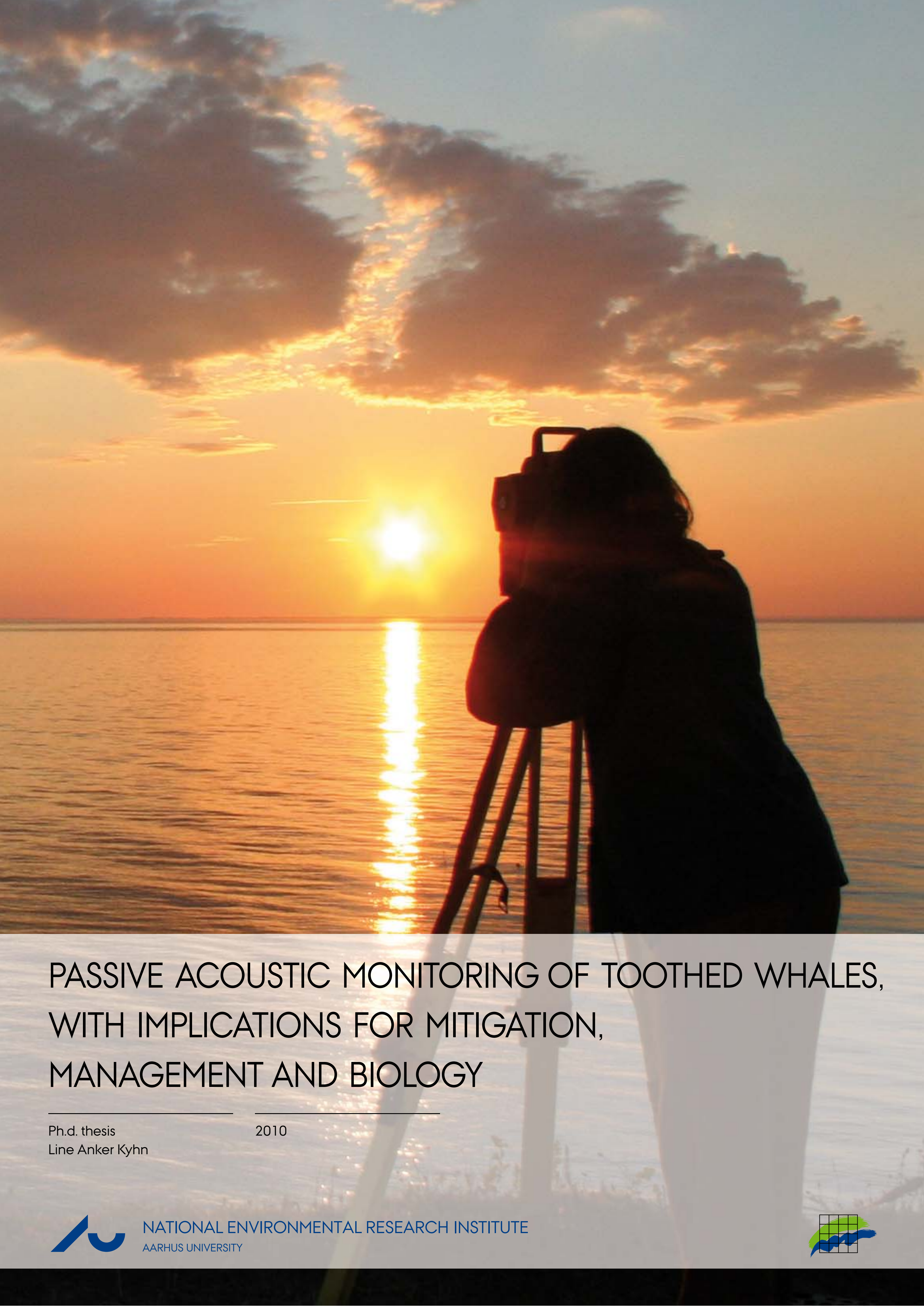

PASSIVE ACOUSTIC MONITORING OF TOOTHED WHALES, WITH IMPLICATIONS FOR MITIGATION, MANAGEMENT AND BIOLOGY

Ph.d. thesis
Line Anker Kyhn

2010

NATIONAL ENVIRONMENTAL RESEARCH INSTITUTE
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Data sheet

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Abstract: Small cetaceans like harbour porpoises are notoriously difficult to study due to various technical, physical and economical constraints in observing them in their marine environment. However, toothed whales are vocal animals and their social life as well as successful orientation and feeding depends on emission and reception of sound. When humans, by means of a hydrophone, are the receivers of these sounds, analysis may provide important information to researchers about the behavioural ecology, social interactions and sensory physiology of toothed whales, as well as it may be the means for acoustic monitoring. This ph.d. thesis presents a novel approach for counting and estimating density of harbour porpoises using acoustic dataloggers. This method is especially valuable for low density areas where traditional visual surveys become very expensive per observation. The thesis further presents thorough descriptions of sounds from six small species that all use the same echolocation signal type, a narrow band high frequency (NBHF) click. Such thorough sound descriptions are a prerequisite of acoustic monitoring. The NBHF click is further discussed in light of possible adaptive values, since the click has evolved by convergent evolution four times. In agreement with previously stated hypothesis it is concluded through modelling that the NBHF click type most likely evolved as acoustic camouflage against predation from killer whales, since all energy in the NBHF click is at frequencies above the upper hearing limit of killer whales.

Keywords: Acoustic monitoring, abundance, density, detection function, harbour porpoise, echolocation, click source parameters, habitat specialization, acoustic species differentiation.

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Dr. Jakob Tougaard, National Environmental Research Institute, Aarhus University

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Content

A. Review

B. Passive Acoustic Monitoring

C. Narrow Band High Frequency Sounds

Ph.d. thesis for the partial fulfilment of the requirements for
the degree of Doctor of Philosophy (ph.d. thesis).

Submitted to the Faculty of Science, Aarhus University, 29th October 2010.

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Assoc. Prof. Angela Fago (Chairman)
Zoophysiology, Dept. of Biological Sciences, Aarhus University

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All photos taken by the author

Preface

This thesis represents the partial fulfilment of the requirements for the degree of Doctor of Philosophy (ph.d.) at the Faculty of Science, Aarhus University. The thesis is written in accordance with regulations outlined by the Faculty of Science, in May 2002, and within the three year frame.

When I was a child I once stumbled upon a dead harbour porpoise on the beach. I was fascinated and astonished – could that really be a whale? The picture has stuck to my mind and the memory of the amazement is clear. But what astonishes me to day is, that there still is so much to be learned about cetaceans: Imagine that in 2007 Jakob Tougaard and I were the first to record sounds from hourglass dolphins! And there are still species that have never been recorded. That more knowledge is ever important is underlined by the fact that one cetacean species have died out since I was a child. As a scientist it is crucial to obtain knowledge by posing and testing hypothesis scientifically in order to objectively assess the problems that many cetacean species encounter to day from for example human encroachment of their habitats. My hope for this thesis work is that I may contribute with knowledge on a cheap methodology to study and count small cetaceans by acoustic monitoring in all parts of the world, and I hope that this may contribute some of the required knowledge to ensure that we shall experience no more extinctions of cetaceans.

This thesis deals with the sounds of six narrow band high frequency species that I have recorded in different parts of the world during the last three years. In this thesis I also present a method to combine acoustics and monitoring with the aim of being able to assess population densities acoustically. The thesis consists of six manuscripts of which three are published in peer reviewed journals (III, IV & V), two are ready for submission (II & VI) and awaits fruitful comments from my opponents, and the last manuscript, chapter I, represents, in accordance with the regulations outlined by the Faculty of Science, a larger review where I put my main results of chapter II to VI in to the context of other studies.

Copenhagen, October 27th 2010

Line Anker Kyhn

Dansk resumé

Dette er et resumé af ph.d. afhandlingen "*Passive acoustic monitoring of small toothed whales, with implications for mitigation, management and biology*" udarbejdet af Line Anker Kyhn på Afdelingen for Arktisk Miljø, Danmarks Miljøundersøgelser, & Zoofysiologi, Biologisk Institut, begge Århus Universitet.

Jeg har arbejdet med en særlig gruppe af små tandhvaler der alle producerer samme ekkolokaliseringssignal. Signalet – klikket - er særligt bemærkelsesværdigt, fordi al energien er indeholdt i et smalt frekvensbånd, med energi udelukkende over hundrede kilohertz (kHz). Klikket kaldes et NBHF klik (Narrow Band High Frequency). Klikkets egenskaber gør det let, at designe et filter, der kan sortere signalet fra den omgivende støj. Der er derfor udviklet dataloggere der automatisk kan opsamle kliks fra eksempelvis marsvin (*Phocoena phocoena*, L.). Metoden anvendes i Danmark til at beskrive relative ændringer i forekomsten af marsvin over tid. Det er dog langt at foretrække, at kunne vurdere ændringer på populationsniveau. Jeg har i denne afhandling arbejdet med, at udvikle en metode til at tælle marsvin ved brug af akustiske dataloggere. Den metode præsenterer jeg i kapitel II. For at omregne akustiske registreringer per tidsenhed til antal dyr per arealenhed kræver det, at man kan beskrive en dataloggers detektionsfunktion. En detektionsfunktion beskriver hvad sandsynligheden er for, at en datalogger registrerer et klik ved en given afstand. Herfra kan man beregne den effektive detektionsradius der angiver sandsynligheden for at detektere et dyr indenfor en bestemt radius af dataloggeren, som videre kan omregnes til densitet af dyr i den givne radius. For at lave en detektionsfunktion observerede vi marsvin fra Fyns Hoved, hvor vi havde sat dataloggere ud i vandet. Marsvinene fulgte vi med en teodolit fra toppen af klinten, så vi kunne beregne afstand mellem marsvin og dataloggere. Ved at sammenligne de visuelle og akustiske observationer opnåede vi en detektionsfunktion, og den brugte vi til efterfølgende, at beregne densiteten af marsvin i området. Metoden viste sig at være pålidelig, og selvom der var individuel variation mellem dataloggerne som udgangspunkt, da de var indstillet til forskellig følsomhed, kunne detektionsfunktionerne udligne disse forskelle på densitetsniveau.

For at kunne bruge denne teknik til andre arter, kræver det, at disse arters lyde er velbeskrevne. Den type datalogger jeg har arbejdet med, er udviklet specielt til marsvin, men fordi de bruger NBHFklik kan metoden potentielt også anvendes til de øvrige 14 NBHFarter. Der er i alt fire grupper af tandhvaler der bruger dette specielle NBHFklik; seks arter af marsvin, seks arter af Cephalorhininae delfiner, pygmæ (og sikkert også dværg) kaskelotter, samt Fransiscana floddelfinen. Det betyder endvidere, at klikket er opstået fire gange ved konvergent evolution, og spørgsmålet er hvorfor? I kapitel III, IV & VI beskriver jeg kliks fra seks forskellige NBHFarter som jeg har lavet lydoptagelser af i det fri under min ph.d. Formålet med lydoptagelserne var tofold; dels at lave præcise artsbeskrivelser til brug i akustisk monitering, dels at opnå større viden om og forståelse for disse arters akustik og for at forstå hvorfor NBHFklikket er udviklet. Herunder om der er artsspecifikke forskelle, der eksempelvis kan være opstået som tilpasninger til de forskellige miljøer dyrene lever i. I kapitel III, IV & VI konkluderer jeg, at der er artsforskelle, og at disse sandsynligvis skyldes forskellige niveauer af støj og *clutter* (uønskede ekkoer). Dette er baseret på, at de mest kystnære arter producerer kliks med de laveste lydstyrker, hvilket er i overensstemmelse med, at det ikke er en fordel at producere kliks med høj kildestyrke, som giver mange ekkoer, i et kystnært *cluttered* miljø. Jeg konkluderer endvidere, at der er artsforskelle som dels kan bruges i akustisk monitering, og som sandsynligvis også kan bruges af dyrene selv til artsgenkendelse, hvilket er en fordel i et miljø hvor synet er kraftigt begrænset. Endelig diskuterer jeg den mulige evolutionære udvikling af NBHFklikket i kapitel I, hvor jeg sammenligner alle de fysiske egenskaber der begrænser lydproduktion og effektiv biosonar i en model for at teste hypotesen om, at NBHFklikket er udviklet som akustisk kamuflage til beskyttelse mod spækhuggere. I modellen sammenligner jeg NBHFklikkets egenskaber med kliks fra andre tandhvaler og konkluderer, at NBHFklikket er stærkt begrænset i detektionsafstand og fungerer bedst til ekkolokalisering under 150 m. Der må derfor være en vægtig grund til udvikling af et klik til ekkolokalisering, der faktisk ikke kan bruges på særlig stor afstand, og på den baggrund accepterer jeg den hypotese, at NBHFklikket er udviklet som en akustisk kamuflage for at undgå at blive ædt af spækhuggere. Spækhuggere kan nemlig ikke høre frekvenser over 100 kHz, og det er jo netop kun der NBHFklikket har energi. Til sidst bruger vi i kapitel V, lydoptageser fra en art der aldrig tidligere har været optaget, tineglasdelfinen (*Lagenorhynchus cruciger*) til at bekræfte resultater fra molekylære fylogenier, at timeglasdelfinen og dens søsterart, Peale's delfin (*Lagenorhynchus australis*), må være tæt beslægtet med Cephalorhynchusslægten, da begge bruger NBHFsignalet.

Summary

This is a summary of the ph.d. thesis "*Passive acoustic monitoring of small toothed whales, with implications for mitigation, management and biology*" by Line Anker Kyhn, Department of Arctic Environment, National Environmental Research Institute, Aarhus University & Zoophysioloy, Department of Biological Sciences, Aarhus University.

Toothed whales are vocal animals and their social life as well as successful orientation and feeding depends on emission and reception of sound. Such sounds may e.g. be clicks used for echolocation or whistles used for communication and they can be monitored in time and space by means of passive acoustic monitoring (PAM). PAM is particularly suited to study small inconspicuous species. Among the small odontocetes, four groups produce the same special echolocation click type, the narrow band high frequency (NBHF) click that has evolved through convergent evolution four times. Clicks of the individual NBHF species are very similar and all these species may thus potentially be monitored by applying the same datalogger systems. However, since some of these species live sympatrically it is essential to identify potential acoustic species differences that may be used for species recognition in PAM.

The focus of chapter II in this thesis was specifically to try to find a method to combine traditional distance sampling technique and acoustic monitoring by means of a snap shot method to be able to estimate densities from datalogger data. The problem is how to derive a detection function, i.e. a function that describes the probability of detecting a porpoise acoustically at a given distance from the datalogger? In chapter II I describe one such possibility where we tracked harbour porpoises visually around dataloggers by means of a theodolite and following compared the visual and acoustic detections in a mark-recapture design to describe the detection function. From the detection function we then calculated the effective detection radius, which we then used to estimate the density of porpoises in the area. From the visual sightings we also estimated density within 100 m radius of each datalogger. The datalogger detection functions were successful in estimating densities of around the same level as we found for the visual observations, and more importantly the detection functions derived per datalogger could level out the sensitivity differences between the dataloggers (chapter II). Knowing that passive acoustic monitoring may be used to derive densities of small odontocetes such as NBHF species, the next step is to obtain accurate click descriptions. A species' sounds must be well defined according to specific sound source parameters to be able to build precise filters for the acoustic dataloggers to sort the correct

signals from noise. Such definitions require that the variation at the level of species is known and therefore that each focal species have been recorded using appropriate equipment under natural conditions. This was the focus of chapter III, IV & VI, where I show that NBHF clicks are very similar, however when applying specific criteria to compare the clicks there a species specific differences at a statistical level. I used these differences to successfully differentiate the species in Monte Carlo simulations, which means that it may also be possible to separate sympatric NBHF species with acoustic monitoring. Secondly, I was interested in examining the species differences in an evolutionary light to see if there were differences pertaining to possible habitat specializations of each species as is seen for Microchiropteran bats and this was the focus of chapter II, IV & VI. It appeared that costal cluttered habitats may be limiting for NBHF species since they produce lower source levels when recorded in cluttered habitats and clutter does not favour production of high source levels. I further argue that the small centroid frequency differences observed between sympatric NBHF species may be caused by character displacement and be the means of acoustic species separation for sympatric species, which appear favourable in an environment where the use of visual cues is greatly reduced. In chapter V we use the fact that two sister species at a disputable position in the dolphin taxonomy both produce NBHF to argue that both Peale’s and hourglass dolphins are closely associated with the Cephalorhynchid dolphins, which is in accordance with new molecular phylogenies. In chapter I use the information I have gathered on spectral source properties as well as on source levels and directionality and use this information to challenge the theories for the evolution of the NBHF click type. I conclude that the NBHF signals likely evolved to meet the dual requirements of operating an effective sonar system and at the same time to minimize the risk of killer whale predation from passive listening. The high frequency part of the NBHF click thus likely evolved as a product of the species’ small body sizes to obtain directionality high enough to yield efficient biosonar, while the narrow bandwidth evolved to restrict energy to frequencies above the hearing range of killer whales.

Acknowledgements

I would like to thank Jesper Madsen, Jakob Tougaard and Frank Rigét for giving me the opportunity to make this ph.d. thesis at the National Environmental Research Institute, Aarhus University, by providing the necessary funding and for believing that I could benefit the department. I am very grateful for the support and good atmosphere that *all* my NERI colleagues have provided me during the past three years, but especially to Jonas Teilmann, Hans Meltofte and David Boertmann for being ever positive and supporting in the ups and downs along the way. Above all Signe Sveegaard; I am so grateful that we can make friendship and science go hand in hand and at least try to laugh when it is hard. Jakob Tougaard I thank you for your fine supervision, good ideas, nice discussions and all the many explanations, but most of all for your compassion and warmth. I would also like to thank my understanding friends and family for patience, as well as for food and heat, in the last weeks, and Steen Andersen for highly needed distractions. I would also like to thank my colleagues at Zoophysiology in Aarhus, my internal supervisor Hans Malte, all the people that has been involved in the various field work in Denmark, the Falklands, Canada and during Galathea3, especially to Frants Jensen, Kristian Beedholm and Len Thomas for help building Matlab and *R* scripts for analysis, to Natacha Aguilar de Soto, Mark Johnson and Patricia Arranz for letting me gain experience from their work at El Hierro and to Mats Amundin, Daniel Wennerberg, Carolina Bordin and Joanna Stenback for the good times during the many hours at Fyns Hoved – it has all been very rewarding. But my warmest gratitude goes to Peter Teglberg Madsen that originally attracted me to this field and ever since patiently has been there for me helping, discussing and encouraging my work, but must importantly for our friendship.

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Chapter I

Kyhn, L.A. Passive acoustic monitoring of Narrow Band High Frequency species. Review (Unpublished manuscript)

How many porpoises are there? Passive acoustic methods to count porpoises! Jammerlandsbugten, Denmark, 2005.

Passive acoustic monitoring of Narrow Band High Frequency species.

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Abstract

Small cetaceans like the Narrow Band High Frequency (NBHF) species are notoriously difficult to study due to various technical, physical and economical constraints in observing them in their marine environment. Monitoring abundance and population development of small odontocetes is further difficult and labour intensive and there is a need to develop alternative methods to the traditional visual line transect surveys, especially for low density areas. However, toothed whales are vocal animals and their social life as well as successful orientation and feeding depends on emission and reception of sound. Such sounds, that may e.g. be clicks used for echolocation or whistles used for communication, convey information about the sender to the receiver or back to the sender in the case of echolocation. When humans, by means of a hydrophone or datalogger, are the receivers of these sounds, analysis may provide important information to researchers about the behavioural ecology, social interactions and sensory physiology of toothed whales, and it may be the basis for acoustic monitoring. Passive acoustic monitoring (PAM) enables efficient monitoring even under poor weather conditions where traditional visual survey methods are not applicable. In addition passive acoustic monitoring provides continuous monitoring in time in contrast to the snap-shots of visual surveys. Rigorous application of methods from distance sampling theory to passive acoustic monitoring provides the tools needed for obtaining estimates of absolute animal densities from acoustic cues recorded by dataloggers. However, in order to use this methodology requires that the sounds of the monitored species are thoroughly described, especially for areas with sympatric species.

Here I review the current methodologies available for calculating detection functions for passive acoustic dataloggers in order to estimate cetacean densities from acoustic cues. I further review and discuss the current knowledge on acoustics of the NBHF species in the light of possibilities for species separation using PAM, but also in the light of the evolution of this remarkable stereotypical signal that has arisen by convergent evolution in four different groups of toothed whales.

1. Introduction

Cetaceans play an important role in the world's oceans and they are present in almost all marine habitats as top predators. It is therefore important to understand their ecological role in various habitats to identify and protect vulnerable species and understand top down and bottom up effects of human encroachment. The relevance of these objectives is underlined by the fact that one cetacean species, the Yangtze river dolphin (*Lipotes vexillifer*, Miller 1918), can be claimed extinct from 2008 (Turvey *et al*., 2007) and two more in either end of the size and habitat spectra are going the same way; the Northern right whale (*Eubalaena glacialis*, Müller 1776) and the Vaquita (*Phocoena sinus*, Norris and McFarland 1958) (e.g. Jaramillo-Legoretta *et al*., 2007). Decline in cetacean populations are caused by a range of different factors of which humans must be held responsible, the most important being incidental as well as direct mortality in fisheries, habitat destruction and vessel collisions. Encroachment of habitats may occur at several levels from reduction of potential prey populations by fisheries over noise from shipping and seismic surveys, to chemical pollution and urban development. Furthermore, it has become important to understand the ecological role of cetaceans as top predators and their predator-prey relations in order to scientifically evaluate competition with fisheries and to provide quality data for evaluating the relevance of proposed cullings in relation to reduction of depredation of commercially exploited fish stocks. It is therefore ever important to be able to accurately assess changes in sizes and compositions of population in time and space. However, toothed whales are notoriously difficult to study due to various technical, physical and economical constraints in observing them in their marine environment and the result is a major data deficiency, especially for the smallest species. New methods are therefore critically required to obtain the needed insights for addressing the above problems scientifically.

Toothed whales are vocal animals and their social life as well as successful orientation and feeding depends on emission and reception of sound. Such sounds may e.g. be clicks used for echolocation or whistles used for communication. When humans, by means of a hydrophone, are the receivers of these sounds, analysis may provide important information about the behavioural ecology, social interactions and sensory physiology of toothed whales. Further, because cetaceans produce sounds they may also be monitored in time and space by means of passive acoustic monitoring (PAM). Especially some of the small odontocetes are very inconspicuous and it is therefore very difficult to address the above questions by visual methods; PAM is therefore particularly suited for these species. Among the small odontocetes, four produce the same special echolocation click type, the narrow band high frequency (NBHF) click that has evolved through convergent evolution. Clicks of the individual NBHF species are very similar and all these species may thus potentially be monitored by applying the same datalogger systems. However, since some of these species live sympatrically it is essential to identify potential acoustic species differences that may be used in species recognition in PAM.

This chapter intends to review and explore how acoustics and in-depth knowledge on acoustic behaviour may be used to convert a count of echolocation clicks to animal density for use in passive acoustic monitoring. The chapter will further review the present knowledge and theories on the acoustics of NBHF species with relevance for aspects of passive acoustic monitoring, the biology and the possible evolutionary driving forces behind this unique echolocation signal shared through convergent evolution by four different odontocete groups.

2. Monitoring of toothed whales

Before the international moratorium on commercial whaling in 1986, populations of large whales were assessed by means of catches per unit effort while biological knowledge was mainly drawn from the carcasses. However, over the last few decades new methods have been developed to provide non-invasive approaches to study cetaceans at sea. Absolute population densities can today be obtained from dedicated surveys from plane or boat (e.g. Hammond *et al*., 2002; Thomas *et al*., 2010), or as relative indexes obtained by means of passive acoustic monitoring (PAM) where a species' vocalizations are detected by specifically designed dataloggers. The basic technique for obtaining densities is that animals are detected by human observers and counted along set track lines by several observers. Such visual surveys provide detailed information on distribution with a high spatial resolution, but in a snapshot of time. The number of animals is afterwards converted to animal density using different statistical approaches. One such approach is called distance sampling.

