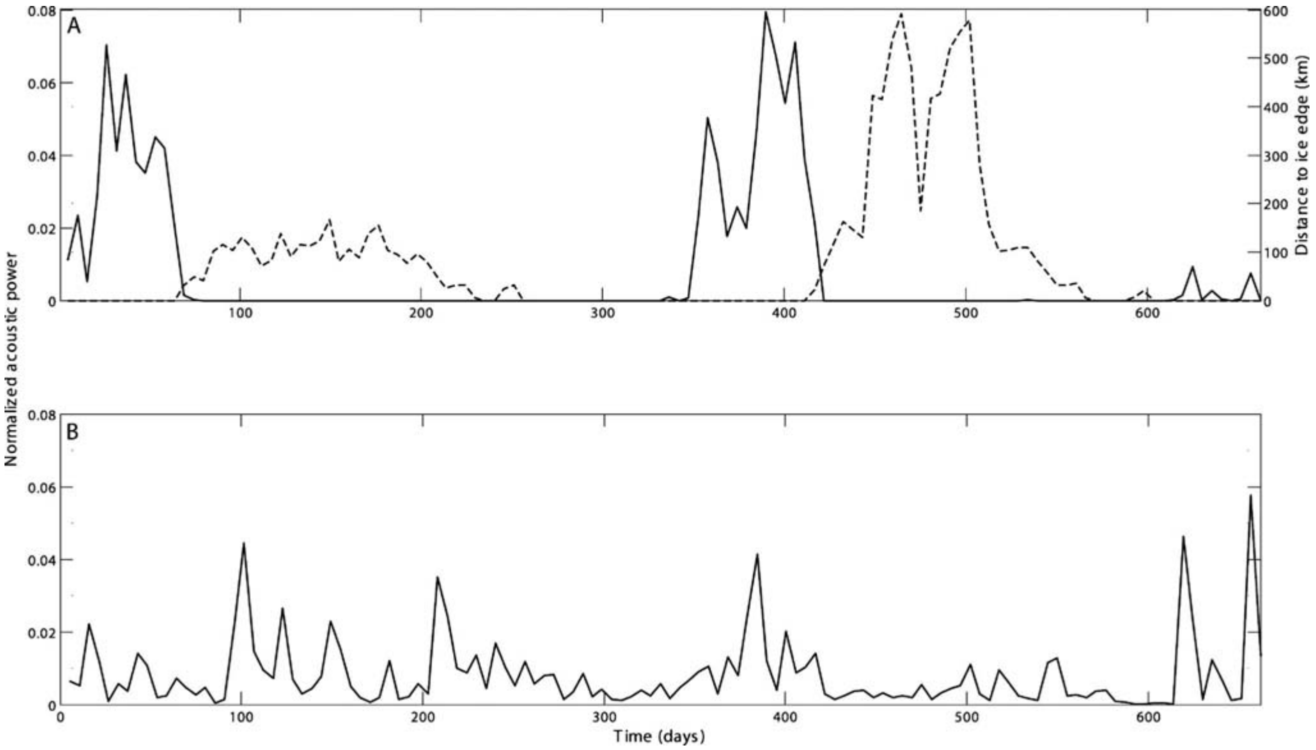


FIG. 5. Dynamics of normalized power in the fin whale (upper panel) and noise (lower panel) frequency bands and the distance to the ice edge (upper panel, broken lines) when the sea ice edge has covered the mooring. The distance was set to zero when the sea ice edge was north of the mooring. All data was computed as the mean of 5 days.

with the primary LF component at 20 Hz. For the same reason, it is not optimal to rely solely on detecting this HF pulse when analyzing data for occurrence of fin whales because of the high risk of missing calls with a changing frequency in the secondary peak on a spatial scale. This concern is accentuated by the fact that we did not always detect the HF component in our recordings, increasing the risk of missing detections.

This raises the question of why the high frequency pulse is not always detected along with the primary pulse at 20 Hz? First, it may simply be that the HF component can be turned on and off by the singing animals. However, if it indeed is a fixed part of the singing, it may relate to differences in source properties and propagation of the two pulses. Given the 6 times shorter wavelength, it may be envisioned that the HF pulse is more directional and thus only recorded when the whale is pointing in the direction of the recorders. Still with a wavelength (11 m) about half the size of the whale that produces it, the signal directionality is expected to be low for the HF component, and with whales in random orientation with respect to the recorders there should at least be a weak spectral band during the months with high peak fin whale detection. Given this, the explanation for the sometimes missing HF component is likely to be explained by differences in the active space of the two song elements; the energy flux density of the HF pulse was about 25 dB lower than the LF pulse within the same call.

Taking the difference in ambient noise at 20 Hz and 130 Hz (Wenz, 1962) into account the noise level is 17 dB higher around the LF pulse (20 Hz) compared to the HF pulse (130 Hz). Assuming spherical spreading, the LF pulse can therefore be detected minimum 3 times further compared to the HF pulse, resulting in a noise limited monitoring area ~9 times smaller, when using only the HF pulse for detection, compared to the LF pulse. We did not take the differences in frequency dependent absorption into account in these estimates, as it is negligible at these low frequencies. If it had been included it would in any case make the detection range of the HF pulse relatively lower (Urick, 1983).

The differential active spaces mean that the song consists of two elements providing different cues when listening for conspecifics. A fin whale closely surrounded by singing individuals will be challenged in extracting directional cues from the LF pulse. That implies that this call component may be used for long-range communication, as suggested by Payne and Webb (1971). The larger active space of the LF pulse will let other whales detect one or more singing males at long ranges depending on ambient noise levels and propagation conditions. When whales close in on the singers, they will start detecting the HF pulses that via a shorter wavelength may be better for telling the direction to individuals, while possibly gaining information on the population identity from the pitch of the HF component.

The interpulse-interval (IPI) distributions of fin whale pulses differ between fin whale stocks and may as such serve as an alternative identification cue for fin whales (Delarue *et al.*, 2009). However, there seems to be a large disadvantage in using a temporal cue for transmitting information in a species often singing in large aggregations, such as the fin whale. As soon as more than a single animal is singing it will