2.1. Distance sampling

Distance sampling is based on the fact that the probability of detecting an animal varies with distance to the observer. The distance sampling methodology is under constant development and its applications, problems, solutions, extensions, statistics, modelling and much more are studied at CREEM, University of St. Andrews (e.g. Buckland *et al*., 2001; Thomas *et al*., 2010). On a ship, the probability of observing an animal is greater on the track line on which the ship sails than at greater distances from the ship. This means that at some distance from the ship some animals will be missed for each animal observed. If the track line is placed at random or systematically with respect to animal distribution in the survey area, it may be assumed that the density of animals is constant with range to the track line. However, due to observer limitations the number of animals actually *observed* per distance decreases with perpendicular range to the track line. Thus, if a perpendicular distance, *r*, can be assigned to each observation during a survey, a detection function, *g(r)*, describing probability of detection per distance can be made allowing adjusting for the number of animals missed per distance in the final density estimate. The detection function (figure 1) is thus the link between observed number of animals per distance and true animal distribution relying on the important assumptions that: 1) the track lines are distributed at random/systematically with respect to animal distribution, 2) that all animals at the track line is detected, i.e. *g(0)*=1 or *g(0)* is known, and 3) that an accurate distance may be assigned to each observation.

Distance sampling is generally used for two types of sampling; *line transect surveys*, as outlined above, and *point transect sampling*. In line transect sampling the ship or plane moves forward a long specified track lines (figure 2), while point transect sampling is conducted from points randomly or regularly distributed in the surveyed area. Point transect sampling is relevant for passive acoustic monitoring by means of stationary dataloggers, while the line transect sampling method may be applied to monitoring by means of hydrophone arrays being towed after a boat.

In line transect sampling, the number of *observed* animals per distance decreases as a function of the perpendicular distance to the track line. In point sampling the relation between true animal distribution and observed distribution is different because the area of each concentric band of fixed width, *dr*, around a point increases with distance to the point. Therefore true number of animals per concentric band increases with distance to the point, if the animals in the area are randomly distributed with regard to the point. Due to observer limitations the number of animals detected thus first increases with distance from the point and then decreases. An illustration of the relationship between true animal distribution, the detection function and the observed distribution of animals as a function of distance is shown in figure 1.

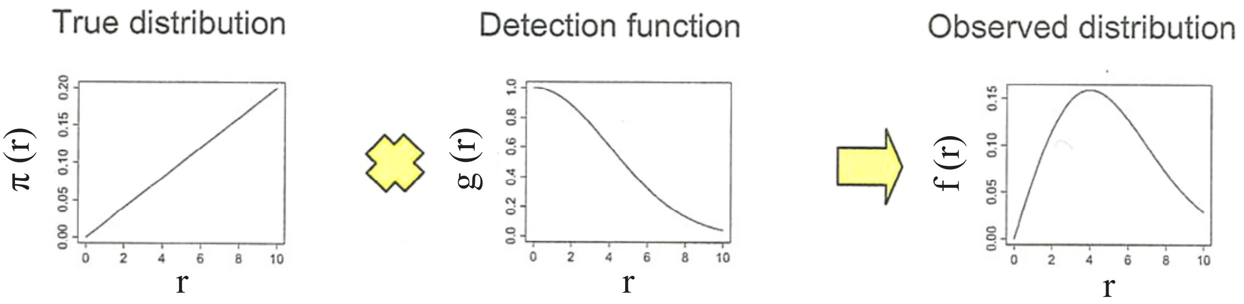


Figure 1. The relationship in point sampling between true distribution of animals π(r), the detection function g(r) and the observed distribution, f(r). *The detection function describes the probability of detection at distance, r, given the animal is present there. The detection function is found empirically and is a prerequisite for converting the observed number of animals/cues back to the true density in the covered area (From Thomas and Martin, unpublished draft, 2006).*

Distance sampling is well established and visually counting cetaceans from plane or boat is presently *the* way to assess abundance, the method is not unproblematic, especially for odontocetes: Except for large baleen whales with blows extending high up into the air, cetaceans are generally difficult to observe and the smaller the species, the more animals are likely to be missed during counts. This difficulty increases greatly with sea state (Teilmann, 2003) restricting the time available for surveys of smaller cetaceans to days with low sea state, which may seriously increase the duration and thus costs of a traditional line transect survey. Further, it is only possible to observe animals under daylight conditions. At higher latitudes daylight is profoundly restricted during winter leaving the temporal coverage rather restricted diurnally and seasonally. Fog, snow and glare may also limit visibility. On top of these physical limitations the human effort is highly dependent on eye sight, training, motivation, fatigue, seasickness, distractions during transects (for example non focal species, icebergs, oil platforms etc.) and may even be predisposed by, perhaps political, yet unconscious, expectations on density or distribution of animals.

The most important problem in distance sampling, however, is the assumption that all animals are detected on the track line or at the point, i.e. *g(0)*=1. This is impossible for cetaceans (Hammond *et al*., 2002; Borchers, 2005; Fan, 2009) for two reasons; either the animals are diving and thus unavailable for detection, i.e. availability bias, or the animals are present but remain undetected, due to for example inconspicuous surface behaviour or small body size, i.e. perception bias. Erroneously assuming *g(0)*=1 has been shown to greatly underestimate cetacean abundance (Fan, 2009). Correct *g(0)* may either be measured (Laake *et al*., 1997; Hammond *et al*. 2002), which is often done using double observer platforms (Hammond *et al*. 2002; Fan, 2009) or the track line may be filmed and *g(0)* assessed from analysing the recordings. *g(0)* is sometimes borrowed from other studies/species (Barlow *et al*. 1997; Barlow *et al*., 2006) for example if the sample size is to low for *g(o)* estimation. Correction factors may also be included in modelling the detection function as covariates, for example effect of dive pattern to adjust for availability bias (Borchers, 2005). However, as long as *g(0)* is known it may be compensated for.

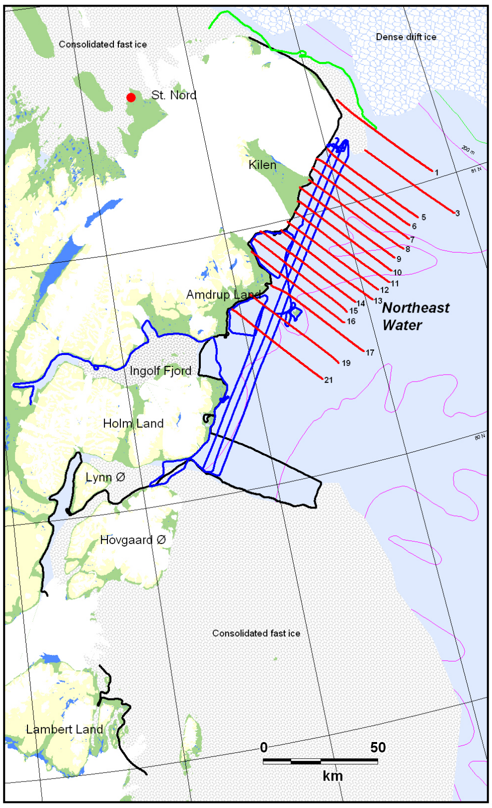


Figure 2. *Example of traditional line transect survey performed from a Twin Otter airplane (Boertmann et al., 2009).*

Another important problem in distance sampling and especially when applied to cetaceans is distance measurement errors. With no trees, buildings etc at sea it is very difficult to assess distances at sea by eye and it requires substantial training. Distance measurement error may be inaccurate, biased and variable between observers and may result in inappropriately fitted detection functions (Williams *et al*., 2007) resulting in biased population estimates. Range is commonly assessed by means of either naked eye or angle below horizon (binoculars with reticules) in ship based surveys and by clinometers measuring angle to observation in aerial surveys, both using Pythagoras by means of known elevated height of the observer. Yet, this method still results in measurement errors (Gordon, 2001) with ranges overestimated close by and underestimated at grater ranges (Leaper *et al*., 2007). Training of observers is thus especially important since differences in range estimations may lead to systematic bias between observers (Thompson & Hiby, 1985; Leaper *et al*., 2007), and therefore tests are often performed for inter-observer calibration during surveys (Ex. Hammond *et al*., 2002). However, also simultaneous visual sighting and video-taping of observations are applied resulting in much more accurate distance measurements (Gordon, 2001; Leaper and Gordon, 2001; Leaper *et al*., 2007)

Violation of the above mentioned assumptions seriously reduce both comparability and validity of obtained densities and are well-known and discussed limitations of visual transect surveys (e.g. Buckland *et al.*, 2002, Marquez *et al.*, 2009). Despite that comparability is essential to assess changes in population sizes over time, visual line transect surveys are still the most used method for obtaining population sizes. The advantages are that the animals are identified to species, and perhaps sex, immediately and that the spatial resolution of visual transect surveys generally is good and may be extensive. The statistical methodology is also advanced and under constant development. However, a valid alternative for obtaining unbiased population densities is being developed in the form of passive acoustic monitoring over the last few years. The use of PAM for density estimations is a powerful method that may reduce many of the inherent limitations of visual surveys; however it requires that a proper methodology is developed which indeed appear possible as we shall see in the next sections.

2.2. Passive acoustic monitoring

Acoustic monitoring provides a valid alternative for visual line transect surveys, yet it faces its own inherent limitations. There are two means of applying passive acoustic monitoring. Either as dataloggers or hydrophones towed behind a boat (here defined as towed arrays) (e.g. Gillespie and Leaper 1997; Hastie *et al.*, 2003; Thode, 2004; Lewis *et al.*, 2007; Mellinger *et al.*, 2007; Gillespie *et al.*, 2009), or as static monitoring where dataloggers (e.g. figure 3) are deployed and remain stationary until retrieved (from here on referred to as static acoustic monitoring (SAM) (e.g. McDonald and Moore, 2002; Carstensen *et al.*, 2006; Moore *et al.*, 2006; Verfuss *et al.*, 2007; Marquez *et al.* 2009; Tougaard *et al.*, 2009; Rayment *et al.*, 2009; Kimura *et al.*, 2010). Both methods imply that incoming sounds are filtered directly using specific filters and only certain features are stored in the internal memory (SAM) or computer (towed arrays), which may be source parameters such as frequency or bandwidth or it may be values such as timing, duration and received level. How fine tuned the filtering process needs to be depends on the species in question and whether there are more species, potentially causing confusions about species identity of individual sounds. Generally speaking the less sharp a filter is the more source parameters should be stored to allow for offline filtering, however this is often not the case. The effective spatial coverage of SAM data is low especially for NBHF species due to their low source level. However, by deploying dataloggers in a robust study design, findings may be extrapolated from individual datalogger points to entire areas increasing the spatial resolution. The resolution in time is oppositely extremely good and at the level of microseconds for some dataloggers (e.g. T-PODs, Chelonia Ltd). SAM may be deployed for months at a time, which can be extended further by duty cycling the data acquisition. SAM thus enables calculation of diurnal or seasonal patterns of presence in an area. SAM is further a cheap alternative since a datalogger may be left at sea for months at a time requiring much less boat time and human involvement. It is further possible to derive objective and thus comparable data with SAM provided that 1) the datalogger detection filters are tested thoroughly and assessed for levels of false positives and negatives, 2) the filters can separate between relevant species in the study area, 3) the datalogger is calibrated to account for sensitivity effects on detection rates and ranges, 4) the off-line data analysis follow pre-set filters and/or definitions for presence and absence of a given species to avoid subjectivity. In Kyhn *et al*., (2008), I presented a method on how to accurately measure datalogger detection threshold and showed how detection threshold and number of detected clicks are directly correlated. I therefore applied this method in chapter II to evaluate the effect of datalogger threshold on detection range and probability of detection showing, not surprisingly, that the lower the detection threshold the greater the detection range and the greater the probability of detection of harbour porpoises (*Phocoena phocoena*, L 1758).

Figure 3. Example of SAM datalogger; a T-POD connected to a laptop for download (courtesy of Jakob Tougaard).

At present passive acoustic monitoring only provides an index of animal presence/absence in the shape of counts of vocalizations divided into different statistical measures (see for example Carstensen *et al.*, 2006; Verfuss *et al.*, 2007; Tougaard *et al.*, 2009). The use of such relative index-values is, however, far from perfect as it will only (at best) provide information on the direction of any development in population size but not the magnitude of the development (Anderson 2001; Anderson 2003). The challenge thus is to combine the qualities of visual distance sampling methods with SAM to develop a method that can convert cost-efficient and objectively sampled SAM data to absolute animal densities. This task is by no means simple and there are many challenges overcome both in regards to optimal filtering process in the datalogger as well as on how to obtain distance to the vocalising animal, how to assess group size and how to obtain cue production rates (see for example review by Mellinger *et al.*, 2007). Five studies have derived a detection function for a SAM datalogger by different methodologies, and three of these used the obtained detection function to estimate density from SAM data (Zimmer *et al.*, 2008; Marquez *et al.*, 2009; Rayment *et al.*, 2009; Kimura *et al.*, 2010; chapter II this thesis). All studies rely on a method derived from point transect distance sampling to convert a number of vocalizations to density, namely cue counting, and I will therefore briefly introduce the methodology in order to discuss results of the mentioned studies. The methodology is explained in full detail by Marquez *et al.* (2009) and in chapter II.

2.3. Cue counting

Cue counting was original developed for counting blows from large baleen whales during line transect surveys since they are easier observable than the whales themselves, however the distance to the cue was measured as the radial distance from the observer on the ship to the cue (Buckland *et al.*, 2002). The methodology therefore closely resembles point transect sampling and may as such be converted to counting toothed whale clicks by a stationary datalogger. The detection function, $g(r)$, is therefore built on radial distances between cue and datalogger and describes the probability of detecting a cue at distance r from the datalogger and P_a is then the probability of detecting a cue within an area, a, with radius, w, and is found as observed number of cues · true number of cues^{-1} within w. Knowing the cue production rate of a species, $\hat{\eta}$ (cues produced · animal^{-1} · time unit^{-1}), animal density can then be estimated from number of cues counted within a specified duration by combining cue counting and point sampling by obtaining the detection function, $g(r)$, for the cue in questions. Thus if number of cues counted, n, and the total time surveying, T, is known for an area, *a*, with radius, *w,* and an effective area $\hat{v}$ ($\hat{v} = a \cdot P_a$), the probability of detecting the cue within *w* is

$$P_a = \frac{\hat{v}}{\left(\pi \cdot w^2\right)} \qquad (1) \qquad \text{(Buckland } \textit{et al.}\text{, 2002)}$$

and then cue density, $\hat{D}_c$, is:

$$\hat{D}_c = \frac{2 \cdot \pi \cdot n}{\hat{v} \cdot T} = \text{cues·unit time}^{-1}\text{·unit area}^{-2} \qquad (2) \qquad \text{(Buckland } \textit{et al.}\text{, 2002)}$$

Animal density, $\hat{D}$, based on cue density, may then be calculated from:

$$\hat{D} = \frac{2 \cdot \pi \cdot n}{\hat{v} \cdot T \cdot \hat{\eta}} = \text{animals·unit area}^{-2} \qquad (3) \qquad \text{(Buckland } \textit{et al.}\text{, 2002)}$$

The formulas for calculating density from cues thus closely resemble point sampling and the same assumptions must be fulfilled:

1) *g(0)*= 1 or *g(0)* is known.
2) Distances to detected cues can be measured without error.
3) Only one distance can be assigned to each detected cue, i.e. animals do not move.
4) Points are located at random or systematically with respect to animal distribution in the study area.

To obtain a detection function for a SAM datalogger the challenges thus are 1) to measure the radial distance, *r*, from the datalogger to the cue, 2) to define a cue that allows species determination, but at the same time is not so long that more than one distance may be assigned the cue and 3) to know whether the acoustic cue at distance, *r*, was detected or not to calculate the probability of detection at distance *r*. To further use the detection function to calculate density the cue, the production rate must be known for the defined cue and be obtained in the study area at the time of the study (Buckland *et al.*, 2002).

In the following sections, I will present and discuss methods and results from the first studies exploring how to obtain a detection function for a SAM datalogger with focus on the applicability for NBHF species.

2.4. Four examples on how to obtain a detection function for acoustic dataloggers

The studies of Zimmer *et al.* (2008), Marquez *et al.* (2009), Rayment *et al.* (2009), Kimura *et al.* (2010) and chapter II (this thesis) have found different solutions on how to define a cue and on how to derive the detection function. However, Zimmer *et al.* (2008) and Marquez *et al.* (2009) used single clicks in their study of beaked whales. The approach by Zimmer *et al.* (2008) is thorough and they model a range of acoustic aspects of sound reception by a SAM device based on DTag data taking account of for example animal orientation, depth of vocalizations and more, however, Marquez *et al.* (2009) take the approach a step further for beaked whales by empirical testing, and I will therefore use their method as an example for using single clicks. Kimura *et al.* used click trains to study finless porpoises (*Neophocaena phocaenoides*, G. Cuvier 1829) and both Rayment *et al.* (2009) and I (chapter II) used click trains per time unit to study Hector's dolphin (*Cephalorhynchus hectori,* van Bénéden 1881) and harbour porpoises, respectively.

The study of Marquez *et al.* (2009) is quite different from the three other studies because they combined two state of the art methods: They mounted digital acoustic dataloggers (DTags (Tyack and Johnson, 2003)) on a number of Blainville's beaked whales (*Mesoplodon densirostris,* Blainville 1817) present in a US Navy testing range located in the Tongue of the Ocean, Bahamas, where 93 cabled hydrophones are mounted on the sea floor of which they could use 82. This is an exceptionally good combination for a SAM study, but the method is hard to transfer to other species or areas of the world. Marquez *et al.* could use individual clicks because they had the exact timing of received clicks on both systems simultaneously and therefore could filter, time and compare data the same way. DTags provide fine-scaled whereabouts in depths and wideband sound recordings (96 kHz sample rate) and high resolution data on heading, pitch and roll of the animal, which may be used to estimate underwater swimming tracks (so called pseudo-tracks) of the focal animal. Arrays of 4+ hydrophones are normally sufficient to localize vocalising animals by time-of-arrival differences between the different hydrophones (Madsen and Wahlberg, 2007). However, the hydrophones in this study were too distantly spaced for the much focused sound beam of Blainville's beaked whale to be recorded on more than three hydrophones simultaneously. The authors therefore modelled the swimming tracks of tagged whales that were recorded on hydrophones within 8 km of the whale position at the time of matched clicks recorded on both DTag and hydrophone. They thus combined acoustic data from DTags and acoustic data on the hydrophones with modelled swim tracks based on the auxiliary data from the DTags to obtain distance to the "SAM logger". They calculated a distance for each matched click in order to arrive at a detection function based on a comparison of clicks recorded in both systems using the DTag as a template for the hydrophone data. The clicks recorded on the DTag were thus the trial and was consequently scored a success if recorded on a hydrophone within 8 km radius and as error if not recorded. The 82 hydrophones therefore only functioned as SAM loggers to greatly increase sample size of click trials. However, the authors did not explain how they ensured that a click recorded on a hydrophone and matched with a click on the DTag did not actually arrive from another whale in the area. In that case, the probability of detection could become artificially high if the DTagged whale was further from the hydrophone than the whale actually was when recorded. They found a maximum detection range of about 6.5 km, which may be valid if beaked whales produce source levels > 210 dB re 1 µPa pp and point directly at the hydrophone. Furthermore, this is provided that sound attenuates with spherical spreading and that the hydrophones could detect sound level as low as 90 dB re 1 µPa pp, as the received level would be when received at 6.5 km distance, however they did not state the sensitivity or self/ambient noise of the hydrophones.

Marquez and co-authors calculated cue production rate from the same DTag data. Their approach was successful building on and complying with the cue counting theory and its assumptions (*Buckland et al., 2002*). However, this approach is expensive (it is difficult to find a suitable military test range in a shallow water habitat where NBHF clicks actually reaches the bottom), laborious and is at present only possible for larger toothed whales, whereto onboard acoustic tags with the DTag auxiliary data acquisition has been designed. Besides these practical issues, the use of individual clicks as cue is in my view not good for NBHF species for several reasons. First, NBHF species, such as harbour porpoises, may reach very high click rates on the order of several hundreds per second, which will require synchronisation at the level of microseconds for comparison of recordings from an onboard tag and a hydrophone array; however, that may be overcome by use of inter-click-interval synchronization. Second and more importantly, at the level of individual clicks, the rate of false detections may be very high and requires assessment of false detection rate at the level of individual click for each habitat where the method is applied, which is very cumbersome. Even in this beaked whale example, the percentage of false detections was almost 50 %. In comparison, I used *click trains per minute* as a cue for porpoise detection in chapter II and found a false detection rate of zero. Thirdly, at the moment there are no dataloggers available for the high frequency clicks of NBHF species that allows examination of individual click source parameters offline. As I describe in chapter IV and VI, there are small differences between clicks of individual NBHF species that may be used to distinguish between sympatric species. However, the differences are small, especially when including off-axis values, but in a simple Monte Carlo simulation, I did find that Dall's and harbour porpoises, that lives sympatric in British Columbia, may be accurately separated using only 32 clicks (100% correct). It is therefore necessary to use more than a single a click as cue and the method employed by Marquez *et al*. is consequently not in my view applicable for any of NBHF species at the moment.

Kimura *et al*. (2010) used Atags (Akamatsu *et al*., 2005) as SAM dataloggers to calculate density of the finless porpoise in a shallow water river habitat in China (the Yangtze River). The Atag is a stereo click detector with a detection threshold of 140 dB re 1 µPa pp. (Akamatsu *et al*., 2005). Kimura *et al*. used a sound propagation model of porpoise clicks to obtain the probability of detection per distance. To take the directional sound transmission properties of the finless porpoise into account they assumed that all clicks from 0º to 16º were on-axis and that clicks in the remaining angles were off-axis. Off-axis clicks were defined to have source levels of 47 dB below on-axis source level of 209 dB re 1 µPa pp (Li *et al*., 2009). Thus for all distances the porpoises were pointing on-axis towards the datalogger 4.4 % of the time and off-axis 95.6 % of the time. To be detected by the Atag the received level had to exceed 140 dB re 1 µPa pp. To make the detection function they thus calculated the distribution of theoretically detected click trains per distance from the Atag for on- and off-axis source levels, respectively, based on the above assumptions and an absorption coefficient of 0.004 dB·m^{-1} (@ 125 kHz centroid frequency in freshwater), resulting in a *g(0)*=1 for on-axis clicks and max detection range of 1250 m and for off-axis clicks *g(0)*= 0.91 where max detection range was 5 m. Using the percentage of on- and off-axis click trains they then combined the two theoretical detection functions to obtain *g(0)*= 0.92. This *g(0)* value is high, and may be overestimated because the effect of off-axis angle is likely to be underestimated for angles above 135° (Hansen *et al*., 2008) and because the variation in swimming movements as well as the natural variation in emitted source levels are unaccounted for. At least in captivity, harbour porpoise source levels may vary with more than 30 dB during a single prey capture event (Atem *et al*., 2009) or during stationing in (Beedholm and Miller, 2007) and when recorded from wild unrestrained animals source levels are generally higher but varies within 30 dB as well (chapter VI). The same natural variation appears to exist for finless porpoises as well (Akamatsu *et al.*, 2007; Linnenschmidt, 2007). Kimura *et al.* did use some variation of source level, where minimum six clicks in a click train should have received level above the detection threshold of the Atag of 140 dB to be detected.

In order to compare the theoretical detection model of Kimura *et al.* with a similar model for detections on a T-POD and further relate that to the empirical T-POD detection function I have derived (chapter II), I here derive a simple theoretical detection function for harbour porpoises and T-PODs. For simplicity, I assume the same on- and off-axis source level criteria as used by Kimura *et al.*, and use a high harbour porpoise source level of 190 dB re 1 µPa pp. I then calculated the probability of detection by a T-POD with a detection threshold of 125 dB re 1 µPa pp (i.e. 15 dB lower detection threshold than an Atag) by randomizing 10,000 click angles and distances between 0-500 m assuming spherical spreading and an absorption coefficient of 0.035 dB/m. The resulting model is in effect similar to the one made by Kimura *et al.* and with a similar high *g(0)* value (figure 4), however, the detection function is very different from the one I obtained empirically for the same species and datalogger as discussed below and in chapter II. A theoretical detection function may be a valuable tool to predict detection ranges in the field, but should at least be tested for example by playbacks at varying distances or better by visually observing porpoises around dataloggers in the field as done by Rayment *et al.* (2009) and in chapter II.

Kimura *et al.* used on-axis source levels for the finless porpoise of 209 dB re 1µPa pp, which exceeds what have been found for any NBHF species (Villadsgaard *et al.*, 2007, chapter III, IV & VI herein) and if this source level is actually too high it may bias the final density estimate positively. The source level of the finless porpoise was calculated by Li *et al.* (2009) from two Atags fitted on a towed array and spaced 17 m apart, 63 and 80 m behind the boat, respectively. The porpoise-to-Atag distances used for source level calculations were up to 200 m, which means that the time-of-arrival differences, that the localizations are calculated from, are very short. A very important point using arrays to estimate distance to a vocalising animal is that the distances and angles between the hydrophones are absolutely fixed. In the case of Li *et al.* (2009) the Atags were towed after a boat, and despite that they tried to take account of the zig zagging of the Atags, by

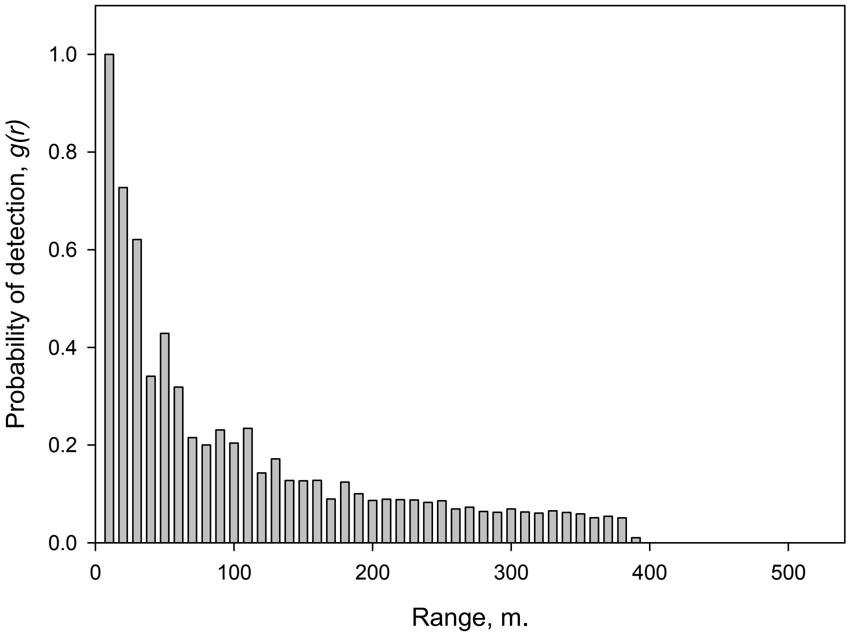


Figure 4. A theoretical detection function for a T-POD *assuming a harbour porpoise echolocating at various distances and angles from a T-POD. The model was made only to compare with results of Kimura et al. (2009) and thus used her assumptions, i.e. on-axis source level at angles from 0-16° and off-axis source levels 47 dB lower of 153 dB re 1 μPa pp from16-344° using an on-axis source level of 190 dB re 1 μPa pp, which is 15 dB lower than the highest found for harbour porpoises.*

measuring distances to several clicks arriving closely spaced in time, it may have had some effect on the accuracy of the distance calculations, thus affecting source level estimations. Kimura *et al.* thoroughly tested different click train parameters before deciding on a robust click train definition by comparing results in receiver operating characteristics plots. For this they used a dataset from SAM Atags and calculated also false alarm ($8.62 \cdot 10^{-2}$) and correct detection probability ($7.47 \cdot 10^{-1}$). They found variation in inter-click-intervals to have the greatest effect on detection probability. However, despite the thorough testing it remains a problem that a click train recorded on the animal will be different from click trains recorded by SAM loggers due to the directional odontocete sound transmission properties. That the click train definition itself is essential when used for density estimations is further strengthened by the fact, noted by Kimura *et al.*, that they found finless porpoises to emit a new click train every 3 s, whereas Akamatsu *et al.* (2007) found that emission of a click train every 6 s, due to the use of different click train definitions. Kimura *et al.* used the found click train definition to calculate cue production rate with the unit '*number of click trains produced* *by a porpoise per day*‘ and found a cue production rate of $2.87 \cdot 10^4$, from Atags fitted to eleven finless porpoises in another part of the Yangtze River. They also tested the correlation between cue rate and group size from the SAM Atags and found it to be 1. Because an Atag contains two hydrophones, bearings can be made to individual click trains if there are more animals in the area. Using these parameters they then used the theoretical detection function to calculate density for a test dataset and found densities matching the expected based on bearings to individual porpoises. Nevertheless, despite that they were very thorough in testing the definition of the click train to be used as cue and that they successfully found densities at the expected level, I find that the validity of their theoretical detection function would gain from being tested in a field trial to confirm the high *g(0)* value and the long maximum detection range, especially in the light of the comparably very low empirically derived *g(0)* of 0.3 that I found in chapter II for harbour porpoises.

The method applied by Rayment *et al.* (2009) to obtain a detection function resembles the method I used in chapter II. Rayment *et al.* made a detection function for Hector’s dolphin by comparing acoustic detections on a T-POD (Chelonia Ltd.) with synchronised visual detections geo-referenced by means of a theodolite. A T-POD is a click detector designed specifically for detection of harbour porpoises that produce NBHF signals. Hector’s dolphin also produce NBHF clicks and they can be therefore be monitored by T-PODs as well. The T-POD detection filter utilises the narrow bandwidth of NBHF clicks by basing detection on a comparison of two band pass filters centred at 130 and 90 kHz, respectively. I have previously explained the T-POD detection process in detail in Kyhn *et al.* (2008). To establish a detection function Rayment *et al.* used the visual detections as trials that were scored a success if there was an acoustic detection on the T-POD within 10 s of the visual sighting. Visual detections were assigned to distance bins and probability of detection was then calculated as number of periods in a distance bin with detections/ total number of periods in that distance bin. A period was the time a group spent in a given distance bin and the distance to a group was taken as the distance from the T-POD to the middle of a group of dolphins.

This setup was not intended to be used to assess dolphin density based on cue counting, but to test how well T-PODs work for detection of Hector’s dolphins. A cue per se was thus not defined, but only periods greater than 60 s was used. Acoustic detections were click trains as defined by the T-POD software and a cue could thus be said to be click trains per time unit. They found a maximum detection range of 431 m and a detection function was fitted to the probability of detection per distance bin, which gave *g(0)*~0.9 for detection of a group of dolphins within 100 m from the T-POD. The validity of this detection function is difficult to assess since it was not used to estimate a density. A density estimation would immediately have shown how well the detection function worked since the density estimate could be compared directly to the visual observations. However, it appears from the distribution of visual sightings that the dolphin groups spent most time in the distance bin closest to the datalogger, i.e. in the distance bin of smallest area 0-100 m (their figure 4), where one should expect fewer animals closest to the point (see figure 1 above). It may thus be that the dolphins were attracted to the boat and mooring of the T-POD. If so, such a left biased detection function could result in overestimating dolphin density depending on the fitted detection function (Buckland *et al.*, 2001; Thomas *et al.*, 2010). Further, since probability of detection increases with the time a group spends in a given distance interval it becomes important to define cue duration to make the probabilities comparable between the distance bins.

Another drawback of the methodology of Rayment *et al.* is the lack of precision of the distance measurements where some dolphins are actually closer to the T-POD than the measured distance to the midpoint of the group. This means that the distance is overestimated which will give an artificially high probability of detection for a given distance since the dolphins closer to the T-POD is more likely to be detected. Again this may result in overestimated densities. However, the effect of this type of error may be reduced by dividing the measured distances into intervals exactly as the authors did, though provided that measurement precision is are correct close to the cutting points between intervals (Buckland *et al.*, 2001). Given that probability of detection was less than one even for groups of dolphins spending several minutes within 100 m of the T-POD it is likely that Hector's dolphins are silent for shorter or longer time periods or that their behaviour reduces the probability of detection, which reinforce the use of a period of time with clicks as a cue to increase probability of detection. That toothed whales may be silent for periods of time has been observed for harbour and finless porpoises (Akamatsu *et al.*, 2007) as well as for three beaked whale species (Tyack *et al.*, 2006; Gillespie *et al.*, 2009), and it may well be that Hector's dolphins also have silent periods.

The last study attempting to make a detection function for a SAM logger is my study presented in chapter II. In short, we chose a high observation point (Danish standard - 20 m above sea level) overlooking a high density harbour porpoise area and deployed eight T-PODs in three clusters in front of the observation point. At the hill top, observers monitored the area and tracked porpoises with a theodolite connected to a computer. In an earlier study, we showed that T-POD detection threshold affects number of clicks detected on a T-POD (Kyhn *et al.*, 2008). I therefore calibrated the eight used T-PODs and deliberately changed their sensitivity to conform to three levels of detection thresholds to examine the effect of detection threshold on detection probability. T-PODs of different thresholds were placed in each of the three T-POD clusters to distinguish possible effects of cluster position and T-POD detection threshold. Since the study is one of the first of its kind, there is no established cue definition and I therefore chose to test three different cue definitions based on discussions with Dr. Len Thomas (CREEM) who is a recognized expert in analysis of distance sampling data (e.g. Thomas *et al*., 2010). The cues were defined as 15 s, 30 s and 60 s intervals containing click trains. As click train definition I used the definition of the T-POD software (T-POD.exe, Chelonia Ltd.), however, this software divides incoming clicks into click trains based on an unpublished and unverified algorithm that is inaccessible to users. The software further divides the detected click trains into five categories based on a probability of arising from porpoises, but again based on an undocumented algorithm. I therefore divided the T-POD data into two combinations of these click train categories for the analysis to examine if click train category affected probability of detection. The final T-POD datasets thus consisted of three data divisions based on three variables; T-POD detection threshold (three categories), click train category (two categories) and cue definition (three categories). On top of this dataset, I obtained a dataset conducted in 2003 using two T-PODs. However, these T-PODs were not calibrated and I could thus only analyse these data based on the three cue categories and the two click train categories.

The visual data consisted of a number of porpoise surfacing localizations for both years. In order to measure the distance to a cue, we connected all porpoise surfacings by linear interpolation resulting in supposed porpoise swimming tracks. Based on the three cue definitions we then divided each of these swimming tracks into segments of 15 s, 30 s and 60 s, and for each interval calculated the distance from the midpoint of the segment to each of the T-POD clusters or individual T-PODs. Each of these visually derived segments thus served as a trial at a known distance form the datalogger. The trial was classified as a success if there was an acoustic detection in the corresponding synchronised time period on the T-POD and a miss if not. We could therefore calculate the probability of detection per distance from the T-POD and a detection function was then fitted to the data by means of a GLM at the level of T-POD detection threshold, cue interval and click train category.

To calculate cue production rate, we used data from four Danish harbour porpoises that had been fitted with Atag dataloggers (kindly shared by Dr. T. Akamatsu) not far from our study site. Cue production rate was calculated for each of the porpoises as number of periods (15 s, 30 s and 60 s) with click trains per hour. To test the established detection functions I then calculated density based on visual detections within 100 m of each T-POD cluster (for the data obtained in 2007 only). Based on the visual data, I also calculated rate of false detections. For each visual observation period, I calculated the number of minutes without visual detections, but with acoustic detections. The false detection rate was calculated as number of minutes with false detections in percentage of the observation period, and was thus at the level of minutes and not at the level of click trains. The false detection rate was zero for seven of the eight T-PODs, where the last had a single false positive minute. The false detection rate was therefore not considered in the density estimation. Subsequently the derived T-POD detection function for each T-POD was used to calculate density based on T-POD data from the same observation period, but for 24 hours a day taking account of T-POD detection threshold, cue production rate and mean observed group size. The estimated densities were all within the same order of magnitude and corresponded to the visually derived densities. More importantly, the densities were at the same level between the different tested variables, which means that the individually derived detection functions effectively levelled out the differences caused by detection threshold, click train category and cue definition. This means that if a detection function has been derived at the level of datalogger or datalogger threshold, densities estimated from different areas become comparable across studies, if survey designs follow the general assumptions point transect sampling, i.e. that dataloggers are placed at random or systematically with respect to animal distribution in the study area. With this method it thus appears that we have achieved one goal of PAM of NBHF species; to assess absolute changes in population sizes over time.

In my study (chapter II) the highest probability of detection was found for T-PODs with the lowest detection threshold and the longest cue interval. However, since porpoises swim quite fast they may move considerable within a cue interval of a minute and the shortest interval of 15 s is therefore more optimal with regard to the assumptions of point transect sampling (see section on cue counting above) that requires that only one distance can be assigned to each observation. A single click or individual click train would in that sense be even more optimal, but we had several reasons to prefer a time interval with clicks instead: 1) As discussed above the level of false detections is simply too high for single clicks, as was also found for beaked whales, and 2) there is not enough information in a single click, if discrimination between different species should be necessary in an area.

I had three reasons not to use individual click trains as cue. First, it was impossible to obtain an exact distance the way that we calculated distance to the T-POD from the interpolated porpoise swim tracks, and we would therefore have added measurement error. Secondly, I have previously shown that the T-POD click train algorithm does not exclude reflected click trains (Kyhn *et al.*, 2006). This means that entire reflected click trains, so called *ghost trains*, with sometimes two reflections per original click train, are included. Thus, if click trains are used as cue, the final density estimate may be positively biased by these false detections. Thirdly, as discussed for the method employed by Kimura *et al.* (2010) and in chapter II, the use of click trains as cue is complicated since there is no consistent definition that will not depend on the directionality of the produced clicks: click train duration and duration of individual clicks will depend on whether it is recorded on an animal or by a datalogger and cue production rates derived from dataloggers fitted on animals may thus not be representative for the cues recorded on SAM dataloggers. Based on these three points, I found an interval with click trains to be the most reliable cue because it effectively limited the rate of false detections and because it makes estimations of cue production rate more comparable between recordings from a porpoise and from a SAM datalogger.

The finding of the low probability of detection in our study even within 50 m of a datalogger is puzzling. Our *g(0)* values are much lower than the results obtained for Hector's dolphin (Rayment *et al.*, 2009) and finless porpoise (Kimura *et al.*, 2010), and when comparing to the theoretical model (figure 4). By deploying acoustic dataloggers (Atags) on wild harbour porpoises it has been shown that they are silent regularly or that their source level regularly is below the detection threshold (140 dB re 1µPa pp) of the deployed Atag (Akamatsu *et al.*, 2007; Linnenschmidt, 2007). Porpoises are oppositely rarely silent in captivity (Kristian Beedholm, personal communication). However, the silent periods of wild porpoises are short, typically much less than of a minute duration and the availability bias that such silent periods causes is thus not expected to have a large impact on the detection probability especially not when using a long cue interval of 60 s. Along these lines, it is doubtful that Kimura *et al.* (2010) would derive the same high *g(0)* values empirically as they obtained theoretically with their modelled detection function since finless porpoises expose the same level of availability bias being silent for shorter or longer periods in the wild (Akamatsu *et al.*, 2007). Another possibility for our low *g(0)* values, as discussed in chapter II, is that the porpoises performed the so called *bottom grubbing* behaviour where they position their bodies vertically in the water - heads down - in search of demersal prey as has been observed in captivity (Desportes and Amundin, 2003). Due to the highly directional sound transmission properties of porpoises such behaviour could cause the porpoises to only sporadically point their beam in a direction where sound would hit the datalogger. This could cause incoming click trains to be too disrupted to be classified as porpoise click trains by the T-POD train detection algorithm thus resulting in a detection bias. This may perhaps explain part of the low observed *g(0)* values and could be tested by reanalysing the data based on detection of individual clicks per cue interval instead of click trains as defined by the T-POD software. However, given that it is a behaviourally caused detection bias causing the low *g(0)* values, the probability of detection would likely be higher in for example areas with deeper water where porpoises hunt prey in the pelagic.

Our method outlined in chapter II is not without problems; the most important being the assumption that porpoises move in straight lines between surfacings, and secondly, the difficulty of extrapolating this method to other areas, for example areas further from the shore. Future development of e.g. a small DTag (Johnson *et al*., 2010) will hopefully shed more light on how small toothed whales move around below the surface. Until then, it may increase the measurement error unnecessary by trying to model assumed swim paths as we do not have the required knowledge to do so correctly. Since porpoise/dolphin behaviour changes over the year and between areas, for example in response to available prey, group size, mating etc., it is very likely that the acoustic behaviour also change and that both the swimming behaviours and the detection functions will vary between areas, populations and over the year. Detection functions for visual line transect surveys are typically assessed for the individual survey for each observer and the same approach may be necessary for SAM detection functions. This is, however, difficult to achieve for most marine areas using our method, since it requires observations of the animals around the dataloggers. The next step is therefore to test if our detection functions are valid for other areas, i.e. deploy dataloggers systematically in an area that is also going to be surveyed visually by line transect surveys and then compare the final density results. If it turns out that our land based detection functions are invalid for offshore areas, another option is to make the detection function at sea from an anchored silent ship or another static feature such as a lighthouse or a bridge. A problem of that methodology could be that some species avoid or are attracted to platforms which could affect the probability of detection. A second problem would be to accurately measure distance to the animals if a theodolite is out of the question on a boat, but that could be achieved by deploying methods used on normal ship based surveys, for example combined video and visual observations (Gordon, 2003) to measure the angle below the horizon.

2.5. Concluding remarks

The field of applying SAM for assessing densities of toothed whales is in its infancy and the presented studies are the very first of their kind with the potential flaws inherent of new methodologies. Of the four presented methods tested, only the last three really pertains to smaller toothed whales such as the NBHF species. Despite that the lowest probabilities of detection were found using our methodology, it is nevertheless the method I would recommend for monitoring of NBHF species for assessing density because it has an easily defined cue allowing for a comparable cue production rates and because the method is empirically tested with a good correspondence to visual observations.

The best SAM system is a system that allow for localization of each animal cue by means of triangulation of the source from time-of-arrival differences (Madsen and Wahlberg, 2007) between more than 4 SAM dataloggers. The dilemma is, that it requires a large aperture array to be able to calculate distance to animals vocalising at large ranges. However, because toothed whale clicks are very directional, a wide spacing of hydrophones will reduce the chance that a click is recorded by all hydrophones. One solution to this problem may be to deploy SAM dataloggers as a web configuration like the hydrophones in the US Navy test range described by Marquez *et al.* (2009), where the optimal datalogger spacing is decided by trial and error from playback experiments. Such methodology requires exact synchronisation of timing between all dataloggers for example by regular emission of sync pulses. Further, the angles and distances between each datalogger must be fixed over time or all datalogger positions should be calibrated for every received sound for example by making the position of each datalogger known automatically by means of differential GPS. Such a method has the advantage that the distance to each cue is measured exactly; however a problem would be to assess the probability of detection, if some animals pass through the SAM web silently. Work is presently being carried out to test different options in regards of arrays of SAM dataloggers (Mark Johnson working with DMONs and beaked whales. Nick Tregenza working with a web of unconnected CPODs and harbour porpoises), and in the next few years we should hopefully see great advances in how to apply passive acoustic monitoring for obtaining densities of smaller toothed whales.

Now we have seen that passive acoustic monitoring may be used to derive densities of small odontocetes such as NBHF species and it is thus time to look at the sounds of these animals. Meaningful use of passive acoustic monitoring requires that the source parameters and acoustic behaviour of the studied species is understood in details at two levels: First of all a species' sounds must be well defined according to specific sound source parameters to be able to build precise filters for the acoustic dataloggers to sort the correct signals from noise. Such definitions require that the variation at the level of species is known and therefore that each focal species have been recorded using appropriate equipment under natural conditions. If there are several species in an area it is further essential to be able to distinguish between the species which may be possible provided fine frequency resolution of equipment and detailed signal analysis to find and statistically quantify species specific differences. Secondly, the acoustic behaviour of a species must be known to a level where it is possible to obtain cue production rates.

From the basic sound recordings and analysis of some of these species arose questions regarding the origin of this amazingly stereotypic signal across the four evolutionary different groups of cetaceans, which in turn spurred questions on 1) how these species may distinguish each other acoustically in areas where they live sympatrically? and 2) how we may utilise such potential species differences in passive acoustic monitoring?

3. Narrow Band High Frequency clicks of small toothed whales

The NBHF click is used by porpoises (though two species remain to be recorded), six dolphin species in the genera *Cephalorhynchus* and *Lagenorhynchus*, the pygmy sperm whale (*Kogia breviceps,* Blainville 1838) (Madsen *et al*., 2005) and the Fransicana river dolphin (*Pontoporia blainvillei*) (Von Versen *et al*. 1999). Thus likely fifteen species (table 1) use the signal, which must have evolved four times by convergent evolution (see figure 6).

Within the Delphinoidea family the NBHF signal is found in all four species in the genus *Cephalorhynchus* and in two *Lagenorhynchus* species (table 1). The dolphin taxonomy is debated and as I discuss in chapter V the acoustic data available as a whole are consistent with formation of a clade containing the four present *Cephalorhynchus* species together with *L. cruciger* and *L. australis,* and under that scenario the NBHF signal appears to be a synapomorphy of the clade suggesting that the signal evolved only once within delphinids. In the remaining of this outline I will refer to all six delphinid NBHF species as Cephalorhynchids despite that such clade has not been formally named. Excluding the hourglass dolphin, and to some degree Peale's dolphin, all Cephalorhynchids are obligate coastal species and they appear to be opportunistic, feeding near the bottom on dermersal fish, cephalopods and crustaceans (Bastida *et al.*, 1988; Schiavini *et al.*, 1997; Hammond, 2008; Reeves *et al.*, 2008). All Cephalorhynchids are predominantly found in smaller groups from 215 individuals (Goodall *et al.*, 1997; Reeves *et al.* 2002). Cephalorhynchids are, like porpoises, very susceptible to by-catch (e.g. Iñíguez *et al.* 2004; Slooten, 2007), and all of the coastal species are regularly by-caught in gillnets, commercial as well as amateur, leaving Chilean dolphins *near threatened* and Hector's dolphin *endangered* according to the IUCN red list. However, there is still a lot to be learned about these species and half the species are accordingly classified *data deficient* by IUCN.