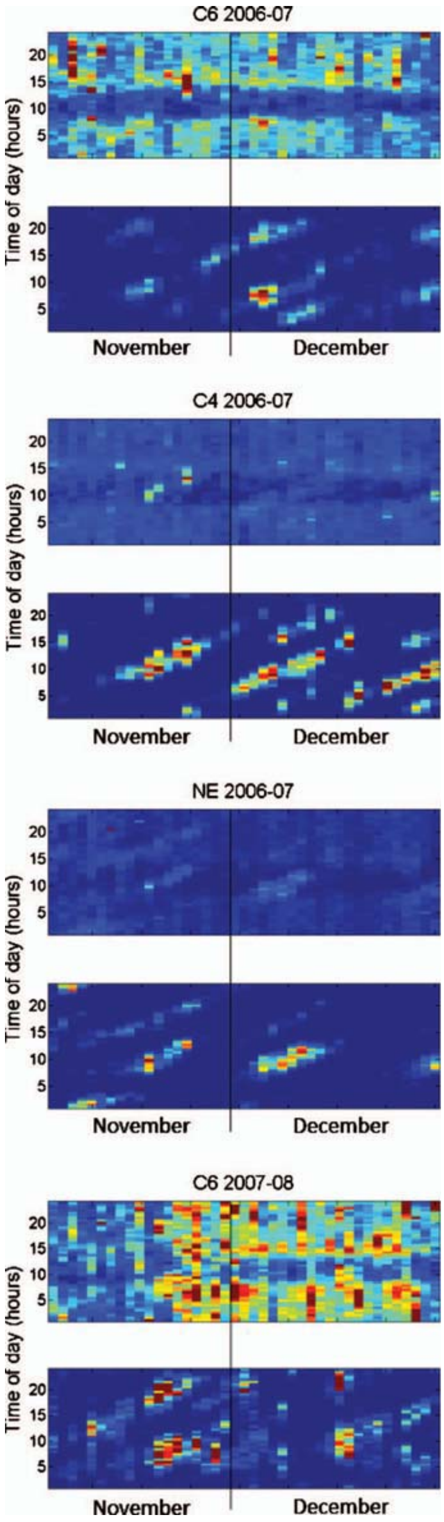


FIG. 6. Diel variation in the power of the F_{fin} (upper panel) and F_{noise} frequency band (lower panel). The x-axis shows the days from 12 November to 22 December. The y-axis shows the time of the day in hours. The image displays show the relative intensity in the frequency bands with increasing intensities illustrated by blue to red color scale. There is a clear diel pattern with the whales singing most of the day with a clear decrease in singing activity a few hours in the middle of the day.

be hard to extract the IPI information and in the peak singing season the IPI would be impossible to extract from the choir of singing whales [Fig. 2(B)]. If the peak singing is connected to mating aggregations, a time where population identity should be important, it seems that the information on population identity in fin whales is better transmitted as a frequency cue perhaps in the form of the HF pulse of the song.

B. Detection ranges of fin whale calls

There were similar power levels of the F_{noise} signal on all three instruments but large differences in the received power levels of the F_{fin} relative to F_{noise} (Fig. 4). The northernmost deployed instrument, NE, had a very weak fin whale signature. Compared to instrument NE the signal was much stronger on instrument C4, and instrument C6 had the strongest signal with the same relative level in the second year of deployment [Figs. 4(A)–4(D)]. The back and forth calibration of the RAFOS signals confirmed that, assuming spherical spreading, the sensitivities of the recorders were similar ($< \pm 3$ dB). Therefore, the large differences in fin whale detections between recorders deployed only 85 km apart likely reflect that more whales were singing closer to the southeastern-most buoy (C6) south of the sea ice edge.

It is reasonable to assume that the detection of 20 Hz pulses both on our recorders and by fin whales are limited by background noise. Therefore the detection range of the recorders also provides a cue to how far fin whales might detect other fin whales. Payne and Webb (1971) estimated that if fin whale song suffered from spherical spreading and the ambient noise was moderate, fin whales should have a detection range of roughly 90 km. The maximum distance for using multiple path propagation of fin whale calls off the western Antarctic Peninsula was modeled to be 56 km while estimated detection ranges of fin whale calls in the Gulf of Alaska varied with ambient noise levels from 10 km–100 km (Širović *et al.*, 2007; Stafford *et al.*, 2007). Here we found that the summed power of fin whale calls was strong on the southeastern instrument (C6) but almost non-detectable on instrument NE, approximately 85 km away. So while the calling fin whales are not necessarily right next to the southernmost mooring (C6), the large drop in summed power in the fin whale call band show that the calling whales must have been much closer to that instrument than to the NE instrument and that their detection range in the physical environment of the Davis Strait in November–December was unlikely to extend much further than 85 km (the distance between the two recorders).

C. Implications for passive acoustic monitoring

The difference in detection range of the two call components is an important point to consider in the light of ambient noise profiles when choosing which part of the song to use for fin whale detections. Knowledge of the range over which a monitoring instrument can detect a sound in question, makes it easier to design a study in accordance with the research questions posed. For instance, if the detection range of fin whale LF calls is about 100 km, monitoring instruments deployed with less than 200 km distance, will result in areas with overlapping coverage from several instruments, potentially allowing for acoustic tracking and localization of singing individuals. On the other hand if instruments are deployed with more than twice the distance of the detection range, areas will be left unmonitored. Under these conditions, however, it is then certain that animals recorded on one instrument are different individuals from those recorded at the same time on another instrument, leading to minimum estimates of the number of singing whales.