Table 1. Species, habitat and acoustic source parameters of all recorded NBHF species*. The habitats are divided into three categories: Coastal is for species with obligate coastal or shallow water affinities. Shelf is for species found coastally, but with sightings offshore as well. Offshore refers to species found predominantly off the continental shelf and in deep waters. Only data on harbour porpoise, Dall's porpoise, Hector's dolphin, hourglass dolphin, Peale's dolphin, Commerson's dolphin and pygmy sperm whale were recorded using on-axis criteria. * Q-value not stated in literature and thus calculated as mean peak frequency/mean -3dB-bandwidth. Data are from: 1)Kyhn et al., (chapterVI); 2) Silber, (1991), 3)Li et al., (2005); 4) Götz et al. (2010); 5) Kyhn et al., (Chapter IV); 6) Morisaka (personal communication); 7) Kyhn et al., (Chapter III), 8) Madsen et al., (2005); 9) von Fersen et al., (1999) (Only "130kHz" stated).*

Family	**Genera**	**Species**	**Habitat**	**Peak frequency kHz**	**Centroid frequency kHz**	**Bandwidth kHz rms**	**Q -value rms**	**Duration µ**
Phocoenidea								
	Phocoena	Burmeister's porp	Coastal & Shelf	?	?	?	?	?
	Phoconoides	Harbour porpoise [1]	Shelf	139±4	140±5	21±4	7±1	54±8
	Neophocaena	Spectacled porpoise	Offshore	?	?	?	?	?
		Vaquita[2]	Coastal	128-139	?	17±5 (?)	8*	136(±41)
		Dall's porpoise [1]	Offshore	138±5	139±5	17±4	9±2	104±37
		Finless porpoise [3]	River & Coastal	125±7	?	20±4	6*	68(±14)
Delphinidae								
	Cephalorhynchus	Chilean dolphin [4]	Coastal	126±2	126±2	12±2	8 (-3dB)	83±30 (-20dB)
		Commerson's dolphin [5]	Coastal	132±6	133±2	12±3	12±3	78±13
		Heaviside's dolphin [6]	Coastal	126±3	127±2	13±2	10±2	71±10
		Hector's dolphin [7]	Coastal	129±5	128±3	18±5	8±2	57±6
	Lagenorhynchus	Peale's dolphin [5]	Shelf	126±3	129±3	12±3	12±3	93±18
		Hourglass dolphin [7]	Offshore	126±2	128±2	11±4	13±5	115±24
Kogiidae	*Kogia*	Pygmy sperm [8] whale (& dwarf ?)	Offshore	130±1	129±1	8±2 (-3dB)	16 (-3dB)	119±9
Pontoporiidae	*Pontoporia*	Fransiscana [9]	River & Coastal	'130'	?	20	6.5	?

Very little is known about pygmy and dwarf (*Kogia sima,* Owen 1866) sperm whales. Since they resemble each other closely and a closely related it is highly likely that they both use the

NBHF signal. Their sound production organ is homologues to the sperm whale, but rather different in proportions. They are deep divers and are found far offshore and thought to feed near the bottom. The pygmy sperm whale is known to rest motionless at the surface and when startled it escapes very fast while ejecting an ink like faecal fluid resembling the anti-predatory behaviour of squid (Reeves *et al*. 2002).

The Fransiscana is an obligate coastal species and with distribution in estuaries and shallow waters along the shores of Brazil, Uruguay and Argentina it is the only river dolphin found in the marine environment and the only river dolphin using the NBHF signal. It lives in small groups of 2-3 up to fifteen individuals and it has an inconspicuous behaviour at the surface. It predominantly eat small dermersal fish species as well as squid and shrimps, depending on season and location. By-catch is a serious threat to the Fransiscana (e.g. Kinas 2000; Bordino and Albareda, 2004) and the species is listed vulnerable by the IUCN redlist (Reeves, 2002).

Porpoises are distributed both on the northern and southern hemisphere and are found in rivers as well as far offshore. The harbour and Dall's porpoises are the best studied of the porpoises due to their coastal distribution in the Western world. Both species have a quite varied diet with prey species depending on exact geographic range, season and habitat (offshore or coastal), but generally speaking both forage for benthic, demersal, as well as pelagic fish (e.g. Aarefjord *et al*., 1995; Walker, 1996; Börjesson *et al*., 2003). Porpoises behave quite inconspicuously and are found in smaller groups. Porpoises appear very susceptible to by-catch (e.g. D'agrosa *et al*. 2000; Vinther and Larsen, 2004; Williams and Winship, 2008), which likely is a combination of their coastal distribution, their acoustics and foraging behaviour. The Vaquita is at present the most endangered (*critically endangered,* IUCN 2008) of any odontocete with a current population estimate of only 150 individuals (Jaramillo-Legoretta *et al*. 2007) and unless effective mitigation is immediately enforced it will be the second odontocete to go extinct in my lifetime.

The NBHF species thus occupy a vast range of marine habitats, but most are found coastally (table 1). The shared features appear to be a small body size, a preferred group size of two - three individuals (max fifteen), inconspicuous surface behaviour, a preference for demersal prey and high vulnerability to by-catch with several of the species under severe pressure with classifications such as *near threatened, vulnerable, endangered, critically endangered* by the IUCN red list. Despite the predominant coastal distribution very little is known about most of the species, likely due to their inconspicuous behaviour and predominant distribution in non-western countries.

We need to ask specific scientific questions in relation to for example by-catch to obtain the knowledge required to protect these species by appropriate mitigation, and one promising and inexpensive method to obtain more knowledge is by passive acoustic monitoring.

3.1. Toothed whale echolocation signals

Sound emissions of toothed whales can broadly be divided into communication and echolocation signals; e.g. whistles, burst pulsed calls and codas (clicks played out in stereotypical fashion by sperm whales), and biosonar clicks. Available data suggests that four different types of echolocation clicks have evolved within in the odontocete suborder. These signals are broad band transient (BBT) clicks from dolphins, river dolphins and monodonts (Au, 1993), multi-pulsed (MP) sperm whale clicks (Møhl *et al*., 2003), long frequency modulated beaked whale (FM) clicks (Zimmer *et al*., 2005) and narrow band high frequency (NBHF) clicks from porpoises, some small dolphins and the pygmy sperm whales as stated above. Echolocation signals are traditionally described in terms of frequency content (e.g. peak and centroid frequency, bandwidth), duration, directionality and source level. Such measures of echolocation clicks are collectively coined source parameters. Examples of the four different signals are given in figure 5 and representative source parameters are found in table 2. Toothed whale echolocation clicks are thus broad band with varying centroid frequency and duration. However, common for these ultrasonic signals are durations between 20 and 300 µsec, high source levels between 160 to 240 dB re 1µPa (pp), and directionality indices (DI) between 20 and 32 dB (Au, 1993; Møhl *et al.,* 2003).

The click types are typical of different families of toothed whales, however, the NBHF signal as explained stands out since it is used in several genera or subfamilies in different families and apparently evolved by convergent evolution four times (figure 6). The NBHF species further do not produce any other sound types than clicks; whether emitted as burst pulsed calls in behavioural contexts (Amundin, 1991; Clausen *et al*., 2010) or during echolocation. The three other sonar clicks are accompanied by either different sonar click types (beaked whales: Johnson *et al*., 2006) and or different communication sounds (BBT species (Au, 1993) and the sperm whale (Madsen *et al*., 2002a,b). This then raises the question of what selective forces acted on NBHF groups and drove the convergent evolution of this peculiar signal?

Table 2. Representative examples of source parameters of the four main types of toothed whale *echolocation clicks. Data from Au 1993; Møhl et al 2003; Johnson et al. 2006; Madsen et al., 2002; Madsen et al. 2005a; Villadsgaard et al., 2007. Duration of the clicks is defined differently between the studies. 95% and 97% duration is defined as the time containing 95% or 97% of the total click energy. -10dB duration is correspondingly the duration within -10dB points below the peak of the click envelope (see appendix 1 for illustration of source parameters).*

Click type	**Centroid frequency, kHz**	**RMS bandwidth, kHz**	**Q-value**	**Source level, dB re 1 µPa (pp) Maximum values**	**Directivity index,dB**	**Duration, µs various def.**	
NBHF	130-142	5-12	12-30	205	22	123-150	(95% energy)
BBT	78	27	3	229	26-32	40	(97% energy)
Sperm whale	15	4	4	240	27-?	120	(-10dB)
FM	38	7	5	200-220*	25*	271	(97%energy)

3.2. Theories for evolution of NBHF clicks

The classic explanation of the narrow band high frequency clicks is that it evolved for navigation and prey capture in acoustically complex habitats such as rivers and inshore waters (Wartzok and Ketten, 1999; Ketten, 2000); since the shorter the wavelength (higher frequency) the smaller the size of the objects that can be resolved by echolocation and high frequency clicks may thus aid the search for small objects in murky water. Only later was the signal found among offshore and deep diving species as well. The NBHF signal is also thought to be the result of symmetrical phonic lips (Cranford *et al*., 1996), however recent data show that porpoises can produce NBHF clicks using only the right pair of phonic lips (Madsen *et al*., 2010). The definite shared features of the species producing the NBHF signal are that none of the species make other sorts of acoustic signals, such as whistles, and that all species are relatively small, less than 3 m. Since they are found in very different habitats the notion of the NBHF signal as a shallow water phenomenon cannot explain a convergent evolution of the signal, but may have been a shared feature of the original species developing the signal. To uncover the possible selective forces responsible for the signal, it is necessary to look in closer detail on its acoustic properties.

The source parameters of all recorded NBHF species are listed in table 1 together with species, genus, family and habitat. The clicks of these small species have evolved to be of very high frequency with a centroid frequency of approximately 130 kHz. NBHF clicks are

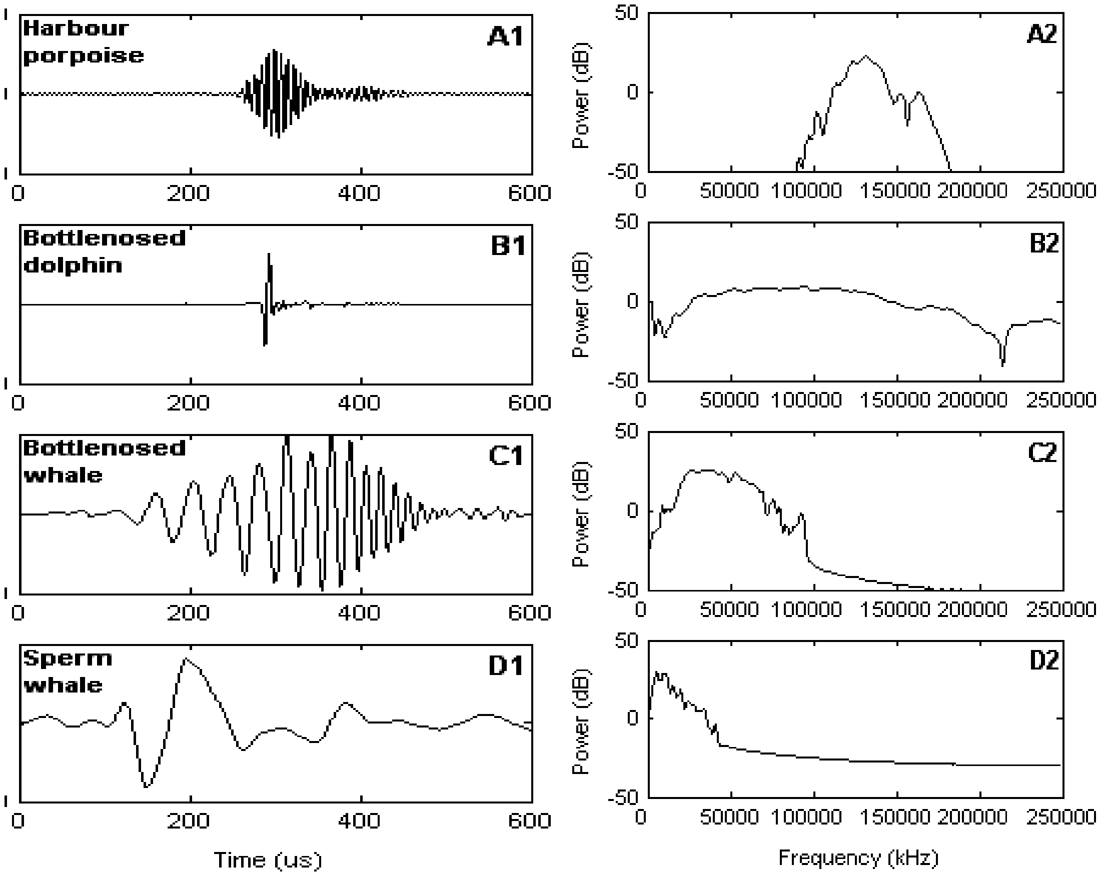


Figure 5. ***Example of the four different toothed whale echolocation clicks****: Waveform (1) and Power spectrum (2) of A) NBHF click from harbour porpoise (Phocoena phocoena), B) BBT click from bottlenose dolphin (Tursipos truncatus), C) FM click from bottlenose whale (Hyperoodon ampulatus) and D) MP click from Sperm whale (Physeter macrocephalus) (Courtesy of Frants Jensen).*

fairly stereotyped with a fast rise phase, of long duration of approximately 50-150 µs, and a narrow bandwidth with respect to the centroid frequency. The source levels of all recorded NBHF species are low relative to the three other click types. However, it is not the high frequency, the bandwidth nor the long duration that makes this signal special; as all these features may be found in some or all of the other three echolocation click types (table 2). It is the combination of the surprisingly stable high centroid frequency and the bandwidth; the quality factor or Q-value (Au, 1993) that singles out this signal from the remaining three click types (table 2). Q_{rms} is defined as centroid frequency divided by the RMS-bandwidth of the signal. The MP, BBT and FM species all have clicks with low Q-values and thus energy covering a broader range of frequencies relative to the centroid frequency. For BBT signals bandwidth and centroid is varying inter and intra-specifically, and in some cases the centroid frequency is comparable to the NBHF signal. Besides the high NBHF Q-value the spectral variation is always maintained above 100 kHz (figure 5 and table 1). NBHF clicks are produced along with a low frequency by-product around 2 kHz, but that is unlikely to play any role for communication or echolocation (Hansen *et al*., 2008). A low source level also seems diagnostic for the NBHF species and the reason may be an inherent limitation caused by the sound production organ necessary for producing NBHF sounds. It may result from how the phonic lips are actuated when producing the NBHF signal or it may somehow be related to the high frequency cut-off that NBHF porpoise clicks are produced with (Madsen *et al*., 2010) (see figure 11 below). The low source level may also be a behavioural adaptation which I will discuss later. However, the notion of low source levels should be viewed in the light that source levels only has been measured for seven out of the assumed 15 NBHF species.

The NBHF signal is thus different from other toothed whale echolocation signals in the combination of a stable high centroid frequency and a narrow bandwidth yielding high Q-value. This raises two important questions:

Why do NBHF species produce echolocation signals with these properties? And why did this signal evolve at least four times to display the consistent features among distantly related species occupying different habitats?

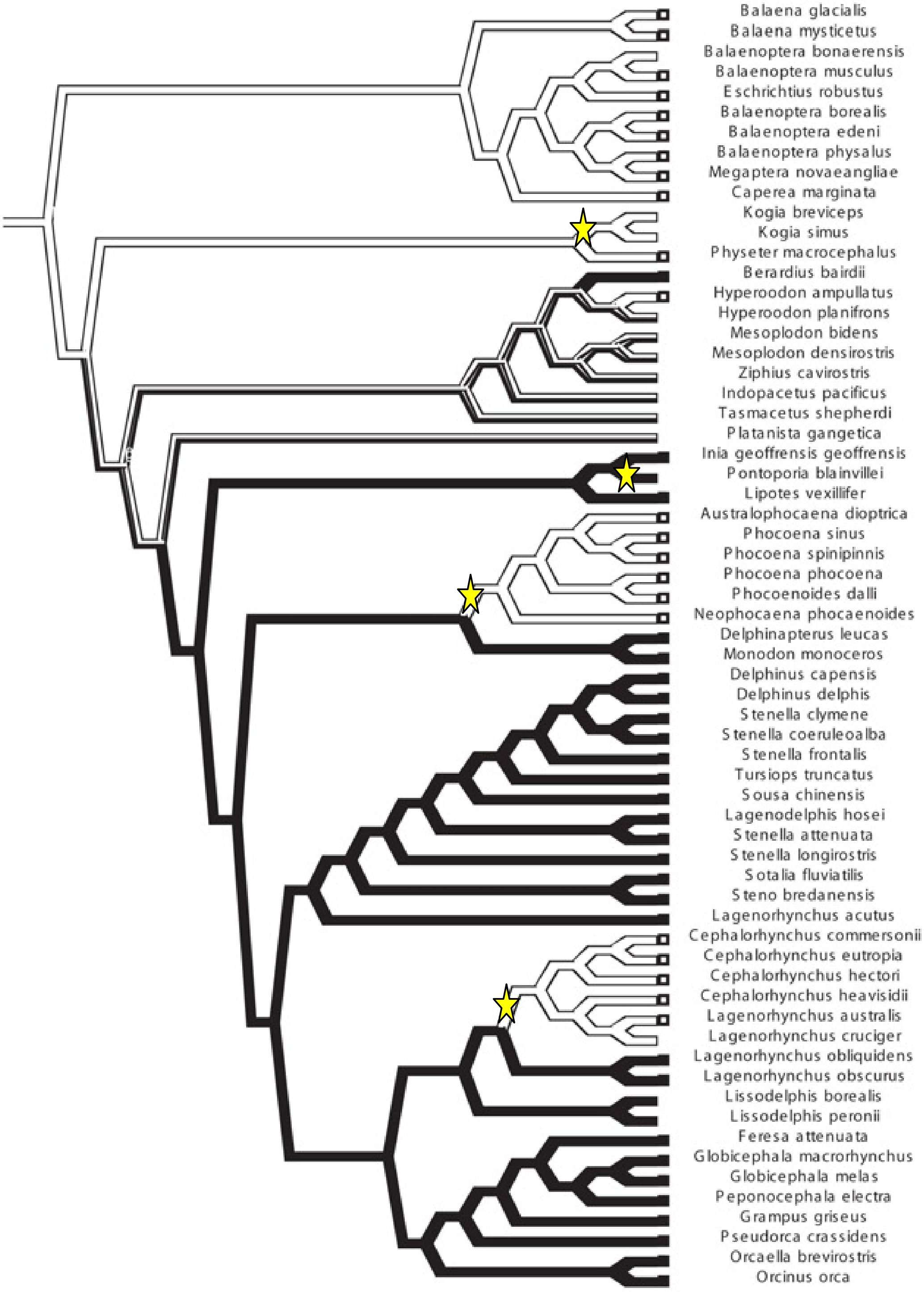


Figure 6. One view of the molecular phylogeny of cetaceans *(May-Collado et al., 2007). The phylogeny is shown to provide on overview of the emergence of the NBHF signal (yellow stars). See manuscript 2 for details on dolphin phylogenies. White lines are families that do not whistle. Open squares are absence of whistles and closed squares are presence of whistles. Both white and black lines together means ambiguous evidence for presence of whistles. The whistling of the Fransiscana river dolphin is an assumption only and has so far not been verified. (Adapted with courtesy of Dr. May-Collado from May-Collado et al., 2007). Whistle loss is also discussed by Morisaka and Connor (2007).*

3.3. *NBHF signals to increase sonar performance?*

Since the special feature of NBHF signal is the high Q-value that consists of two parts, both the bandwidth and the centroid frequency are relevant for the discussion of why NBHF click have evolved.

3.3.1. Why use a high centroid frequency?

A biosonar system requires clicks of high source levels to detect potential prey and obstacles at ranges that allow the animal to find sufficient amounts of food. A high source level can be obtained from pneumatic sound generation by focusing the projected sound pulse into a narrow, forward directed beam of high directionality. The high directionality is a function of the ratio between the size of the transmitting aperture and the wavelength of the projected sound (Au *et al.*, 1999) expressed as the wave number, *ka*, $k = \frac{2 * \pi}{\lambda}$, where λ is wavelength of the sound source, and a is the radius of the effective aperture of the transmitter. The acoustic projection system of toothed whales can be modelled by an equivalent planar transducer that has the same directivity index. A circular piston has traditionally been used to mimic sound production of toothed whales (e.g. Au, 1993; Au *et al.*, 1999) not necessarily because it behaves like a toothed whale, but because it is reasonably straight forward to model (Madsen and Wahlberg, 2007).

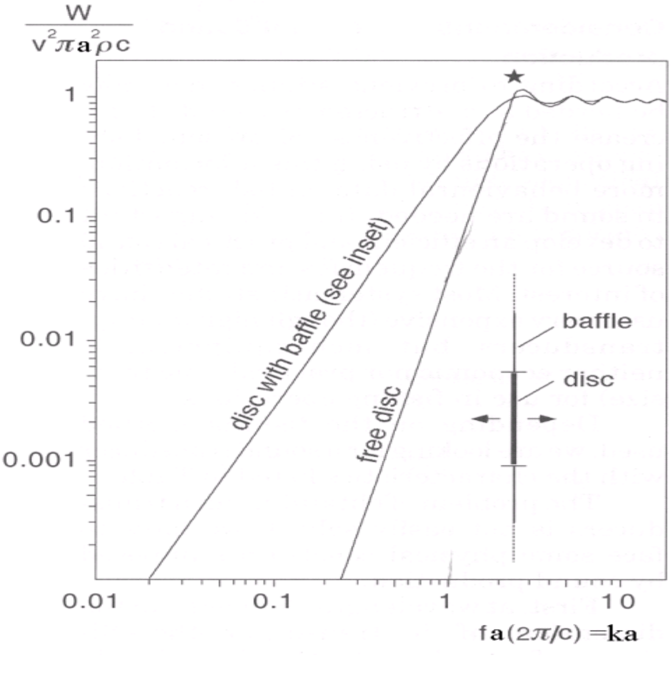
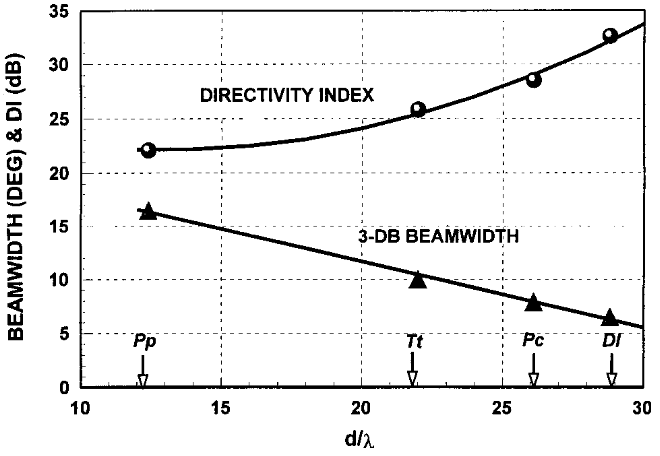


Figure 5. The relationship between sound production efficiency in generating pressure and the size and wavelength emitted for a flat piston vibrating with or without a baffle*. The unit of the y-axis expresses efficiency of sound production. (Wahlberg (2005), but originally adapted from Michelsen, 1983).*

For efficient production of sound pressure (rather than excess particle motion), the product of $k \cdot a$, where a = radius of a piston sound source, has to be greater than 1 (figure 5). However, to achieve a directionality index as found for all measured toothed whale echolocation clicks above > 20dB (figure 6) ka of an equivalent planar transducer has to be larger than 10 (figure 7). DI of a directional source expresses the difference in source level between the source level of a directional source and the source level of an omnidirectional source emitting the same power (Urich, 1983).

Figure 6. Transmission directivity index and 3-dB beam width for four odontocetes. *Pp (Phocoena phocoena), Tt (Tursiops truncates), Dl (Delphinapterus leucas), Pc (Pseudorca crassidens). d is the head diameter. The wavelength, λ, corresponds to the average peak frequency of the animals' echolocation signal. The directivity index is fitted with a second-order polynomial curve and the beam width is fitted with a linear curve. (Figure from Au et al., 1999).*



The greater the DI the higher the SL for the same power, and the larger the sound source the greater the DI for the same wavelength (Urich, 1983). Transmission properties of a biosonar system are thus dictated by the size of the sound production organ and the spectral properties of the transmitted sound pulse (Urich, 1983; Au, 1993). The high centroid frequency of the NBHF species may thus be a result of their small body size and the small equivalent apertures of their sound production organs, which is implied by the fact that the smallest of the non-NBHF species have the highest centroid frequencies (e.g. the 2.7 m short-beaked common dolphin (*Delphinus delphis*) has 112 kHz centroid and spotted dolphins have centroid frequencies at 130 kHz or higher (Jensen and Madsen, pers. comm). Thus, given their size it is not surprising that NBHF species have centroid frequencies above 100 kHz to achieve DI's higher than 20 dB like other, larger toothed whales.