D. Seasonality in fin whale presence in the Davis Strait

It has been assumed that the majority of fin whales migrate south in the fall to warmer waters to mate and breed during winter (e.g., Norris, 1967; Heide-Jørgensen *et al.*, 2008). Sighting surveys and catch statistics have shown that fin whales are numerous in West Greenland from July to October (Heide-Jørgensen *et al.*, 2008; Simon *et al.*, 2007). Ten aerial cetacean surveys were conducted in the Davis Strait in March–April 1981–2008 (Heide-Jørgensen *et al.*, 1993; Koski and Davis, 1994; Heide-Jørgensen and Reeves, 1996; Heide-Jørgensen and Acquarone, 2002; Heide-Jørgensen *et al.*, 2007). None of these surveys had sightings of fin whales, making it unlikely that fin whales were present in the Davis Strait in March–April in the years of the surveys. However, the apparent seasonality inferred from catches and surveys is heavily biased by weather, daylight and sea ice conditions. There is a lack of information on the presence or absence of whales during winter. Except for a single satellite tracked fin whale, that stayed in West Greenland until 20 December, when the tag stopped transmitting (Heide-Jørgensen *et al.*, 2003), we have almost no information on fin whale presence in the Davis Strait from October to February. Here we used acoustics to document the presence of fin whales during these months. As in all PAM studies, a lack of acoustic detections does not necessarily mean that no whales are present, only that they are not singing. We recorded sporadic fin whale calls from June to October; few acoustic detections during a period when fin whales are known to be abundant from catch reports and visual surveys (e.g., Heide-Jørgensen *et al.*, 2008). On the other hand, we also detected a very strong peak in singing activity in November and December, when sighting effort is low or absent. The intense singing activity with overlapping continuous bands of fin whale calls is strong evidence that a large number of singing fin whales are present in the Davis Strait in November and December. This changes the view on fin whale seasonal migratory patterns by showing that at least part of the population does not migrate south in the fall, but rather stay at least until the end of December. This in turn raises the questions of 1) What are they doing until the early winter in the Davis Strait?, 2) When do the fin whales start migration and 3) Which factors drive them to migrate? As for the first question, there are two likely answers: feeding and mating. Here we use the call patterns to test for the hypotheses proposing fin whale feeding and mating in the Davis Strait from October to December.

E. Fin whales and sea ice

Širović *et al.* (2004) reported a negative correlation between the occurrence of fin whale calls and sea ice cover in the Antarctic, implying that fin whales migrate when the sea ice forms. Our data corroborates this finding. Starting in November the sea ice expands in the Davis Strait from the northeast, and all three instruments were covered with sea ice from December 2006 to June 2007 (Fig. 1). The weak fin whale signal on instrument NE compared to instrument C6 (Fig. 4) suggests that the singing whales were closer to instrument C6, south of the sea ice edge during the peak singing period, indicating that sea ice dictates the northern limit of the distribution of singing fin whales in the Davis Strait during winter. Second, we observed that the short period of intense singing activity ended abruptly by the end of December (Fig. 5). That, in combination with the differences in song power on the buoys described above, suggests that the advance of sea ice may possibly affect the fin whales in different ways: i. fin whales stay in the area, despite increasing sea ice cover, but discontinue singing when the sea ice forms. ii. The advancing sea ice triggers fin whales to end their singing and migrate south to lower latitudes or iii. The fin whales continue singing but move further south just ahead of the expanding sea ice. Scenarios i or ii would imply that a certain sea ice distribution threshold exists for fin whale singing and/or migration and that this threshold was reached in 2006 just as the sea ice covered mooring C6. Therefore, if such a threshold exists, we were fortunate enough to deploy the mooring just at the threshold latitude. This seems unlikely, and the third scenario whereby fin whales continue to sing, but move further south when the sea ice moves in from the north, seems to be the most parsimonious explanation. Thus, both Antarctic and Davis Strait fin whale calling activity is strongly negatively correlated with the expansion of sea ice (Širović *et al.*, 2009), suggesting that similar circumstances exist for singing fin whales near the two poles: sea ice limits their distribution toward higher latitudes and changing sea ice may therefore lead to changes in distribution of singing fin whales. Whether this is due to the physical presence of sea ice that impedes normal breathing and surface swimming or if it relates to secondary oceanographic effects on prey availability remains to be tested. Regardless, it seems that changes in sea ice cover related to climate changes are likely to affect fin whale distribution in Davis Strait during winter with the potential to cause overall changes in how these large predators exploit Arctic waters for mating, breeding and feeding in a warmer less icy future.

F. Mating in the cold?

Fin whale calls are usually recorded year round in different areas of the world's oceans, but with a clear seasonal peak in the singing activity, lasting for about four months (Thomson and Richardson, 1995; Stafford *et al.*, 2007; Watkins *et al.*, 1987; Thompson *et al.*, 1992; Moore *et al.*, 1998). The annual peak in fin whale singing coincides with the estimated conception time, suggesting that the song is part of a mating display, possibly to attract mates (Watkins *et al.*, 1987; Moore *et al.*, 1998; Croll *et al.*, 2002; Payne and Webb, 1971). This contention is supported by genetic evidence that all singing fin whales, that have been sexed, were males (Croll *et al.*, 2002). The peak singing period in the Davis Strait in November and December is unusually short compared to fin whales recorded in other areas, including further south in the North Atlantic and Pacific (Watkins *et al.*, 1987; Stafford *et al.*, 2007). The peak conception time in the North Atlantic centers on January (Lockyer, 1984). From the contemporaneous occurrence of the intense fin whale singing and the conception time we infer that at least part of the population of the Davis Strait fin whales may likely mate while still at high latitudes. The bimodal pattern of feeding at high latitudes and breeding/mating at low latitudes is too simplistic to fully account for fin whale ecology and migration patterns.

G. Feeding and singing in the Arctic winter

Several studies have shown that baleen whales have diel variations in their song behavior, with blue and fin whales singing in the dark period of the day from dusk to dawn, suggesting a causal link between song activity and the absence of sunlight (Stafford *et al.*, 2005; Watkins *et al.*, 1987). Fin and blue whales are lunge feeders, ingesting large volumes of prey filled water (Croll *et al.*, 2001; Goldbogen *et al.*, 2006; Pivorunas, 1979). This feeding strategy is most efficient if the prey occur in dense aggregations (Croll and Tershy, 2002). Most baleen whale prey perform daily vertical migrations up and down the water column controlled by the light intensity, appearing in dense aggregations at depth during the day to reduce predation and dispersed in the water column during night when sunlight is gone. Stafford *et al.* (2005) suggested that the higher call rates in blue whales during night/dusk were associated with the vertical migration of the prey. The blue whales fed during day when krill densities were highest and then sang during night when krill were dispersed in the whole water column and perhaps not in great enough concentrations for cost-efficient feeding (Stafford *et al.*, 2005). Sei whales (*Balaenoptera borealis*) are, contrary to fin and blue whales, most vocally active during daytime (Baumgartner and Fratantoni, 2008). This difference among three large closely related rorquals has been explained by the differences in prey choice and feeding behavior. Where the lunge feeding fin and blue whales might benefit from feeding at depth during daylight, when krill swarms are concentrated at depth, sei whales were reported to skim feed on copepods near the surface at night (Baumgartner and Fratantoni, 2008). Despite these differences, the singing activity of all three rorquals seems linked to the light intensity (whether positively or negatively), through the light-induced vertical migration and dispersion of prey.

In the present study, there was a significant diel pattern in the fin whale song activity in November and December with fin whales singing continuously from early afternoon until early morning (Fig. 6). Diel variation in calling activities of rorquals has previously only been reported from temperate and tropical areas (Baumgartner and Fratantoni, 2008; Stafford *et al.*, 2005; Watkins *et al.*, 1987; Wiggins *et al.*, 2005). Here we show that even in the dark Arctic winter with minimal hours of daylight, the calling activity follows the dark period of the day. This provides strong circumstantial evidence that the calling activity is light-induced either directly or through the migratory behavior of the prey.

The clear diel signature in the fin whale singing activity, however, does not directly justify the conclusion that there is a causal correlation between the prey migration and fin whale feeding behavior. A recent study showed that Arctic zooplankton continues the light-induced vertical migration through the polar night (Berge *et al.*, 2009). Fin whales prey on krill that follow the vertical migration of their planktonic prey (Sourisseau *et al.*, 2008). As the song activity follows the same pattern as the vertical migrations performed by fin whale prey it is conceivable that the reduction in fin whale singing during the daylight was due to whales feeding on dense prey patches at depth. If such a relationship exists, it would imply that fin whales that stay in the Arctic during early winter are feeding during the short daylight hours, which contrasts the paradigm that balaenopterids only feed during summer.