One study have conclusively shown that bottlenose dolphins can steer their sound beam (Moore *et al.* 2008), and several studies have shown variation in sound beams or results indicating that both BBT delphinids and monodonts (Au, 1993; Au *et al.*, 1995) as well as harbour porpoise can steer their beam (Madsen *et al.*, 2010). Whether NBHF dolphins and porpoises also may change their DI purposefully is more doubtful, yet as I have shown in chapter IV and VI the

DIs of five groups of wild NBHF species was of higher DI than expected based on data from captive harbour porpoise (Au *et al*., 1999) (DIs given in figure 6). If the animals can change DI it means that animal size and signal wavelength likely only provides a basis for the directivity. Another explanation for the lower DI measured by Au *et al*. (1999) may be that they averaged over many clicks recorded both on and off-axis, whereas we measured DI directly for each on-axis click and its five off-axis representations, knowing the angle and distance to the animal. It remains to be shown if NBHF dolphins and porpoises besides steering the beam also may change the directionality.

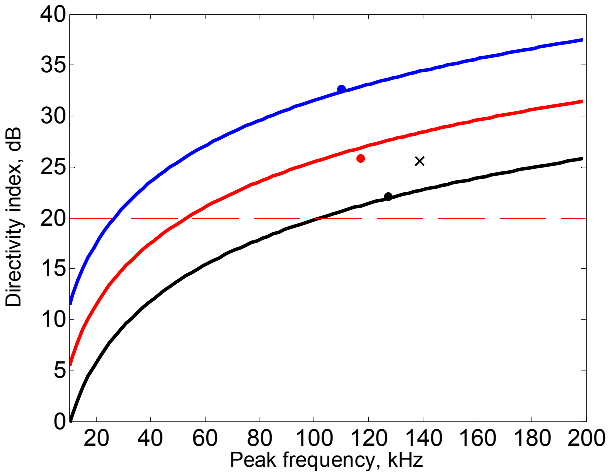


Figure 7. Effect of size of piston and centroid frequency on directivity index (DI). *DI is calculated as* $DI=10\log(a^2 * k^2)$*, where k is the wave number* $(2\pi/\lambda,)$*, a is radius of piston and λ is wavelength = speed of sound(m/s) / frequency(Hz). DI is calculated for three theoretical equivalent apertures with the same radiation properties as the odontocete sound production organs:* ***Black*** *(Porpoise) = 2.3cm,* ***Red*** *(Bottlenose) = 4.0cm,* ***Blue*** *(Beluga) = 9.5cm. Dots are DIs and peak frequencies from Au et al. (1999) of the respective species. The black cross is DI and peak frequency of wild Danish harbour porpoises (chapter VI). The broken red line is DI = 20, which may represent a minimum DI for toothed whales (see text). It is seen that the larger the equivalent aperture the lower the frequency that can be used to produce a given DI. For a small odontocete like the harbour porpoise, only a frequency greater than 100 kHz would generate DIs comparable to larger toothed whales.*

Background noise level in the deep ocean reaches a low somewhere between 30 kHz and 180 kHz, and with increasing sea states the lowest noise levels are found at increasingly higher frequencies (Urich 1983). Figure 8 is the only general noise curve available for frequencies above 100 kHz. However, it describes the deep ocean situation, which is not relevant for most NBHF species. Nevertheless, while the background noise level in shallow water is generally much higher than for deep seas, the spectral noise levels drop with increasing frequency, at least up to the highest measured frequency of 100 kHz (Urich, 1983, fig. 7.8), and the inferences about NBHF exploitation of low ambient noise levels at high frequencies (Madsen *et al.*, 2005) are thus likely to apply for most marine habitats, deep or shallow. It is thus possible that the specific properties of the NBHF signal with a high Q and the signal energy above 100 kHz are adaptations for this low-noise window.

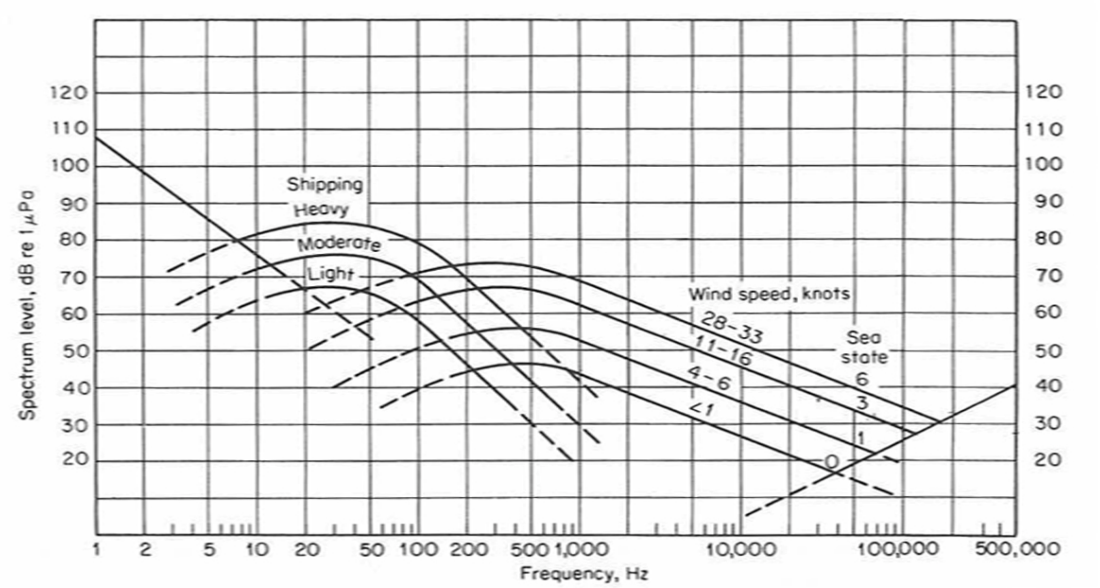


Figure 8*. *Average deep water ambient noise spectral levels *(N_0). Urich (1983, figure 7.5).*

3.3.2. Why the narrow bandwidth?

Møhl and Andersen (1973) first suggested that the narrow band click of harbour porpoises could be an adaptation to improve echo to noise ratio (ENR) of returning echoes since the masking noise that interferes with detection of a signal increases with bandwidth of the signal. The mammalian auditory system can be viewed as a filter bank with overlapping frequency bands centred at different frequencies (Nachtigall *et al*., 2000). A sound stimulus will be masked by noise in such a band if the masking noise is above the hearing threshold at the given frequency. Thus, for echolocation signals; the smaller the click bandwidth the better detectable a signal is from background noise of a given spectral noise level provided that the signal is matched with a similar auditory bandwidth on the receiving side.

The auditory filter bank composition is inferred by two means of measuring bandwidths: From critical ratios (CR) or by measuring critical bandwidths (CB). Critical ratio builds on the assumption that at the threshold level where a tone is just audible in white noise, the bandwidth can be derived as the difference in amplitude between the sound pressure level (SPL) of the signal (dB re 1 μPa, rms) and the noise spectrum level (N_o) (dB re 1 $\mu Pa^2 Hz^{-1}$) by CR = SPL - N_o (Fletcher, 1940; Scharf, 1970; Kastelein *et al.*, 2009). Critical bandwidth is found by reducing signal-to-noise ratio for a range of noise bandwidths until S/N threshold is constant with increasing noise bandwidth. The critical bandwidth is then judged as the bandwidth where threshold no longer increases with increasing bandwidth, and that bandwidth is assumed to be of same width as the auditory filter. Both CR (Kastelein *et al.*, 2009) and CB (Popov *et al.*, 2006) have been measured for porpoises and different BBT species. The general picture for mammals is that critical bandwidth increases with centroid frequency of the tested tone resulting in constant Q (Scharf, 1970; Au, 1993). Popov *et al.* (2006), however, found that the critical bandwidths of finless and harbour porpoises only increased from 3 to 4 kHz going from a centroid frequency of 32 all the way to 140 kHz. This means that porpoises have constant bandwidth filter bank where other mammals have constant Q-filter bank. One function of this difference appear to be that threshold not nearly to the same extend increases with centroid frequency as observed for mammals in general (Popov *et al.*, 2006). Porpoises have thus preserved high sensitivity hearing even to the highest measured tone frequencies, which makes sense given their high frequency echolocation signals. The function of the constant bandwidth filter bank is likely to match the frequency of best hearing to the frequency and bandwidth of the NBHF signal. Since best sensitivity normally is at lower frequencies where the critical bandwidths are narrower (Kastelein *et al.*, 2002; Popov *et al.*, 2006) the high frequency sensitivity may have evolved by shifting the narrow auditory filter bands up in frequency over time resulting in a constant bandwidth filter bank over the entire auditory spectrum. There is still a lot to be learned about hearing in toothed whales, and future auditory studies on different NBHF species should provide us with better means to interpret the evolution of their hearing in connection to their click source properties.

The apparently matched auditory filter and narrow band properties of the porpoise NBHF signal, however, suggests an advantage in noisy shallow water areas, since the narrow bandwidth has the effect of decreasing the absolute detection threshold of returning echoes from NBHF signals in relation to the broader BBT signals of the same echo level. For the same SPL the NBHF signal thus seems to be of advantage in terms of improving the echo-to-noise ratio (ENR) due to the smaller bandwidth on both transmission and receiving sides. However, since absorption increases with frequency (figure 9) there must be a trade-off for maximizing detection range between absorption and the effects of reducing masking noise by pushing a given bandwidth up in frequency.

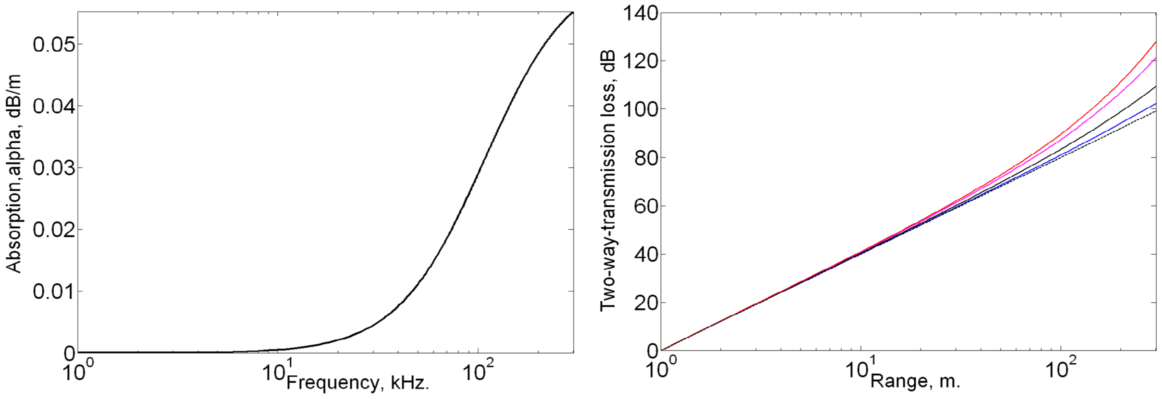


Figure 9. *A) Effect of centroid frequency on absorption and B) effect of absorption on transmission loss (TL). In B)* ***Red*** *line is 200 kHz,* ***Magenta*** *is 130 kHz,* ***Black*** *line is 65 kHz and* ***blue*** *is 32.5 kHz.* ***Dotted line*** *is TL= 40·log(range). It is clear that absorption and thus transmission loss increases with centroid frequency.*

3.4. Model of target detection range for signals of different centroid frequency

There are thus many physical consequences that have to be integrated to evaluate possible selective forces driving the evolution of the NBHF signal. Here I introduce a model to incorporate as many of these constraints on sound emission and reception as possible to explore the consequences of the trade-off between the relative effects of 1) the possible low-noise window at 100-150 kHz, 2) the lower detection threshold effects of a narrow bandwidth signal and 3) the negative effects of increased absorption with increasing frequency. This comparison will make it easier to see the relative advantages and disadvantages of the NBHF signal in relation to the other types of echolocation signals. First I assume a single signal of fixed bandwidth (15 kHz) resembling a NBHF click and compare the effects of varying the centroid frequency on absorption for the same source energy flux density. Since the ear operates as an energy detector (Au, 1993; Au *et al.*, 1999) different click durations with the same peak pressure will yield different detection thresholds because the energy content of a click increases with click duration (Au, 1993). To simplify the model I have therefore expressed SL as the energy flux density of the click with unit dB re 1μPas^2. Thus a NBHF click with a duration of 100 μs and a source sound pressure level of 200 dB re 1uPa (pp) will have the same source energy flux density as a BBT click with a duration of 25 μsec and a source sound pressure level of 206 dB re 1uPa (pp) due to the longer duration. Secondly, I include a click with a three times wider bandwidth (45 kHz) resembling a BBT click and again vary the centroid frequency to see effects of the increased bandwidth of a BBT click compared to a NBHF for each centroid frequency and for the same source energy flux density.

The model is based on the following assumptions:

1. Masking noise (NL) was estimated as; $NL = No(Fc) + 10\log(BW_{RMS})$ (Møhl *et al.*, 2003), where *No* is the background spectral noise level at the centroid frequency, Fc. *No* was read of figure 8 for sea state 3. BW_{RMS} is the rms-bandwidth of the emitted click/returning echo and was kept constant at 15 kHz to represent a NBHF click or at 45 kHz to resemble a BBT click.
2. Source energy flux density level (SL), receiving directivity index (DI) and target strength (TS) were assumed constant.
3. Detection threshold (DT) for the animal was assumed to be at the same echo to noise (ENR) level above the masking noise for all centroid frequencies.
4. That the spectral noise is lowest in the environment around 130 kHz.

I will start by introducing some more general biophysical considerations to justify the assumptions. During transmission back and forth to the target, part of the intensity of an echolocation click is lost as a result of absorption and geometric spreading and this is termed transmission loss (TL). Absorption increases with frequency and the absorption coefficient, α, can be estimated from Fisher and Simmons (1977) for a given centroid frequency and water temperature. The centroid frequency of a signal thus affects the received level of the returning echo, and the centroid and bandwidth will determine the masking noise level, which will affect the detection range of a given target keeping all other things equal. This is formalized in the active sonar equation:

$$ENR = SL - 2TL + TS - (NL - DI) \qquad \text{(Urich 1983)}$$

where transmission loss is $TL = 20 \cdot \log(R) + \alpha \cdot (R)$, *R* is range to target in meters and α is the absorption coefficient in dB/m at the centroid frequency of the signal. NL is noise level, TS is target strength, SL is source level and DI is directivity index. For detection of a signal of a given frequency the echo level has to exceed the noise level with some factor (ENR) by which the detection threshold (DT) can be defined as a certain dB level of ENR above the masking noise level at the center frequency of the echo. Thus, the echo-to noise ratio goes up when SL, TS and DI go up or when TL or BW goes down. Here it is assumed that ENR for detection on a statistical basis is the same for all centroid frequencies. In the model, SL, receiving DI and TS were assumed to be constant (assumption 2), while TL and NL were varied (as a function of varying bandwidth) and thus changing ENR. To see these changes most easily the resulting changes in ENR were normalised relative to the ENR of a NBHF signal at detection threshold. Thus at 0 dB in figure 10 the NBHF echo is just detectable for a given range, SL and target, so when a value ΔENR on the y-axis is higher than zero, it means that the animal would need to increase SL by that dB difference to detect that specific target. If the ΔENR is below zero it means a better echo to noise ratio by that dB difference than for the NBHF signal for the same source energy flux density, target and range. It is thus a way to quantify the effects of centroid frequency and bandwidth as a function of range all other things equal. Assumption 1) requires that masking noise level *can* be calculated from the bandwidth at each centroid frequency given white noise conditions in that frequency band, yet as discussed above this assumption may not be valid for all situations.

Results of the model are shown in figure 10 as a function of target range (x-axis). Changes in echo-to-noise ratio (ΔENR) (y-axis) was normalised relative to the NBHF signal to aid interpretation (**magenta solid line**). The following was modelled:

a) The effects of absorption and masking noise on detection threshold was modelled for signals of different centroid frequencies (**32.5**, **65**, **130** and **200** kHz) and equal bandwidths (15 kHz) and source energy flux densities. Go from magenta solid line to any other solid line to see the effect on ΔENR (y-axis) and target range (x-axis) from the change in frequency with effect on absorption and background noise.

b) Test of effects for BBT click: Bandwidth was assumed three times wider for the same four frequencies. Go from solid magenta to any broken line to see the effect of increased bandwidth and thus increased masking noise on ENR relative to the NBHF signal (solid magenta).

With the inherent limitations and weaknesses of the listed assumptions, several points can be made about the apparent advantages of the NBHF signal from this model (figure 10):

1) For the same source energy flux density level and bandwidth, a click at 130 kHz will have the best echo to noise ratio for ranges shorter than some 100 meters compared to the

other frequencies. Beyond target ranges of some hundred meters, for the same BW, the absorption will render poorer echo to noise ratios compared to clicks at lower centroid frequencies, whereas a centroid frequency of 200 kHz will perform worse than NBHF clicks regardless of the range.

2) If the NBHF signal is compared to a BBT signal of the same centroid frequency and source energy flux density, but with a bandwidth three times wider, it is seen that the echo to noise ratio for the same range is 5 dB worse at shorter ranges and that the BBT first yield the same echo to noise ratio at target ranges of more than 200 meters.

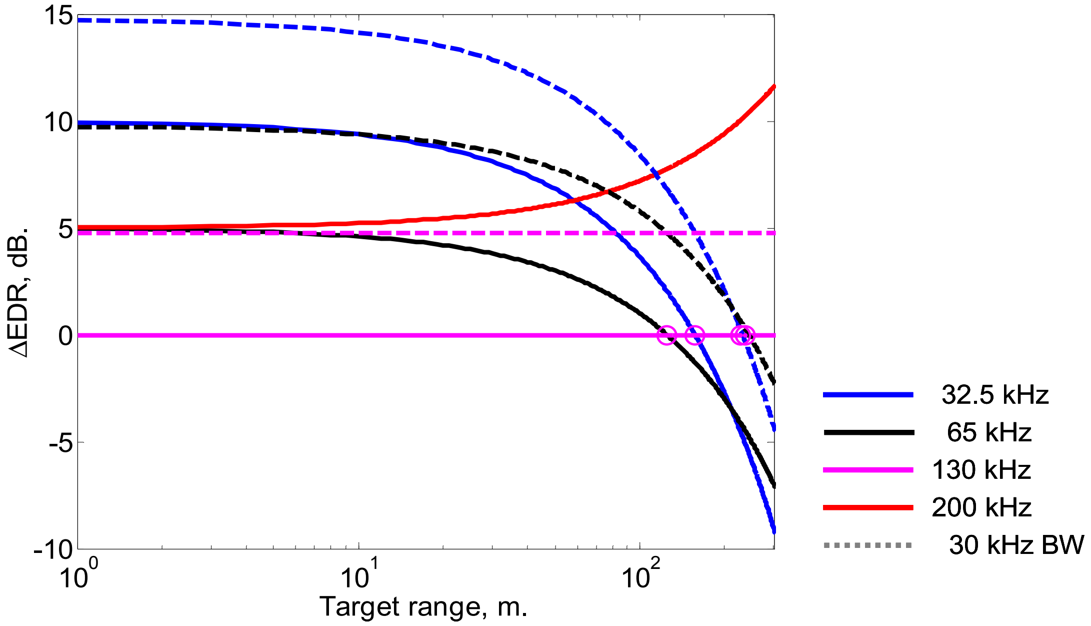


Figure 10. Effects of absorption and masking noise on detection range. *The effect is calculated as summed costs/benefit in dB with respect to the echo-to-noise ratio (ENR) at detection threshold (DT) of a NBHF click (*ΔENR*) (y axis) with bandwidth of 15 kHz as a function of target range (x-axis). The figure assumes fixed source energy flux density level and TS. Making noise levels (NL) are calculated from fig. 7.5 in* Urich (1983) *for sea state 3 in deep water assuming a fixed BW of 15 kHz. Absorption is calculated by equations given by* Fisher and Simmons (1977) *for relevant centroid frequencies (31.25, 62.5, 130 and 200 kHz) and 14°C.* ***Magenta*** *solid line is for centroid frequency of* ***130*** *kHz.* ***Black*** *solid line centroid frequency of* ***65*** *kHz.* ***Blue*** *solid line centroid frequency of* ***32.5*** *kHz.* ***Red*** *solid line centroid frequency of* ***200*** *kHz.* ***Broken lines of colour x mimics the effect of switching to a BBT type click*** *with a BW of 45 kHz (3 x NBHF BW) for same centroid frequency and source energy flux density as colour x.*

It is thus clear that a centroid frequency of 200 kHz is of little use for toothed whale biosonars due to the high absorption, and that a centroid frequency of around 130 kHz likely represent an upper centroid frequency border for efficient sonar due to increasing absorption and spectral noise. In this respect it is interesting that the high pass filtering of porpoise signals allows frequencies above 160 kHz off-axis, while energy on-axis is sharply restricted to frequencies between 110-160 kHz, with essentially no energy at frequencies below 100 kHz (Madsen *et al*., 2010, figure11). Because frequencies above some 150 kHz are increasingly inefficient for biosonar and because the animals cannot hear them anyway there is no low pass filter applied off-axis. Further, it is clear that for a fixed bandwidth there is a positive effect of the low-noise window at 130 kHz in terms of a decreased masking noise, which is seen as the difference in ENR at 1m target range. Additionally, a three times wider bandwidth (broken lines) has a clear negative effect on ENR irrespective of centroid frequency compared to the NBHF signal type with 15 kHz bandwidth (magenta solid). Yet, if bandwidth of a 130 kHz signal is three times wider (magenta broken line) the low-noise window only offers a small advantage in detection range in relation to the lower centroid frequency signals at 15 kHz bandwidth, and only for very short ranges. Thus for a fixed source energy flux density level the low noise window at 130 kHz offers an advantage of the NBHF signal out to about 100m. The signal is as such very well suited for short range sonar. However, it is also clear from the high absorption that NBHF signals are very unsuited for long range sonar, where lower frequency biosonar systems are much better (Madsen *et al*., 2002a) irrespective of signal bandwidth.

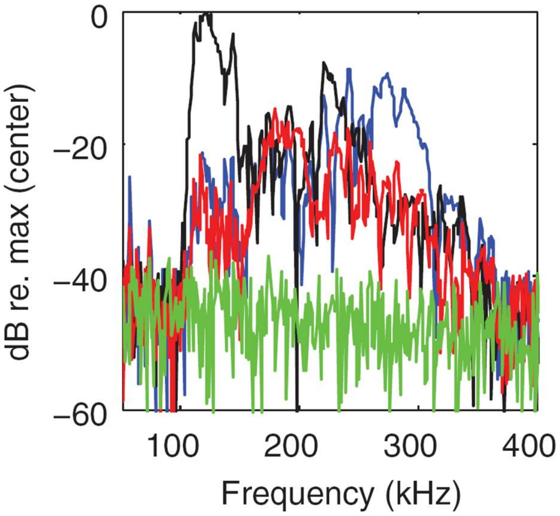


Figure 11. Harbour porpoise high pass filtering*.* *Power spectra of the same click recorded with suction cup hydrophones at three locations on a porpoise head; on-axis (black line), right (blue) and left (red). Green line shows relative spectrum of the noise recorded in a section preceding the clicks. The figure illustrates the extreme hi-pass filtering – there is plenty of energy above 130 kHz, but essentially no energy at frequencies below 130 kHz in the on-axis angle (Madsen et al., 2010) illustrating the importance of only removing energy below about 100 kHz.*

Compared to BBT type signals of different centroid frequencies, it is seen from figure 10 that the NBHF signal for the same source energy flux density renders ENRs that are between 5 and 15 dB better for short ranges. This then raises the question of why all delphinids do not use very narrow band signals at different centroid frequencies depending on their size and needs of sonar ranges? The BBT species will due to a shorter click duration require 3-6 dB more pressure to generate the same energy flux density as NBHF species, so if all toothed whales were peak pressure limited, NBHF species would have an overall advantage due to their narrow bandwidth, long duration and the low-noise window around 100-150 kHz. However, if production of NBHF clicks somehow is peak pressure limited (table 1) (some 200 dB re 1uPa (p.-p.) according to all available data (Madsen *et al*., 2005; Villadsgaard *et al*., 2007; Li et at., 2009; chapter III, IV and VI herein)) compared to similar sized BBT species (SLpp up to 225 dB re 1uPa (p.-p.), (Au 1993; Au and Herzing, 2003), it seems that BBT species can overcome that 3-6 dB difference AND the 5-15 dB poorer ENR from a larger masking bandwidth simply by making a higher peak pressure. Then if the long duration of NBHF clicks should serve to increase energy flux density, why not just make normal BBT dolphin clicks, where the energy goes up with the square of the pressure (i.e. 6 dB more source energy would either require four times longer duration or twice the pressure)? Rather it seems that the long duration of NBHF clicks has evolved to generate a narrow bandwidth rather than increasing energy flux density as proposed by Au (1993). The evolution of the NBHF signal may therefore not only be explained by the enhanced echo to noise ratio for target ranges below 100 m.