V. CONCLUSIONS

We have demonstrated that fin whales are acoustically active and hence present in the Davis Strait from June to December, much later in the year than previously thought. The contemporaneous peaks in song activity and estimated conception time suggest that not all fin whales migrate south to mate, but rather stay at high latitudes perhaps to exploit food niches that are not available at lower latitudes while mating. The latter notion is supported by the fact that the singing activity of fin whales in the Davis Strait is strongly linked to daylight hours, and could be controlled possibly by the vertical migratory behavior of their prey. This suggests that fin whales might feed during the few daylight hours of the late fall and early Arctic winter. The difference in magnitude of fin whale signal detections among the three recorders shows that the distribution of fin whales in the Davis Strait may in part be controlled by the advance of the sea ice edge during winter. Further, we observed a negative correlation between fin whale song and sea ice whereby the song stopped when the sea ice covered the mooring. Consequently, changing sea ice conditions may change the winter distribution of singing fin whales in the future and such changes may be monitored successfully by using PAM.

ACKNOWLEDGMENTS

We thank the captain and crew of the R/V KNORR and the mooring team for their skilled support. F. Ugarte and two anonymous reviewers provided valuable comments on previous versions of the manuscript. The project was funded by the Oticon Foundation (Denmark) and the U.S. National Science Foundation OPP Award No. 0532611.

Alerstam, T., Hedenström, A., and Åkesson, S. (**2003**). "Long-distance migration: Evolution and determinants," Oikos **103**, 247–260.

Bannister, J., Pastene, L. A., and Burnell, S. R. (**1999**). "First record of movement of a southern right whale (*Eubalaena australis*) between warm water breeding grounds and the Antarctic Ocean, South of 60 °S," Marine Mammal Sci. **15**, 1337–1342.

Baumgartner, M. F., and Fratantoni, D. M. (**2008**). "Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders," Limnol. Oceanogr. **53**, 2197–2209.

Berge, J., Cottier, F., Last, K. S., Varpe, Ø., Leu, E., Søreide, J., Eiane, K., Falk-Petersen, S., Willis, K., Nygård, H., Vogedes, D., Griffiths, D., Johnsen, G., Lorentzen, D., and Brierley, A. S. (**2009**). "Diel vertical migration of Arctic zooplankton during the polar night," Biology Letters B **5**, 69–72.

Brodie, P. F. (**1975**). "Cetacean energetics, an overview of intraspecific size variation," Ecology **56**, 152–161.

Charif, R. A., Mellinger, D. K., Dunsmorre, K. J., Fristrup, K. M., and Clark, C. W. (**2002**). "Estimated source levels of fin whale (*Balaenoptera physalus*) vocalizations: Adjustments for surface interference," Marine Mammal Sci. **18**, 81–98.

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

Clark, C. W. (**1995**). "Application of US Navy underwater hydrophone arrays for scientific research on whales," Rep. Int. Whal. Comm. **45**, 210–212.

Clark, C. W., Borsani, J. F., and Notarbartolo-Di-sciara, G. (**2002**). "Vocal activity of fin whales, *Balaenoptera physalus*, in the Ligurian Sea," Marine Mammal Sci. **18**, 286–295.

Croll, D. A., Acevedo-Gutiérrez, A., Tershy, B. R., and Urbán-Ramírez, J. (**2001**). "The diving behavior of blue and fin whales: Is dive duration shorter than expected based on oxygen stores?," Comp. Biochem. Physiol., Part A: Mol. Integr. Physiol. **129**, 797–809.

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

Croll, D. A., and Tershy, B. (**2002**). "Filter feeding," in *Encyclopedia of Marine Mammals*, edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen (Academic, London), pp. 428–432.