3.4.1. Concluding remarks on the model of target detection ranges for signals of different centroid frequency

It seems likely that the NBHF signal evolved as a result of small body size in terms of the high frequency, whereas the narrow bandwidth and long duration does not seem to be explained only by exploitation of a low noise window at the 100-150 kHz, since e.g. BBT species of the same size apparently just turn up peak pressure and overcome the negative effects on ENR of short signal duration and larger masking bandwidth. On top of this a broader bandwidth yields an echo of greater spectral resolution, which at least in man-made sonar provides better target discrimination, and the lower spectral resolution of the NBHF signal may thus also be of potential disadvantage for NBHF species. Hence it seems at least partially that another explanation must exist for the evolution of the narrow bandwidth of the NBHF signal.

3.5. Acoustic crypsis

The second theory for evolution of the NBHF signal proposes that the signal evolved as an acoustic crypsis against killer whales (*Orcinus orca*, L., 1758). That idea was first advanced by Andersen and Amundin (1976), subsequently by Madsen *et al*. (2005) and then Morisaka and Connor (2007). Killer whales overlap in distribution with all NBHF species and the associated risk of predation is thus a factor joining all NBHF species. So called *transient* killer whale pods are known to kill or attack cetaceans regardless of their size (e.g. Jefferson *et al*., 1991; Barret-Lennard *et al*., 1996; Reeves *et al*., 2002). The term *transients* strictly apply to mammal eating killer whale pods in British Columbia, Canada, but I will use this term in general for mammal eating killer whales and the term *residents* for fish eating killer whales (*sensu* Ford *et al*., 1998).

Transient killer whales communicate with whistles and burst pulsed calls of fundamental frequency below 20 kHz (Deecke *et al*., 2005; Riesch *et al*., 2008), but with many harmonics at higher frequencies. Echolocation clicks of *residents* have broadband bimodal frequency spectra with low and high frequency peaks at 24 and 108 kHz (Au *et al*., 2004; Simon *et al*., 2007) and the same likely apply for transients when they echolocate. Hearing sensitivity has been measured for a few toothed whales in captivity. Audiograms (figure 12 and 13) of mammals generally have a u-shape, where the left side slopes down gradually to some minimum threshold; whereas the right site has a steep high frequency cut-off of about 100 dB/octave (Au, 1993). This means that hearing sensitivity at frequencies above the high frequency cut-off quickly becomes very limited and then practically non-existent. The difference in audiograms between species is the position of the high-frequency cut-off. The hearing sensitivity below the high frequency cut-off is more similar, but in general the higher the best frequency of hearing the poorer the very low frequency hearing will be. The harbour porpoise has its best hearing sensitivity around 90-100 kHz (Kastelein *et al*., 2002) and the finless porpoise is most sensitive around 45 kHz and 108 kHz (Popov *et al*., 2005) (with unexplained dips in between – maybe the two tested animals has experienced hearing trauma at the intermediate range?). It is possible that this mismatch between click centroid frequency and frequency of best hearing is an artefact caused by animals' clicking during the auditory experiments possibly masking their own hearing. An incomplete ABR-audiogram of a stranded pygmy sperm whale calf showed that of the measured frequencies it was most sensitive at 90-150 kHz (Ridgway and Carter, 2001). These are the only audiograms of NBHF species and the echolocation clicks of killer whales are thus well within the hearing range of at least the porpoises and most likely also of all other NBHF species.

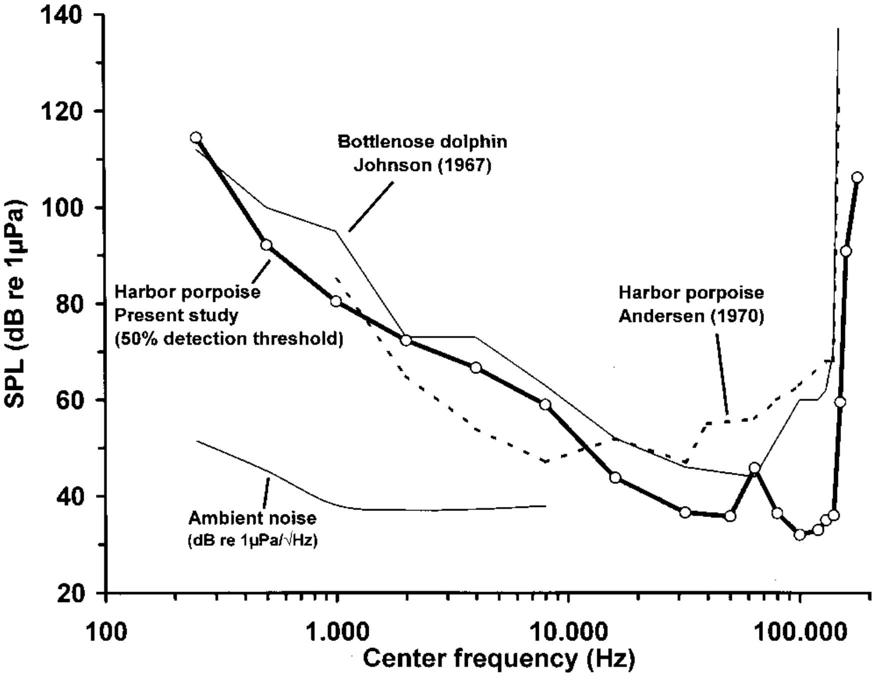


Figure 12. Audiogram of a harbour porpoise *measured with narrow-band frequency-modulated signals, measured on one 2-year old captive male porpoise. The area of most sensitive hearing is from 32-50kHz and from 100-140kHz. It is unclear whether the lower area of sensitivity was special for that specific porpoise or whether it is general for porpoises. (Figure from Kastelein et al., 2002).*

The best hearing sensitivity of killer whales is at 16-42 kHz (based on two captive females (Szymanski *et al.*, 1999), and the sensitivity drops above app. 40 kHz with a less pronounced high frequency cut-off than normally observed. The audiograms were made as both ABR measurements and as psychophysical testing. I plotted the mean ABR killer whale audiogram next to five NBHF power spectra in figure 13 and it seen that there is no frequency overlap between killer whale hearing and NBHF click energy (the Y-axis are not comparable). The two killer whales responded behaviourally to 0.5 ms tone bursts of 100-120 kHz if played out at very high source levels half a meter from the animal. However, this could be the result of the broad band nature of such a short pulse (figure 14) or distortion of the transducer if it was approaching its maximum output. Thus what the killer whales actually heard might be radiated energy at frequencies below 100 kHz.

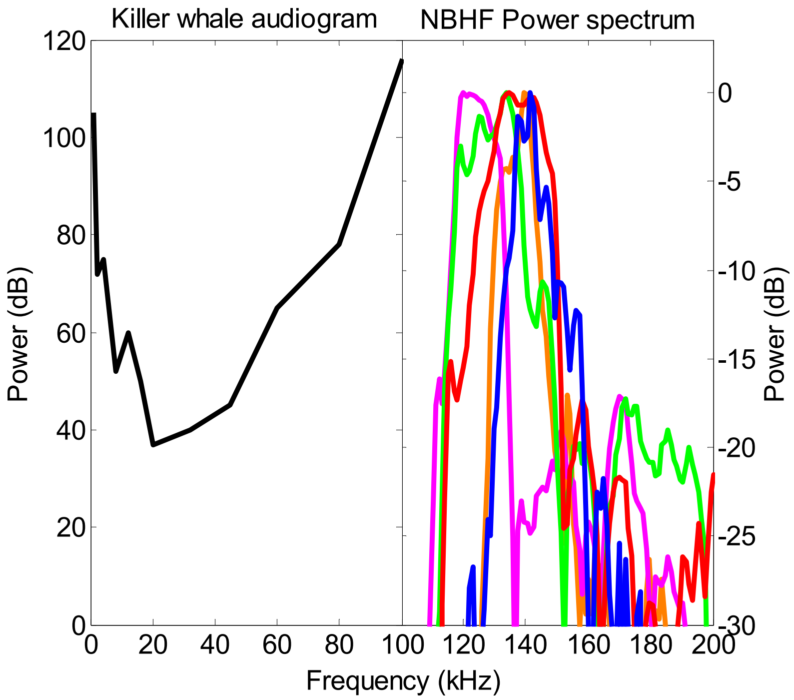


***Figure 13. Mean hearing sensitivity of two killer whales and power spectrum of five NBHF species**. Mean ABR audiogram of two killer whales (black line) in the left panel and power spectra of five NBHF species (coloured lines) in the right panel. The X-axis is thus continuous for the two plots, while the left Y-axis represent hearing threshold and the right normalised power, where 0 dB is most power. The two tested killer whales were most sensitive at 20 kHz, the peak frequency of their own echolocation clicks and only one of the whales responded to frequencies higher than 100 kHz behaviourally, however, at a high sound pressure level. If these two audiograms are general for killer whales, it is clear that NBHF species have to be very close in order to be perceived. (The audiogram is adapted from Szymanski et al., 1999).*

Even if the killer whale can hear tone burst of 0.5 ms duration at frequencies above 100 kHz they have to be played out very close by and be of high received level. (The tone bursts of 0.5 ms are app. five times longer than NBHF clicks, which means that for a NBHF click to be of similar RL for the killer whale as the tone bursts it would have to be at least 7 dB higher). This means that for all practical purposes killer whales likely can not hear NBHF clicks.

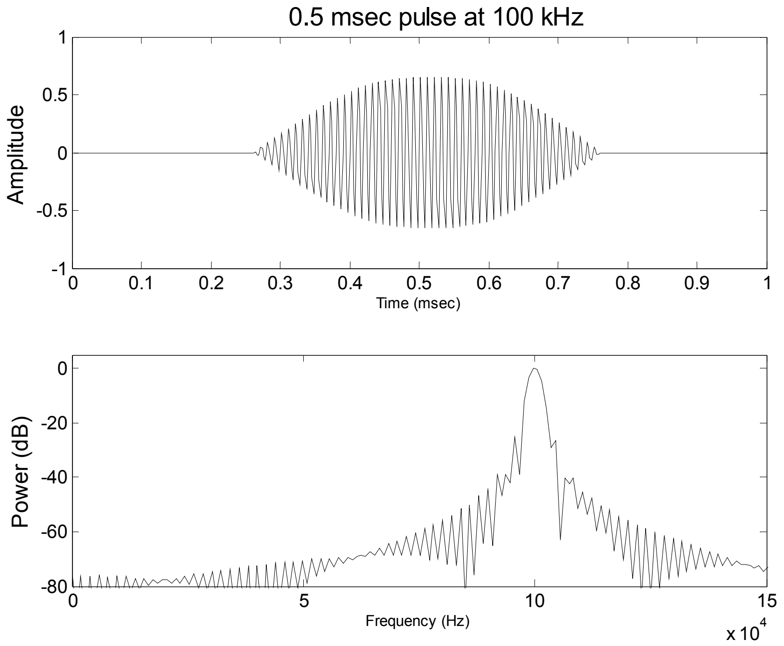


***Figure 14. Power spectrum of 0.5ms tone pulses centred at 100 kHz**. Notice the energy content of frequencies below 100 kHz, where killer whales can hear.*

According to the anti predatory hypothesis the advantage of the NBHF signal is that all click energy is kept at frequencies above the upper hearing range of the killer whale. Given that all measured NBHF species have almost identical centroid frequencies of around 130 kHz it is likely to satisfy a short range sonar optimum between the costs of absorption in terms of detection range and having a high enough centroid frequency and narrow enough bandwidth to keep all energy above killer whale hearing threshold (app. 100 kHz).

There are several lines of evidence to suggest that predation by transients may have caused the Q change of NBHF clicks. First, the threat of transient attacks is real. In for example Southeast Alaska Matkin *et al*., (2007) witnessed 43 *transient* attacks & kills and of these 28 % were on Dall's and harbour porpoises.

Despite their larger body size the source levels of killer whale whistles only reach 168 dB re µPa (likely RMS) (Miller, 2006); however, since the peak frequency and thus absorption is low, a porpoise should be able to hear communicating killer whales at large enough ranges to be able to flee or make other behavioural changes to avoid detection. In all cases at much larger ranges than where killer whales may detect porpoises by echolocation or passive listening. And these acoustic predator prey interactions may likely have forced the predator to either hunt in silence or change to frequencies outside the hearing range of its prey (Deecke *et al*., 2005). Likely for this reason there is a difference in vocalization rates between hunting *transients* and *residents*. Whereas *residents* actively find and chase their piscivorous prey using echolocation and communicate at the same time (Barret-Lennard *et al*., 1996; Simon *et al*., 2007; Au *et al*. 2004), *transients* hardly vocalize until the prey is killed (Deecke *et al*., 2005) and they do not use echolocation when hunting mammals (Barrett-Lennard *et al*, 1996), despite that they hunt in very skilled and coordinated fashion. This silent hunt has been interpreted as a means to avoid detection by their prey (Barrett-Lennard *et al*., 1996). Accordingly where fish eating killer whales use echolocation to detect and track down their prey, their mammal eating con-specifics seem to rely on passive acoustics, likely to decrease the risk of being detected by their prey. If so, the small-group living and inconspicuous behaviour of NBHF species at the surface could be seen in this light (Morisaka and Connor, 2007) since the primary cue for killer whales besides listening is vision. The effect of the echolocation signal of the NBHF species and the silent hunting behaviour of killer whales is as such an evolutionary arms race between predator and prey to avoid being eating by the NBHF species and to avoid being detected by the prey for the killer whale, if indeed the NBHF signal is inaudible for killer whales.

In conclusion, it seems likely that the NBHF signal evolved convergent in several cetacean families as a signal that would provide acoustic crypsis against killer whales, by employing a narrow bandwidth for a centroid frequency adaptive according to the physical constraints inherent of a small sound production apparatus, to yield effective active sonar for short range prey capture and orientation. The constant bandwidth auditory filters may then have evolved secondarily to match the narrow click bandwidth. If the auditory bands were of constant Q with increasing centroid frequency, as for other mammals, the narrow band echoes would result in higher detection thresholds with frequency due to the greater masking potential of wider auditory filters.

In chapter VI I show that one of the differences in echolocation source parameters between harbour porpoises from a killer whale free Danish habitat and a habitat with transient killer whales in British Columbia is that the source level is much lower where there are killer whales. I suggest that this difference is due to a potentially higher clutter level in the BC habitat, since sympatric Dall's porpoises also used quite low source levels in spite of their otherwise offshore range and larger body size. However, if there is the slightest chance that a prey may be heard by its predator it should lower the source level. Such a strategy is seen in the Asian corn borer moth (*Ostrinia furnacalis*) where males whisper during courtship to reduce risk of predation and thus increase chance of mating (Nakano *et al.*, 2008). Despite that it seems unlikely that killer whales may actually hear porpoises, it is intriguing to think that porpoises may employ a similar strategy and whisper if there are killer whales nearby. This could be investigated in two playback experiments:

One to test whether killer whales *can* hear NBHF clicks at a level where it makes sense for porpoises to react by lowering their source levels. In such an experiment different sound types including a normal as well as a down-played NBHF click is played back to killer whales that then respond behaviourally or by auditory evoked brainstem responses, while the received SPL at the whale is recorded simultaneously.

The second experiment should test how porpoises react to killer whale sounds. If there is no reaction in terms of changes in either vocalization rates or source level it would imply that they already are cryptic to killer whales. Oppositely, if they react by either being silent or by lowering source level it would indicate that killer whales in fact may hear NBHF clicks and that it is favourable to change acoustic behaviour for example by whispering. In that case we need to look for a different explanation for the evolution of the NBHF click type. Since bottlenose dolphins also are known to predate on harbour porpoises (Patterson *et al.*, 1998) and since they can hear such high frequencies (Au *et al.*, 2002) porpoises may regardless of killer whale hearing abilities benefit from a lower source level in areas where they overlap with bottlenose dolphins.

Since killer whales prey on all cetaceans we should also expect that similar anti-predatory measures have evolved in other cetaceans. However, all other odontocetes produce sound audible to killer whales and they have thus evolved behavioural adaptations to reduce the risk of predation instead. The gregariousness of most dolphin species has been seen as such as a strategy to reduce risk of predation by the dilution effect (re Norris and Schilt, 1988). Following this premise the individual thus depends on conspecifics to avoid predation and it thus appears adaptive that these species are highly social with rich acoustic vocabularies that may facilitate group cohesion, and there is indeed a positive correlation between sociality and acoustic repertoire (May-Collado *et al.*, 2007). The conspicuous jumping and “playful” surface behaviour could be to spot killer whales from the air, where the long dorsal fin of male killer whales should be visible long before the whale itself is sighted or heard underwater. The behaviour of gregarious BBT dolphins is consistent with the notion that inconspicuous behaviour of NBHF species living in very small groups may be an anti-predatory measure (Morisaka and Connor, 2007). Sperm whales also have a range of social behaviours associated with protection against predation from sharks and killer whales (Gordon, 1998). Female sperm whales remain in matrilineal family units throughout life and take turn babysitting while others are foraging. If threatened or attacked they form a circle to protect their calves in the middle (Gordon, 1998). The dive patterns and acoustic behaviour of Blainville's beaked whale (*Mesoplodon densirostris,* Blainville, 1817) and Cuvier's beaked (*Ziphius cavirostris,* G. Cuvier, 1823) whales have also been interpreted as a strategy against killer whale predation (Tyack *et al*., 2006). Beaked whales do not begin to echolocate until at a depth of minimum 200 m when descending and when ascending they stop clicking already 600-800 m below the surface and ascent at a low pitch angle whereby they surface away from the last point they clicked (Johnson *et al*., 2004). Despite this, they remain close together in small groups in the short periods they spend at the surface with no sounds made at all at shallow depths (Tyack *et al*., 2006). Maybe the risk of predation from killer whales also in part has caused the Monodonts to move into the pack ice on the Northern Hemisphere and the small river dolphins to move up rivers? It is in any case quite remarkably that the only river dolphin – the Fransiscana river dolphin - with marine living has evolved to use the NBHF signal and not the BBT signal used by the three other species of river dolphins living in a killer whale free environment.

3.6. Concluding remarks on theories for the evolution of the NBHF signal

Available evidence so far suggests that the NBHF species evolved these special echolocation click source properties to meet the dual requirements of operating an effective sonar system from a small head and at the same time to minimize the risk of killer whale predation from passive listening. Given the size of the NBHF species the high centroid frequency is required to produce a directionality index comparable to that of other toothed whales. However, since the signal will suffer from increasingly high absorption with increasing centroid frequency there is an upper limit on centroid frequency for efficient sonar, which may help explain that all known NBHF species have centroid frequency around 130 kHz. The narrow bandwidth does yield a lower masking noise level, compared to BBT signals of similar and other centroid frequencies. However, one of the special source parameters of NBHF clicks or the sound apparatus necessary for making these sounds are apparently limiting peak pressure. The effect is that the low source level in combination with the high centroid frequency limits NBHF sonar systems to short ranges. Either way; the entire lack of energy below 100 kHz and the low source level will likely reduce the risk of predation from killer whales significantly. The sonar requirements may have driven the selection for the high centroid frequency to begin with, whereas the bandwidth has been narrowed subsequently to reduce risk of predation from killer whales both accompanied by a matched sensitive hearing at the frequency of echolocation by evolving a constant bandwidth auditory filter bank of narrow bandwidths for the entire hearing range.

Trying to figure out why a particular trait evolved is inherently problematic since evolution and adaptations are recurrent events taking place as you read, but with some effects only measurably over thousands of years. For small insects with fast lifecycles we may experiment and see some reactions fast over generations, however, it becomes a lot more complicated when working with large mammals. Yet, in being so eager to understand and describe there is a danger that we end in *just so stories* that may well be interesting reading, but also wrong. I have recorded and analysed clicks of six NBHF species in the wild, as shown in table 1. As discussed in chapters III, IV and VI the clicks are remarkably similar across the species of both Cephalorhynchids and porpoises. However there are small differences between species, and also within the same species recorded in different habitats. In the chapters III, IV and VI I discuss the differences in relation to species recognition, but also in regards to habitat differences. Yet, despite the very thorough and consistent choice of clicks and analysis I have performed one big problem remains, and that is to be able to test what the differences means for the animals in their natural habitats? I argue that the very narrow bandwidth and high DI clicks of the Falkland dolphins (chapter IV) may be an adaptation for efficient biosonar in a cluttered coastal habitat, since clutter will not favour production of high source levels. Oppositely, the offshore hourglass dolphins use clicks of much higher source level as do the Danish harbour porpoises when found in more open/deep habitats, and I argue that such habitat will favour production of high source levels to increase detection range. The problem however is that I have no means to evaluate these conjectures. As a future study it would therefore be extremely interesting to fit small DTags to these animals to be able to quantify the actual amount of clutter they receive in their coastal environment by analysing the incoming echoes (e.g. Madsen *et al.*, 2005b), as well as to measure the levels of background noise in different habitats, especially in relation to human impacts such as seismic surveys, vessel noise, noise from bridges. Such a study would enable a better understanding of how flexible the NBHF species are and what may cause them to change source parameters.

We have now examined how the NBHF signal may have evolved and how it may benefit the species utilising the signal. There are however more serious threats to many NBHF species than predation; namely human induced encroachment of their habitats such as for example by gill nets along the coast. By-catch is a serious problem that reduces the population sizes of many of these coastal species and it is therefore prudent that we adopt new and cheaper ways to study and monitor them to enforce mitigation, especially for the countries that do not have the economic means to perform traditional visual surveys. However, many of the NBHF species overlap in distribution and we therefore need to be able to separate them acoustically in order to apply passive acoustic monitoring to accurately measure changes in population sizes over time.

4. The acoustic unit of species separation

The prerequisite for separating NBHF species is to have detailed knowledge of the sound source parameters of each species. This requires high quality wide band recordings made with a hydrophone array of more than four hydrophones to be able to distinguish between on- and off-axis clicks. Further the source parameters of clicks must be described according to specific definitions (Madsen and Wahlberg, 2007). Definitions of source parameters are necessary because they can be applied in automatic detection routines which eventually will be the foundation of the species separation in SAM. Thus the criteria for detection and inclusion in SAM data and the definitions used for describing the click source parameters must be comparable.

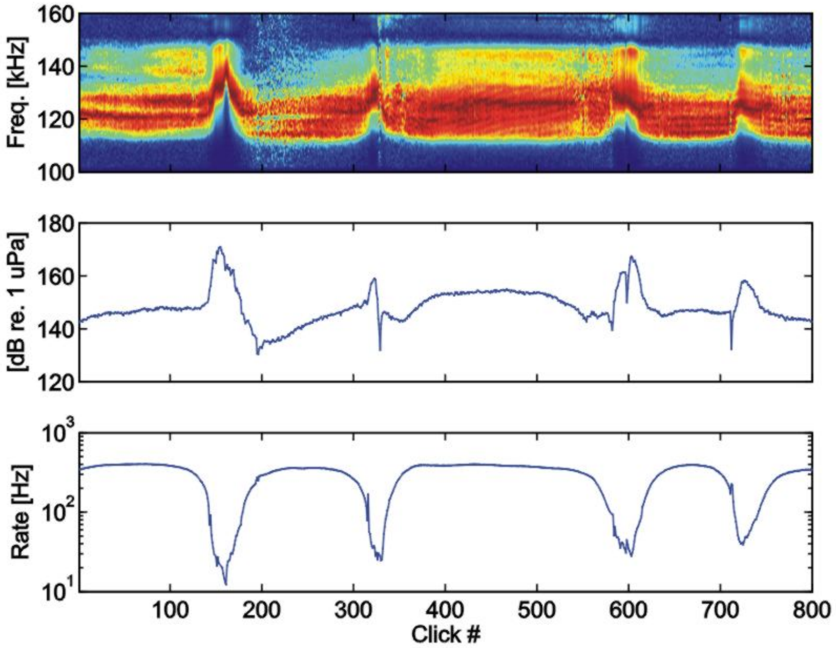


Figure 15. Spectral content of harbour porpoise clicks *change with click repetition rate: When click rate goes down (bottom panel) source level increases (middle) and frequency goes up while bandwidth decreases. (Courtesy of Kristian Beedholm).*

As I discuss in chapter VI the first step in finding species differences should involve the level of variability of clicks within an individual. Studies of harbour porpoises in captivity have shown that the spectral content of clicks changes with click repetition rate and source level (figure 15 Beedholm, 2010). Within a click train centroid frequency goes up and bandwidth narrows down as source level increases in amplitude with falling click repetition rate, however this has only been observed at lower source levels and for click repetition rates much higher than used from the wild in my studies. Nevertheless, it potentially means that differences in spectral content could be the result of recording different behavioural stages instead of being genuine species differences. To avoid this I based my species comparisons in chapter III, IV and VI on clicks that complied with a set of pre-set criteria optimising the chances that the clicks were recorded on-axis. In figure 15 I would for example only choose *the one click* of highest source level (middle panel) for further analysis. Doing that for all click trains and doing it the same way for all recordings should thus reduce the inter-click-train variation if the highest source levels also are correlated with the lowest click rates in the wild. Yet, for the porpoises I studied in chapter VI there was no correlation between inter-click-interval and source level and the values were above those observed in captivity. However, since that was the case for all the species I find that the species descriptions I have made, may be used to find acoustic species differences.

All recorded NBHF clicks are seemingly identical, however, when applying the on-axis criteria statistical differences do occur (Table 2). Dall’s and harbour porpoises recorded in British Columbia had a mean difference in centroid frequency of 5 kHz and the likewise sympatric Falkland Island dolphins, Peale’s and Commerson’s dolphins, were distinguishable by a mean centroid difference of only 4 kHz. In chapter IV and VI I used these centroid frequency values to differentiate between the species. From a mix of on- and off-axis clicks I randomly picked 100 click pairs of varying number of clicks. For each click pair size I then calculated mean centroid frequency for the 100 click pairs. The resultant mean centroid frequencies were then submitted to a Monte Carlo simulation where correct species ID was based on whether the mean centroid frequency of a click pair was above or below a threshold found from a ROC plot. The Monte Carlo simulation was based on 1:5 on-axis-to-off-axis clicks. It turned out to be easy to separate the species and quite small click pairs could give a high percentage of correctly identified click pairs, even with inclusion of off-axis clicks (see chapter VI, fig. 4). The Monte Carlo simulations were however based on combinations of randomly selected clicks and it would be expected that click trains with less variation between individual clicks would require more clicks to obtain the same results. Species separation could be supplemented by discriminate analysis (principal component analysis) that seeks to describe variables that maximally discriminate between groups, i.e. discriminate analysis can be used to find a variable that may be consistently different among minimum two groups. This variable is then used for assigning single observations of variable *m* to either group (McGarigal *et al*., 2000). The advantage of discriminate analysis is that it may be applied to sets of clicks in a click train, which will increase the precision of the mean by reducing variation among clicks and thus make it easier to decide which group of parameter belongs to. This methodology will be tested on some of the available NBHF data sets that I have recorded. The next challenge is then to design dataloggers that may exploit these fine spectral differences at these high frequencies.

Conclusively, it is possible to separate pairs of sympatric NBHF species where the clicks have been thoroughly described. Acoustic monitoring of sympatric NBHF species thus seems very promising. Yet, it requires dataloggers that may sample the entire frequency spectrum of the clicks. Thus new and better dataloggers are required in order to test SAM in areas where several NBHF species overlap, as for example in South America.

4.1. Species separation by the species

An interesting question arose while analysing the spectral differences between echolocation clicks and that was whether the species themselves may use the small spectral differences to find the right species for mating, for example during the night? The theory of character displacement (Brown & Wilson, 1956) predicts that in areas where closely related species overlap characters that allow species recognition should shift in regards to areas where the species is found alone in order for the species to avoid wasting energy on hybridization. Since there are significant differences in for example centroid frequency between each of the two pairs of sympatric species I have studied, it appears possible that the differences evolved to allow species identification especially since the Danish harbour porpoise and the British Columbian harbour porpoise had different centroid frequencies. This however does not prove that the animals can tell the difference or that they make use of the differences, and that makes it inconclusive as to whether the differences may in stead result from founder effects.

We have a general lack of knowledge on both BBT dolphins' and porpoises' ability to separate between clicks of different frequency and duration (DeLong *et al*. 2003) and it is therefore difficult to validate if they may use the small, but consistent, centroid frequency differences, I have found between the species (chapter III, IV & VI), for species recognition. When looking at results from blind target discrimination experiments it is clear that bottlenose dolphins easily can discriminate between targets based on echo information alone (Au, 1993; Helweg *et al.* 1996; Harley *et al.*, 2003). Further, in a phantom-target study a bottlenose dolphin had to discriminate echoes from a 7.6 cm diameter solid stainless steel sphere that was filtered with different high and low pass filters before being projected back to the animal. The dolphin was apparently able to correctly separate phantom echoes differing by only 1 kHz in frequency content from the unfiltered phantom echo projected back to the animal using the same equipment. The frequency content was compared on the basis of spectrograms of both phantom echoes (Ibsen *et al.*, 2009). Given that bottlenose dolphin clicks are on the order of 25 µs in duration they must generally be able to assess the spectral and time information contained in somewhat longer echoes (about 0.3 ms in the study by Ibsen *et al.*, 2009), for example by assessing small frequency differences (DeLong *et al.*, 2006) or by integrating information over several echoes (Helweg *et al.*, 1996) to discriminate between targets. That odontocetes can make use of frequency information is evident from clutter experiments where beluga whales can distinguish target echoes of lower received level than clutter echoes received from a clutter wall (Au, 1993). The ability to distinguish frequency differences is measured as frequency limens, where a frequency modulated (FM) signal is played out synchronously with a constant frequency (CF) signal. The FM signal is centred at the centroid frequency of the CF signal and the modulation is then decreased until the animal no longer can distinguish between the signals. This point is defined as the frequency limens threshold and is expressed as the max frequency minus the min frequency of the FM signal in percentage of the CF signal, i.e. the perceived difference in percentage of the standard. Bottlenose dolphins have frequency limes of less than 0.008 for carrying frequencies up to 130 kHz using 2.5 s signals (Thompson and Herman, 1975). However, ability to assess frequency differences has not been established for short duration sounds like clicks, yet based on the above studies it appears likely that bottlenose dolphins may have good frequency discrimination also for transient clicks and echoes.

One line of evidence that the centroid frequency differences between the NBHF species are large enough to be exploited for species differentiation, at least by porpoises, is their constant bandwidth auditory filters of 4 kHz (Popov *et al.*, 2006; Kastelein *et al.*, 2009). For both of the pairs of two sympatric NBHF species I have measured, the centroid frequency difference was 4-5 kHz. These findings in combination with the narrow auditory filters (Kastelein *et al.*, 2002; Popov *et al.*, 2006) suggest that they may use such small frequency differences. However, as discussed above there appear to be a mismatch between click centroid frequency and frequency of best hearing for porpoises (figure 12) (Kastelein *et al*., 2002; Popov *et al*., 2006). To test whether the 4-5 kHz differences in centroid frequency may be of use to the animals we therefore filtered clicks from Dall's and harbour porpoises with the audiogram of Kastelein *et al*., (2002) in chapter VI and calculated new source parameters, and submitted the new centroid frequency values to a Monte Carlo simulation to see if the differences in centroid frequency were persistent and still large enough for species separation. The results were even better than before the filtering. The apparent lower frequency around 130 kHz in the porpoise audiogram, whether based on an artefact or not, thus does not seem to hinder species differentiation based on 4-5 kHz centroid frequency differences. Lastly, despite of yet another line of circumstantial evidence, the most convincing argument, however, that the NBHF species may use such small centroid frequency differences for species separation comes from the fact that harbour porpoise accurately (>90 % correct) can distinguish between balls of equal size but of different materials (brass, steel, pvc, plexiglass) when blindfolded (Danuta Wisniewska, personal communication, figure 16).

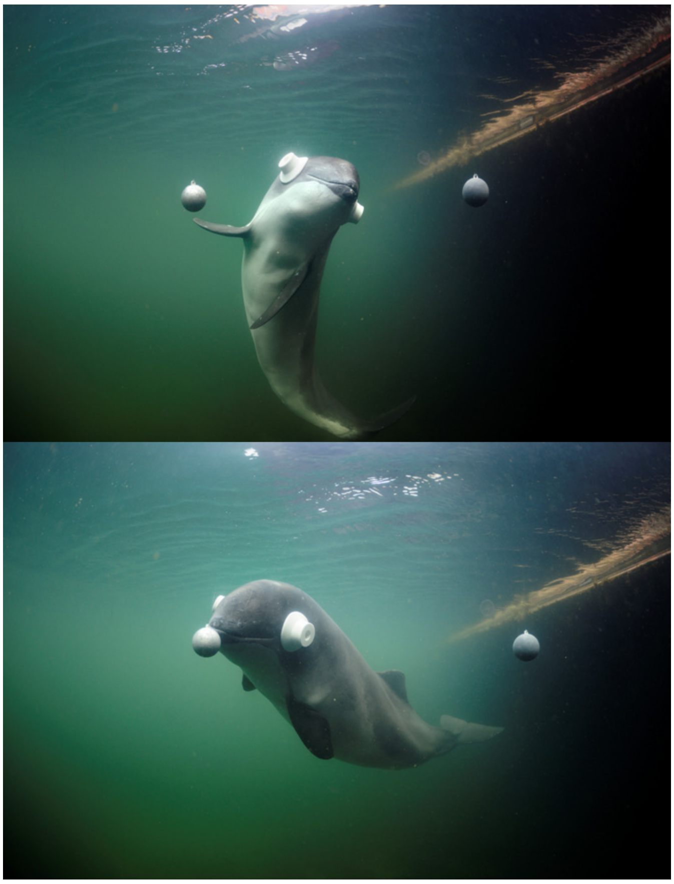


Figure 16. Blind folded harbour porpoise in target discrimination experiment *where it has to choose one of the two balls based on material only. Balls of four different materials (brass, steel, pvc and plexiglass) were included and the balls were shifted around in random fashion. The porpoise was blind folded and chose the ball of the correct material based on echolocation alone. (Courtesy of Danuta Wisniewska, pictures taken by Solvin Zankl and shown with permission from Fjord & Belt).*

Being able to do that, makes it hard to believe that they cannot also separate between friend and foe based on spectral click differences alone, even they always, naturally, will use all senses available. If they further integrate frequency information over several clicks they may perceive such spectral differences at the level of burst pulsed calls, as is used during different behaviours in captivity (Amundin, 1991; Clausen *et al*., 2010) or they may be able to recognise species based on such different click repetition rate patterns. Above all they will likely not restrain themselves to a single sense, nor a single acoustic cue, such as centroid frequency, neither generally when echolocating, nor when making such important choice as to whom to mate with. With regards to different acoustic cues, for the time being the frequency resolution of the clicks I have recorded is simply not high enough to include differences in for example bandwidth.

4.2. Concluding remarks on acoustic species differentiation

We have now seen that different NBHF species may accurately be identified to species based on differences in centroid frequency alone and we have consequently made the grounds for making passive acoustic monitoring available for sympatric NBHF species. As discussed previously the next few years will hopefully see advances in SAM dataloggers, and now knowing that small spectral differences of about 4 kHz exist on a statistical basis, should be taken into account when designing new equipment. The dataloggers in use at present for NBHF species, such as TPODs and CPODs (Chelonia Ltd.) unfortunately does not have the required frequency resolution and cannot separate sympatric NBHF species (Munro, 2010).

Secondly, circumstantial evidence suggests that porpoises may be able to distinguish between species based on species specific differences in echolocation clicks. In line with the results of the target discrimination experiment by Wisniewska *et al*. (personal communication) it would be very interesting to make a similar experiment where the porpoises are asked to discriminate between clicks of different centroid frequency to find their click frequency limens as well as to make a classic frequency limens study to examine how similar/different the frequency resolution is in relation to signal duration. If they integrate frequency information over several clicks, they may then make use of entire communication burst pulsed calls (Amundin, 1991; Clausen *et al*., 2010).

5. Conclusion

I have here shown that echolocation clicks can function as cues for animal presence to assess density by combining the methodology of cue counting and point transect sampling conforming to the distance sampling assumptions. This method is especially valuable for counting small inconspicuous odontocetes like the NBHF species since these are especially prone to the inherent perception bias of traditional visual line transect surveys. I have further discussed the methods available at present to obtain a detection function describing the probability of a detecting a cue at a given distance from a datalogger and showed that a detection function derived by comparing visual and acoustic detections around a datalogger accurately can assess density of harbour porpoises in a coastal high density area. It is the first time this methodology has been tested and it is the first time a density estimate of harbour porpoises has been obtained from acoustic cues alone. I am therefore hopeful that the next few years will show significant developments in dataloggers and advances in the use of passive acoustic monitoring to obtain cheaper and unbiased data for measuring odontocete densities, even in parts of the world where traditional visual line transect population assessments are economically infeasible. Assessment of population sizes and the ability to measure changes over time is a prerequisite for successful conservation and both are badly needed in many parts of the world where cetacean habitats from day to day suffer increasingly from encroachment especially in terms of by-catch and human developments.

I have shown how state of the art wide band sound recordings of wild odontocetes provide the basis for acoustic monitoring given that they provide the means to accurately measure source parameters and describe species differences. However, such recordings may also add pieces to the puzzle of the life in a world where human senses are of little use. I have shown that recordings of wild odontocetes may provide knowledge on spectral source properties as well as on source levels and directionality and I have here used this information to challenge the theories for the evolution of the NBHF click type. I conclude that the NBHF signals likely evolved to meet the dual requirements of operating an effective sonar system and at the same time to minimize the risk of killer whale predation from passive listening. The high frequency part of the NBHF click thus likely evolved as a product of the species' small body sizes to obtain directionality high enough to yield efficient biosonar. Whereas the narrow bandwidth evolved to keep all click energy at frequencies above the upper frequency hearing limit of killer whales. The constant bandwidth auditory filters of porpoises (Popov *et al.*, 2006) may thus have evolved to match the resultant narrow band high frequency echoes by gradually shifting the frequency of highest sensitivity upwards to the highest frequencies, and since the best sensitivity normally coincides with the narrowest auditory bands the narrow bandwidth filters were maintained while shifted upwards in frequency. As such predation from killer whales may have caused the evolution of a unique mammalian hearing system. However, since audiograms have only been obtained for two captive killer whales I have put forward different ways to test the theory experimentally.

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Appendix

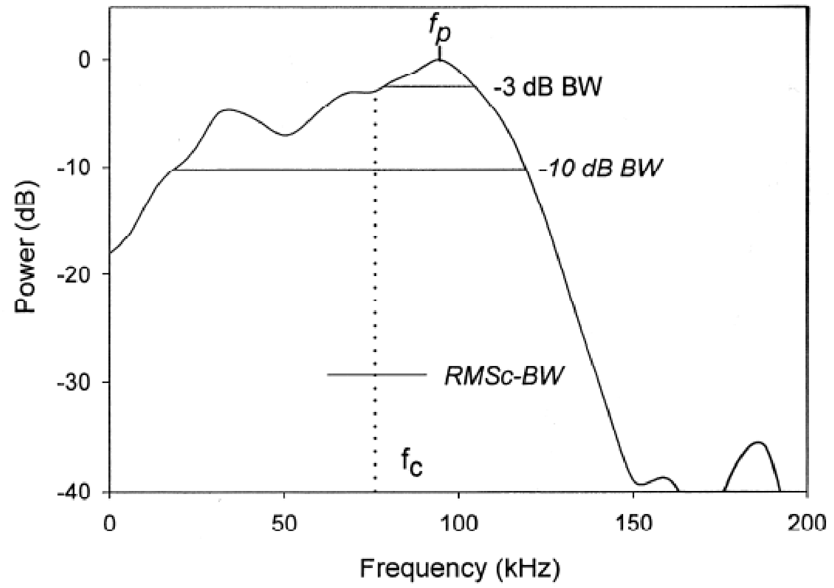

Illustration of the different source parameter terms: **Fc** is the centroid frequency, the frequency at which the spectrum can be divided in two equal halves based on energy on a linear scale, expressed in kHz. **RMS-BW** is the RMS bandwidth, the spectral standard deviation around the centroid frequency. **Fp** is peak frequency, the frequency of greatest amplitude expressed in kHz. **-3dB BW** is the bandwidth of frequencies within -3dB from the peak frequency. **-10dB BW** is the bandwidth of frequencies within -10dB from the peak frequency (Madsen and Wahlberg, 2007).

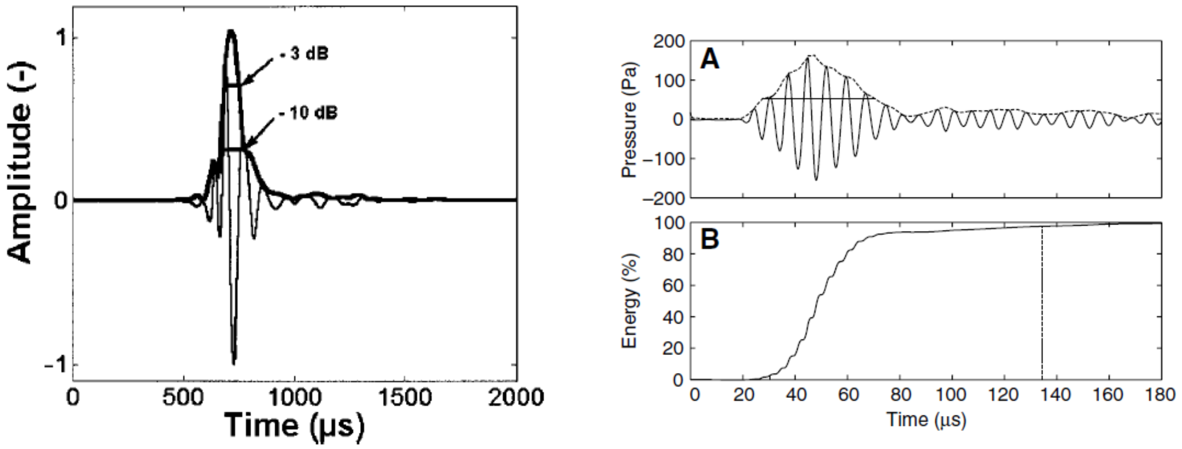

Illustration of -3dB and -10 dB durations of a sperm whale click (Møhl et al., 2003) and illustration 95% energy duration for a porpoise click (corresponding to the horizontal line in figure A) and the vertical dotted line in figure B (Villadsgaard et al., 2007).

Chapter II

Kyhn, L.A., Tougaard, J., Thomas, L., Duve, L.R., Steinback, J., Amundin, M., Desportes, G. and Teilmann, J. From echolocation clicks to animal density – acoustic sampling of harbour porpoises with static dataloggers. (Drafted for Applied Ecology)

Harbour porpoises, Little Belt, Denmark, June 2010

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From echolocation clicks to animal density – acoustic sampling of harbour porpoises with static dataloggers

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Abstract

1) Monitoring abundance and population development of small odontocetes, like the harbour porpoise, is notoriously difficult and labour intensive. There is a need to develop alternative methods to the traditional visual line transect surveys, especially for low density areas. Rigorous application of methods from distance sampling and cue counting theory to passive acoustic monitoring provides the tools needed for obtaining estimates of absolute animal densities.

2) Passive acoustic dataloggers (T-PODs) were deployed and harbour porpoises were concurrently tracked visually. The data were analysed in a mark-recapture approach, where a visual sighting constituted a "mark" and a simultaneous acoustic detection a "recapture". As a distance could be assigned to each visual observation the probability of acoustic detection with increasing distance from the T-POD could be estimated.

3) Effective detection radius of T-PODs ranged from 22 to 104 m and depended on T-POD type, T-POD sensitivity, train classification settings and time window of cue counting.

4) Using cue production rate obtained from acoustic dataloggers on wild porpoises, a realistic density estimate was obtained from T-POD recordings and corresponded to density derived from the visual observations. With more dataloggers and adequate design of survey layout a density estimate would be obtainable for a larger area.

5) Passive acoustic methods enable efficient monitoring even under poor weather conditions where traditional visual survey methods are not applicable. In addition passive acoustic monitoring provides continuous monitoring in time in contrast to the snap-shots of visual surveys.

6) *Synthesis and applications.* The prospect of obtaining robust density estimates for small cetaceans by passive acoustic monitoring is demonstrated. Passive acoustic dataloggers, record the vocalisation of animals over extended periods of time and are thus particularly appropriate for low density areas. By estimating the relationship between distance from animal to detector and the probability of detecting the animals' vocalisation, the so-called detection function, the density of animals can be estimated from echolocation clicks recorded on the datalogger. This provides a method suitable for monitoring in areas with densities too low for visual surveys to be practically feasible, for example harbour porpoises in the Baltic proper and the vaquita in the Gulf of California.

Keywords: abundance, acoustic datalogger, cue counting, low density area, odontocetes, Passive acoustic Monitoring, PAM, *Phocoena phocoena*, radial detection function, static acoustic monitoring. (Max 10 key words)

Running Title: From porpoise clicks to density

Word count: 6510 **(**JAE: max 7000 words)

Introduction

A central element in conservation and management of any organism is an ability to evaluate the effectiveness of measures taken to protect the species. The most direct overall measure of effectiveness is to monitor population size and trends, by conducting regular surveys or other continuous monitoring. Indirect, relative measures of abundance are discouraged, as it will only (at best) provide information on the direction of development in population size but not the magnitude of the development (Anderson 2001; Anderson 2003). Survey techniques that can provide absolute numbers, either as total number of animals within a designated area or as densities of animals per unit area, are to be favoured, whenever possible. However, this is not a straight-forward task and is usually very costly especially when applied to cetaceans.

Harbour porpoises (*Phocoena phocoena*, L 1758) are small inconspicuously behaving cetaceans that are difficult to observe and count at sea. During the last decade, Passive Acoustic Monitoring (PAM) has therefore been used increasingly to account for presence or absence of harbour porpoises, for example in connection to construction of offshore wind farms (Carstensen, Henriksen & Teilmann 2006; Tougaard *et al.* 2009) and spatial distribution and migration (Verfuss *et al.* 2007). Passive acoustic monitoring of odontocetes exploits the fact that they echolocate regularly and porpoises (family Phocoenidae) are particularly well suited for such acoustic monitoring due to their unique sonar signals. Porpoise sonar signals are extremely stereotypic and have features that separate them from most other sounds in the ocean. They are of short duration (approx. 100 µs), peak frequency around 130 kHz and with no energy below 100 kHz (Møhl & Andersen 1973; Villadsgaard, Wahlberg & Tougaard 2007). No other species of cetaceans, which occur regularly in the eastern North Atlantic produce sounds with similar characteristics. Furthermore, porpoises apparently produce sound almost continually, with silent gaps rarely exceeding 1 minute (Akamatsu *et al.* 2007).