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

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

Fox, C. G., Matsumoto, H., and Lau, T. K. (**2001**). "Monitoring Pacific Ocean seismicity from an autonomous hydrophone array," J. Geophys. Res. **106**, 4183–4206.

Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A., and Hildebrand, J. A. (**2006**). "Kinematics of foraging dives and lunge-feeding in fin whales," J. Exp. Biol. **209**, 1231–1244.

Heide-Jørgensen, M. P., and Acquarone, M. (**2002**). "Size and trends of the bowhead whale, beluga and narwhal stocks wintering off West Greenland," in *Belugas in the North Atlantic and the Russian Arctic*, edited by M. P. Heide-Jørgensen and Ø. Wiig (Scientific Committee-North Atlantic Marine Mammal Commission-NAMMCO Scientific Publications, Tromsø, Norway), Vol. **4**. pp. 191–210.

Heide-Jørgensen, M. P., Borchers, D. L., Witting, L., Laidre, K. L., Simon, M. J., Rosing-Asvid, A., and Pike, D. G. (**2008**). "Estimates of large whale abundance in West Greenland waters from an aerial survey in 2005," J. Cetacean Res. Manage. **10**, 119–129.

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., Lassen, H., Teilmann, J., and Davis, R. A. (**1993**). "An index of the relative abundance of wintering belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, off West Greenland," Can. J. Fish. Aquat. Sci. **50**, 2323–2335.

Heide-Jørgensen, M. P., and Reeves, R. R. (**1996**). "Evidence of a decline in beluga, *Delphinapterus leucas*, abundance off West Greenland," ICES J. Mar. Sci. **53**, 61–72.

Heide-Jørgensen, M. P., Witting, L., and Jensen, M. V. (**2003**). "Inshore-offshore movements of two fin whales (*Balaenoptera physalus*) tracked by satellite off West Greenland," J. Cetacean Res. Manage. **5**, 241–243.

Jakobsson, J., and Østvedt, O. J. (**1999**). "A review of joint investigations on the distribution of herring in the Norwegian and Icelandic seas 1950–1970," Rit Fiskideildar **16**, 209–238.

Kellogg, R. (**1929**). "What is known on the migrations of some of the whalebone whales?," Smithsonian Institution Annual Report No. 1928, Washington: U.S.G.P.O., pp. 467–494.

Kosky, W. R., and Davis, R. A. (**1994**). "Distribution and numbers of narwhals (*Monodon monoceros*) in Baffin Bay and Davis Strait," Medd. Gronl. Biosci. **39**, 15–40.

Kraus, S. B., Prescott, J. H., Knowlton, A. R., and Stone, G. S. (**1986**). "Migration and calving of right whales (*Eubalaena glacialis*) in the western North Atlantic," Rep. Int. Whal. Comm. **10**, 139–144.

Laidre, K. L., Heide-Jørgensen, M. P., Heagerty, P., Cossio, A., Bergstrom, B., and Simon, M. (**2010**). "Spatial associations between large baleen whales and their prey in West Greenland," Mar. Ecol.: Prog. Ser. **402**, 269–284.

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

Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P., and Matsumoto, H. (**2007**). "An overview of fixed passive acoustic observation methods for cetaceans," Oceanogr. **20**, 36–45.

Mizroch, S. A., Rice, D., Zwiefelhofer, D., Waite, J., and Perryman, W. (**2009**). "Distribution and movements of fin whales in the North Pacific Ocean," Mammal Rev. **39**, 193–227.

Moore, S. E., Stafford, K. M., Dahlheim, M. E., Fox, C. G., Braham, W., Polovina, J. J., and Bain, D. E. (**1998**). "Seasonal variation in reception of fin whale calls in five geographic areas in the North Pacific," Marine Mammal Sci. **14**, 617–627.

Moore, S. E., Stafford, K. M., Mellinger, D. K., and Hildebrand, J. A. (**2006**). "Listening for large whales in offshore waters of Alaska," BioScience **56**, 49–55.

Norris, K. (**1967**). "Some observations on the migration and orientation of marine mammals," in *Animal Orientation and Navigation*, edited by R. M. Storm (University of California Press, Berkeley), pp. 320–380.

Oleson, E. M., Wiggins, S. M., and Hildebrand, J. A. (**2007**). "Temporal separation of blue whale call types on a southern California feeding ground," Anim. Behav. **74**, 881–894.

Payne, R., and Webb, D. (**1971**). "Orientation by means of long range acoustic signaling in baleen whales," Ann. N.Y. Acad. Sci. **188**, 110–141.

Pike, G. C. (**1962**). "Migration and feeding of the gray whale (*Eschrichtius gibbosus*)," Bull. - Fish. Res. Board Can. **19**, 815–38.

Pivorunas, A. (**1979**). "The feeding mechanisms of baleen whales," Am. Sci. **67**, 432–440.

Salomonsen, F. (**1967**). "Migratory movements of the Arctic Tern (*Sterna paradisaea Pontoppidan*)," Det Kongelige Danske Videnskabernes Selskab Biologiske Meddelelser **24**, 1–42.

Simon, M., Kingsley, M., and Witting, L. (**2007**) "Seasonal and spatial distribution and sex ratio of fin whale catches off West Greenland, 1987–2006," in 59th Annual Meeting, Anchorage, Alaska.

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.

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., Part II **51**, 2327–2344.

Širović, A., Hildebrand, J. A., Wiggins, S. M., and Thiele, D. (**2009**). "Blue and fin whale acoustic presence around Antarctica during 2003 and 2004," Marine Mammal Sci. **25**, 125–136.

Sourisseau, M., Simard, Y., and Saucier, F. J. (**2008**). "Krill diel vertical migration fine dynamics, nocturnal overturns, and their roles for aggregation in stratified flows," Can. J. Fish. Aquat. Sci. **65**, 574–587.

Stafford, K. M., Mellinger, D. K., Moore, S. E., and Fox, C. G. (**2007**). "Seasonal variability and detection range modeling of baleen whale calls in the Gulf of Alaska, 1999–2002," J. Acoust. Soc. Am. **122**, 3378–3390.

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., Nieukirk, S. L., and Fox, C. G. (**1999**). "Low frequency whale sounds recorded on hydrophones moored in the eastern tropical Pacific," J. Acoust. Soc. Am. **106**, 3687–3698.

Strelkov, P. P. (**1969**). "Migratory and stationary bats (*Chiroptera*) of the European part of the Soviet Union," Acta Zoology. Cracoviensia **14**, 393–435.

Thompson, P. O., Findley, L. T., and Vidal, O. (**1992**). "20-Hz pulses and other vocalizations of fin whales, *Balaenoptera physalus*, in the Gulf of California, Mexico," J. Acoust. Soc. Am. **92**, 3051–3057.

Thomson, D. H., and Richardson, W. J. (**1995**). "Marine mammal sounds," in *Marine Mammals and Noise*, edited by W. J. Richardson, C. R. Greene, C. I. Malme, and D. H. Thomson (Academic, New York), pp. 159–204.

Urick, R. J. (**1983**). *Principles of Underwater Sound* (Peninsula, Los Altos).

Urquhart, F. A., and Urquhart, N. R. (**1977**). "Overwintering areas and migratory routes of the monarch butterfly (*Danaus p. plexippus*, lepidoptera: danaidae) in North America, with special reference to the western population," Can. Entomol. **109**, 1583–1589.

Watkins, W. A., Moore, K. E., Sigurjónsson, J., Wartzok, D., and Notarbartolo di Sciara, G. (**1984**). "Fin whale (*Balaenoptera physalus*) tracked by radio in the Irminger Sea," Rit Fiskideildar **8**, 1–14.

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

Wenz, G. M. (**1962**). "Acoustic ambient noise in the ocean: spectra and sources," J. Acoust. Soc. Am. **34**, 1936–1956.

Wiggins, S. M., Oleson, E. M., McDonald, M. A., and Hildebrand, J. A. (**2005**). "Blue whale (*Balaenoptera physalus*) diel call patterns offshore of Southern California," Aquat. Mamm. **31**, 161–168.