Detecting sounds from porpoises by a passive acoustic monitoring device in a fixed position does not in itself provide information on density of animals as the surveyed area isn't automatically known. As with visual observations more and more animals remain undetected as the distance from the observation point increases. In addition, not all animals are necessarily detected, even at distance zero, which for example would be the case for a porpoise passing a passive acoustic detector without echolocating. The first step towards an animal density estimate is thus to derive the detection function, $g(r)$, describing the probability of detection as a function of distance, r, to the datalogger (Buckland *et al.* 2001; Marquez *et al.*

2009). Given that *g(r)* can be estimated, it is possible to compensate for the animals that remain undetected, by estimating an effective area of detection and thus convert the relative index of abundance to an absolute density. See Marquez *et al.* (2009) for a thorough account of the theory underlying the conversion of acoustic cues to animal density.

Estimating *g(r)* can be achieved in various ways (see e.g. Marquez *et al.* 2009; Rayment *et al.*, 2009; Kimura *et al.* 2010). Essential to the estimation is that a distance *r* can be associated to each acoustic detection. This distance can be estimated by visually keeping track of porpoises while in the vicinity of a datalogger, by means of triangulation with a theodolite from a fixed observation point, as was done in the present study.

The second step from acoustic data (cues) to animal densities is a conversion from echolocation clicks per time unit to number of animals. This conversion requires knowledge of the cue production rate. The cue production rate is the average number of cues produced by each animal per unit time and must be obtained independently from determination of the detection function. An ideal method to determine cue production is by means of acoustic tags attached to free-swimming animals, as has been done for harbour porpoises (Akamatsu *et al.* 2007; Linnenschmidt 2009).

In the following a feasibility test of application of cue counting and detection modelling to passive acoustic monitoring of harbour porpoises is presented. Success of the feasibility test lies in obtaining robust density estimates considered realistic for the experimental site during the experiments.

Materials and methods

Observations were made at Fyns Hoved, northern Great Belt, Denmark (55°37'9"N 10°35'26"E) in May 2003 and in August 2007. The area was chosen due to its high abundance of porpoises and the presence of a cliff offering a good overview of the experimental area. The sea bed in the area is sandy-muddy with small and large boulders and slopes gently down to about 15 m. The experimental area was marked with buoys in an effort to keep boats out of the area during observations.

THEODOLITE OBSERVATIONS

Visual observations, using a team of at least three observers, were made from a 22 m high cliff top overlooking the experimental area. When a harbour porpoise was sighted one person tracked it with a digital theodolite (Geodimeter 468) which was connected to a computer with the tracking software Cyclopes 2004 (University of Newcastle, Australia) which was connected to a computer running the custom made tracking software Cyclopes (University of Newcastle, Australia). Each position of a surfacing porpoise was entered into Cyclopes automatically when the observer pushed a button on the theodolite after aiming the theodolite sight at the porpoise or the “foot print” left in the surface. Timing was essential for the comparison between visual and acoustic detections and any delay in entering a position of a surfacing animal was commented in Cyclopes. Other observation notes, such as total number of animals visible in the area, behaviour of the focal animal and accompanying calves were also commented. Observations were made only at sea states below three.

ACOUSTIC DATALOGGER DEPLOYMENT

The dataloggers to obtain the acoustic detections were three versions of the T-POD (Chelonia, U.K.). In 2003 one version 1 and one version 3 were used. In 2007 eight version 5 were used. The T-POD is specifically designed to detect harbour porpoise clicks taking advantage of the narrow bandwidth of the clicks. The fundamental construction is a hydrophone connected to an amplifier and two band-pass filters, a comparator/detector circuit and a microprocessor with attached memory to store information on the time of occurrence of possible porpoise clicks. Clicks are detected based on a comparison between the output of a target bandpass filter centred at 130 kHz and a reference filter at 90 kHz. There are slight differences between the different T-POD versions, but the general mode of operation is the same. Settings were as follows. Version 1: target filter sharpness 5 (arbitrary unit); reference filter sharpness 18 (arbitrary unit); selectivity ratio: 5, threshold 0 (arbitrary unit), minimum click duration 10 µs. Version 3: target filter integration time ‘short’; reference filter integration time ‘long’; selectivity ratio 5; sensitivity 6 (arbitrary unit); minimum click duration 10 µs. Version 5: as version 3, except minimum click duration 30 µs and sensitivity adjusted individually, see below.

T-PODs are known to have individual differences in sensitivity and hence detection thresholds (Dähne *et al.* 2006; Kyhn *et al.* 2008). From the trials in 2003 it was clear that threshold differences transferred to detection probabilities: therefore, sensitivity of all T-PODs used in 2007 were measured in a tank according to Kyhn *et al.* (2008). Detection thresholds were then adjusted accordingly by changing the sensitivity parameter so that detection thresholds fell in three groups: 115, 121 and 125 dB re 1 μPa peak-peak, respectively. T-PODs were deployed in three clusters, each cluster with minimum two different thresholds.

In 2003 the two T-PODs were deployed app. 150 m from the coast at a depth of approximately 6 meters. The T-PODs were deployed with the hydrophone of each T-POD positioned about 2 meters above the seafloor. The eight T-PODs used in 2007 were deployed in three clusters at different distances (up to 180 m) from the observation point and at 8-10 m of water depth with the hydrophones suspended app. 2 m above the sea bed.

T-POD DATA ANALYSIS

T-POD data were downloaded to a computer by the associated software (T-POD.exe, Chelonia Inc., version 5.41 in 2003; version 8.23 in 2007). All data were subsequently analysed with version 8.23 of the software (train detection algorithm 4.1). The software groups detected clicks into clusters termed “trains” and assigns each train to one of six different categories: ‘Click trains with high probability of arriving from cetaceans (Cet Hi)’; ‘Click trains with lower probability of coming from cetaceans (Cet Low)’; ‘Cetaceans and trains of doubtful origin (d)’; ‘Cetaceans and very doubtful trains (dd)’; and ‘Trains with features of boat sonar (Sonar)’. The grouping of clicks into trains and classification of trains is largely undocumented by the manufacturer, but is primarily based on analysis of inter-click interval statistics. Detection functions were estimated for two different data sets: based on all clicks except sonar clicks (‘All trains’) and based only on the categories Cet Hi and Cet Lo (referred to as ‘Cet All’). The time of occurrence of each click train was exported from the software for further analysis.

ESTIMATION OF DETECTION FUNCTION

Visual observations resulted in a number of observed surfacings for each animal. The track between two consecutive surfacings of a porpoise was interpolated as a straight line, with a constant swimming speed. Each whole track of each porpoise was then divided into segments of constant duration. The analysis was repeated three times with different segment durations to test different cues, either 15 s, 30 s or 60 s. A distance x was assigned to each segment being the distance from the midpoint of the segment track to the T-POD. Analysis was right truncated by exclusion of segments with distances greater than 350 m to the T-POD, as accurate estimation of location at such ranges was difficult and very few acoustic detections were made as these ranges. Segments included in the analysis were paired with T-POD data for the same time interval. One such pair constitutes a trial. A trial was successful if there was an acoustic detection corresponding to the visual observation and failed if there was no acoustic detection. Such a pair of one visual sighting at distance x and either a successful or failed detection constitutes one observation in a binary regression analysis (see below). The trials can also be thought of as a kind of mark-recapture experiment: the visual sighting is equivalent of a "mark", a positive acoustic detection a "recapture", and analysing all data thus provides a measure of the probability that an animal sighted at distance x from the T-POD is detected acoustically. For the 2003 dataset each segment produced two observations, one for the version 1 and one for the version 3 T-POD, both assigned the same distance x. For the 2007 data each segment produced eight observations, one for each of the T-PODs and assigned one of three different distances, as the T-PODs were grouped in three clusters.

False detection rate (expressed as percent of total observation time) was calculated per T-POD for 2007 data in order to take account of false detections in the density estimations. A false detection was defined as a minute without visual observations within the observation period, but with acoustic detections. False detection rate was calculated for the period with observations with no truncation distance around each T-POD cluster.

The detection function was modelled using a binary GLM (Generalized Linear Model) with trial distance as the explanatory variable, success/failure as the response, and a logit link function. Both 2003 and 2007 data was stratified by T-POD. Because the same track segments were used multiple times (once for each T-POD present in the relevant year), analytic variance estimates from the GLM were not valid; instead variance and 95 % confidence intervals (CIs) were calculated using a non-parametric bootstrap, treating the porpoise track as the unit for resampling and with 1000 bootstrap replicates.

The above procedure yields estimates of the detection function $g(x)$, i.e., probability of detecting a cue given it is at distance x. However, the quantity required for density estimation (below) is the average probability of detecting a cue given it is within distance w of the detector, denoted P. As is standard in distance sampling applications, this was estimated from the detection function by assuming that animal density is uniform over space within the area surveyed by the detector (the circle of radius w), and then integrating out distance:

$$\hat{P} = \int_{x=0}^{w} x\hat{g}(x)dx \Big/ w$$

An equivalent quantity often computed in the distance sampling literature is the effective detection radius, ρ, which is the distance at which as many cues are missed within this distance as are detected outside it. To ease interpretation of results, this quantity was also computed, using the relationship

$$\hat{\rho} = \sqrt{\hat{P}w^2}$$

The above analysis was repeated 6 times for each T-POD: once for each combination of segment duration (15s, 30s and 60s) and click train category ("All trains" and "CetAll"). Analyses were performed in the software R v2.11.1 (R Development Core Team 2010).

CUE RATE AND DENSITY ESTIMATION

As the T-POD records porpoise clicks and not porpoises, the density of porpoises must be obtained by a conversion from clicks to porpoises. The cue detection method (Buckland *et al.* 2001; Hiby & Hammond 1989), illustrated and discussed in detail by Marques *et al.* (2009) was used for this conversion. The latter authors give the following estimator of animal density, D:

$$\hat{D} = \frac{n_c(1-\hat{c})}{K\pi w^2 \hat{P} T \hat{r}}$$

where n_c is the number of cues detected on K detectors over T time periods within distance w, P is the average probability of detecting a cue within distance w, c is the proportion of false positive detections and r is the cue rate (i.e., the average number of cues produced per animal per unit time). The equivalent, using effective detection radius rather than detection probability is:

$$\hat{D} = \frac{n_c(1-\hat{c})}{K\pi \hat{\rho}^2 T \hat{r}}$$

In the current study, estimates of density were made separately for each T-POD using each of the 6 detection functions computed in the previous section. Number of detected cues, n_c, was calculated for the entire experimental period and thus included periods where no synoptic visual observations took place. This gave a much larger dataset, but is under the assumption that the detection probabilities were unrelated to visual observation times. Cue production rate was estimated separately for each cue duration (15, 30 and 60s), using four data sets collected by acoustic dataloggers (W20-AS A-tag, Little Leonardo, Tokyo, Japan) fitted to the dorsal fin of free-ranging porpoises in Inner Danish Waters (Akamatsu *et al.* 2007; Linnenschmidt 2007). The A-tag recorded echolocation sounds from the tagged porpoises by means of two attached hydrophones for periods between 4.5 and 61 hours following attachment. Individual A-tags had detection threshold of either 142 or 148 dB re 1 μPa peak-peak. Each of the four data sets were divided into periods of 15, 30 and 60 s and cue production rate was calculated as the mean number of intervals which contained at least one click train, expressed per hour and weighted by deployment time.

For estimating variance in $\hat{D}$, it was assumed that the density estimate applied only to the time period and area monitored, and hence that spatial or temporal variance in the counts n_c was not relevant. This would not be the case for a larger monitoring exercise, where dataloggers might be placed randomly over a larger study area and/or be active over a sample of time periods. Variance was estimated by combining variances of the remaining random components of D, assuming they are mutually independent, using the delta method (Buckland *et al.* 2001; Marques *et al.* 2009):

$$\hat{\operatorname{var}}(\hat{D}) = \hat{D}^2\left(\frac{\hat{\operatorname{var}}(\hat{P})}{\hat{P}^2} + \frac{\hat{\operatorname{var}}(\hat{c})}{\hat{c}^2} + \frac{\hat{\operatorname{var}}(\hat{r})}{\hat{r}^2}\right)$$

Confidence intervals on $\hat{D}$ were calculated by assuming the density estimate follows a lognormal distribution (Buckland *et al.* 2001; Marques *et al.* 2009).

INDEPENDENT VISUAL ESTIMATE OF DENSITY

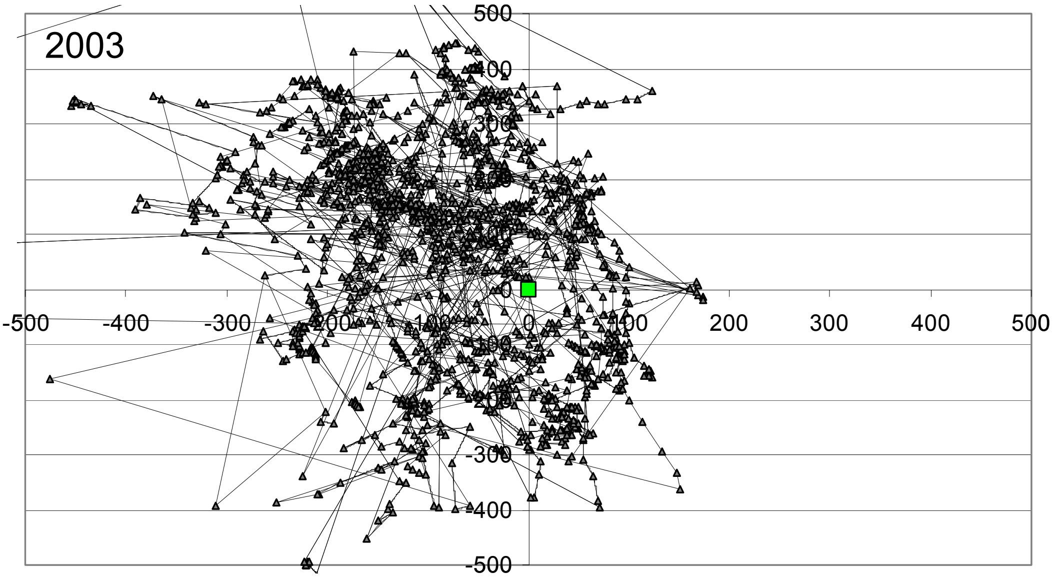
For the 2007 survey, porpoise density was also estimated from the visual observations within a 100 m radius around each T-POD cluster. It was assumed that all animals were observed within this radius, and density was then estimated as

$$\hat{D}_v = \frac{n_v \cdot s}{T_v \cdot a}$$

where n_v is number of times that a porpoise group was observed within 100 m of the T-PODs for each observation minute, s is mean group size, T is the total observation period in minutes and a is the observation area (0.031 km^2). No attempt was made to estimate a variance on this quantity.

Results

After right truncation at 350 m the data set consisted of 91 tracks from 2003 and 32 tracks from 2007. All tracks shown in Fig 1. Each track consisted of between 2 and 128 sightings per track.



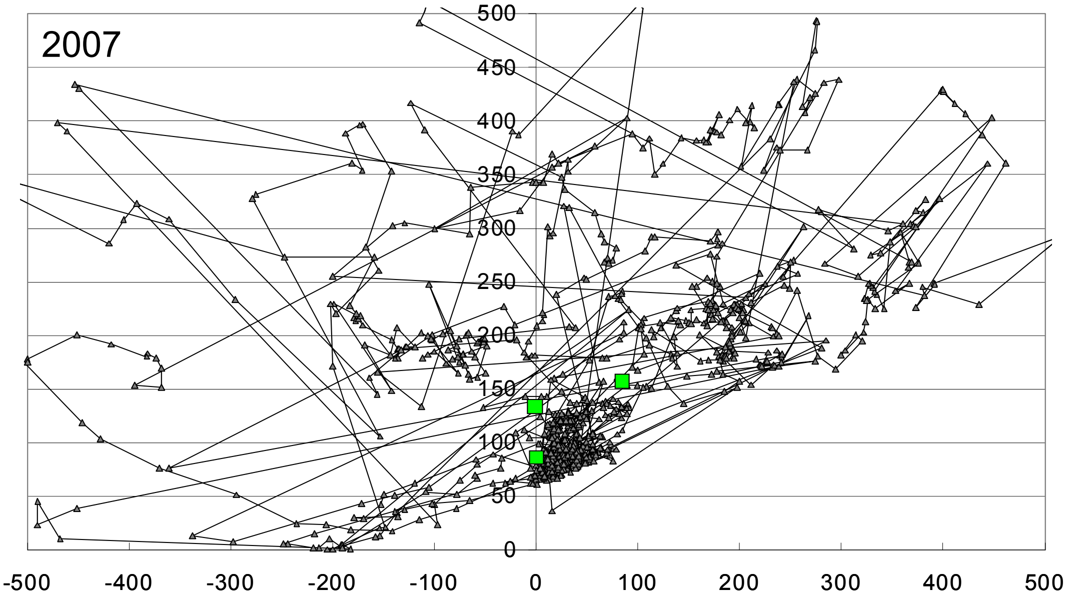


***Figure 1. All tracks** from a) 2003 and b) 2007. Only tracks within 350 m of each T-POD were used for the detection functions. The green squares mark T-POD clusters.*

The T-PODs reliably detected harbour porpoises in the vicinity. Fig. 2 shows an illustrative example of one animal tracked in 2003, together with indication of its location when clicks were detected on the version 3 T-POD. The porpoise swam past the T-PODs at close range, turned and swam back. Only when the animal moved toward the T-POD or was within 50 m of the T-PODs were clicks detected.

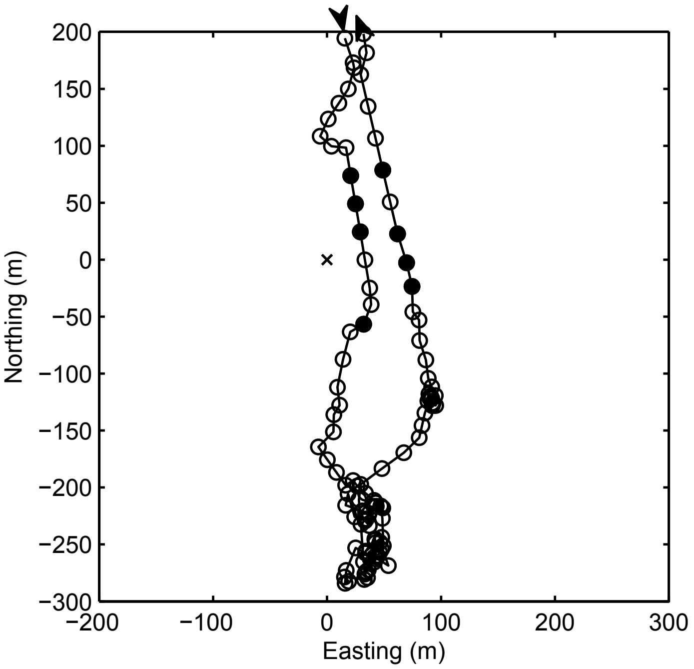


Figure 2. Representative track *from 2003 of a porpoise around a version 3 T-POD (indicated by×). Each circle represents a 15 second interval, with filled circles indicating that clicks were recorded simultaneously on the T-POD. Arrows at the top indicate direction of swimming.*

Fig. 3 shows a small sample of clicks recorded in 2003 simultaneously on the two different T-PODs. Although the version 1 T-POD was less sensitive than the version 3 T-POD, there is a close match between recordings and almost all clicks recorded by the less sensitive version 1 were also recorded on the more sensitive version 3. Duration of the recorded clicks are considerably longer in the version 3 recording than the version 1 recording, which is an effect of the difference in datalogger sensitivity.

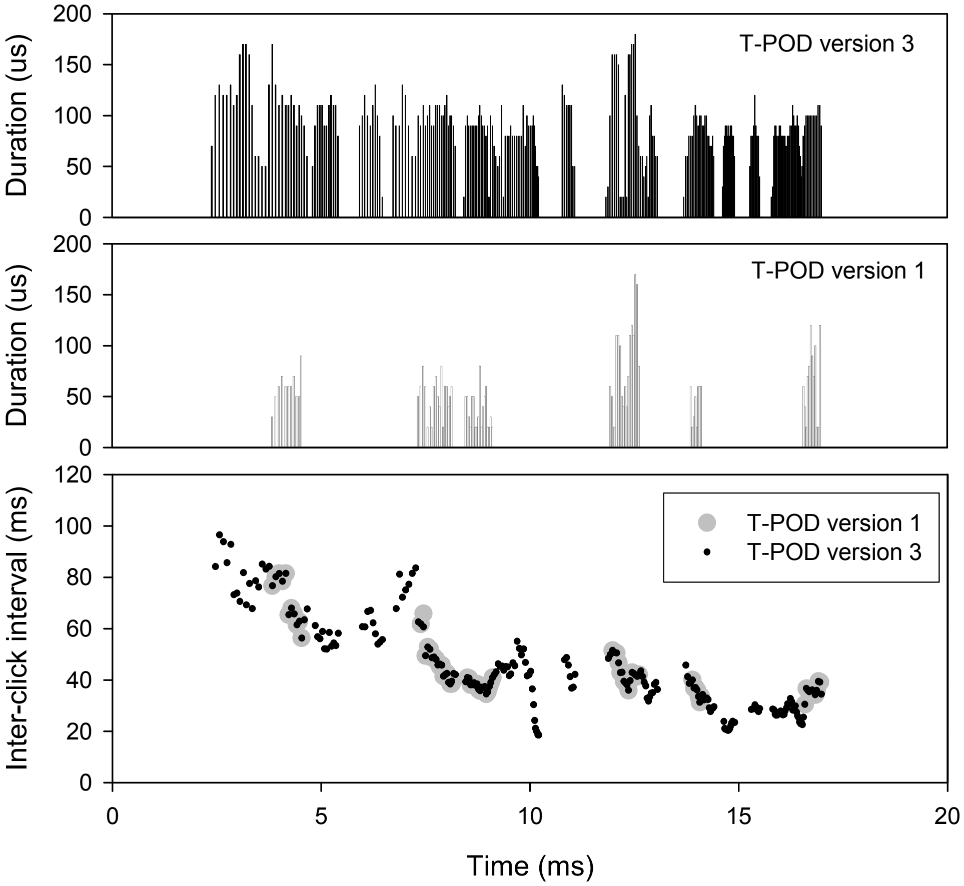


Figure 3. Examples of click trains *recorded by the two T-PODs during tracking of a porpoise. A) shows individual clicks on the version 3 T-POD, B) clicks from the version 1 T-POD and C) shows inter-click intervals for both recordings superimposed. As the drift of the internal clock of the T-POD becomes significant on the scale of milliseconds, the two recordings were aligned in time to obtain best possible fit.*

FALSE DETECTION RATE

The level of false detections calculated for 2007 data was very low, in fact only one T-POD had a single minute with detected click trains when no porpoises were observed by the trackers. The level of false detection was thus essentially zero for both click train categories and is thus not included in the density estimations.

CUE PRODUCTION RATE

Cue production rates for all four data sets are shown in Table 1. There was some variation among the four porpoises in cue production rate and a weighted mean for each cue interval was used as input to the density estimates.

***Table 1**. Cue production rate calculated from four A-tag deployments on wild harbour porpoises in inner Danish Waters. A cue is a 15, 30 or 60s period during which one or more porpoise click was produced. (Tag data provided by T. Akamatsu)*

A-tag deployment			*Cue production rate, cues*hour^{-1}*		
	Tagging date	Tag duration, hours	15 s	30 s	60 s
Porpoise ID 6420_05	8. June 2005	5.5	120.2	96.0	51.8
Porpoise ID 6422_06	23. April 2006	24.8	162.4	113.0	59.1
Porpoise ID 6172_06	26. April 2006	62.0	145.6	106.7	58.8
Porpoise ID 6170_07	19. May 2007	66.6	228.1	120.0	60.0
Weighted mean			182±46	113±10	59±4

DETECTION FUNCTIONS

Estimated detection functions for the 15 s period are shown in Fig. 4. Probability of detection, P, and effective detection radius, ρ, for all detection thresholds and combinations of cue intervals and train classifications are shown in Table 2. The highest probability of detection was not unexpectedly found for the most sensitive T-POD, the longest cue duration and the click train category “All trains” (as opposed to the more restrictive “Cet All trains” category.

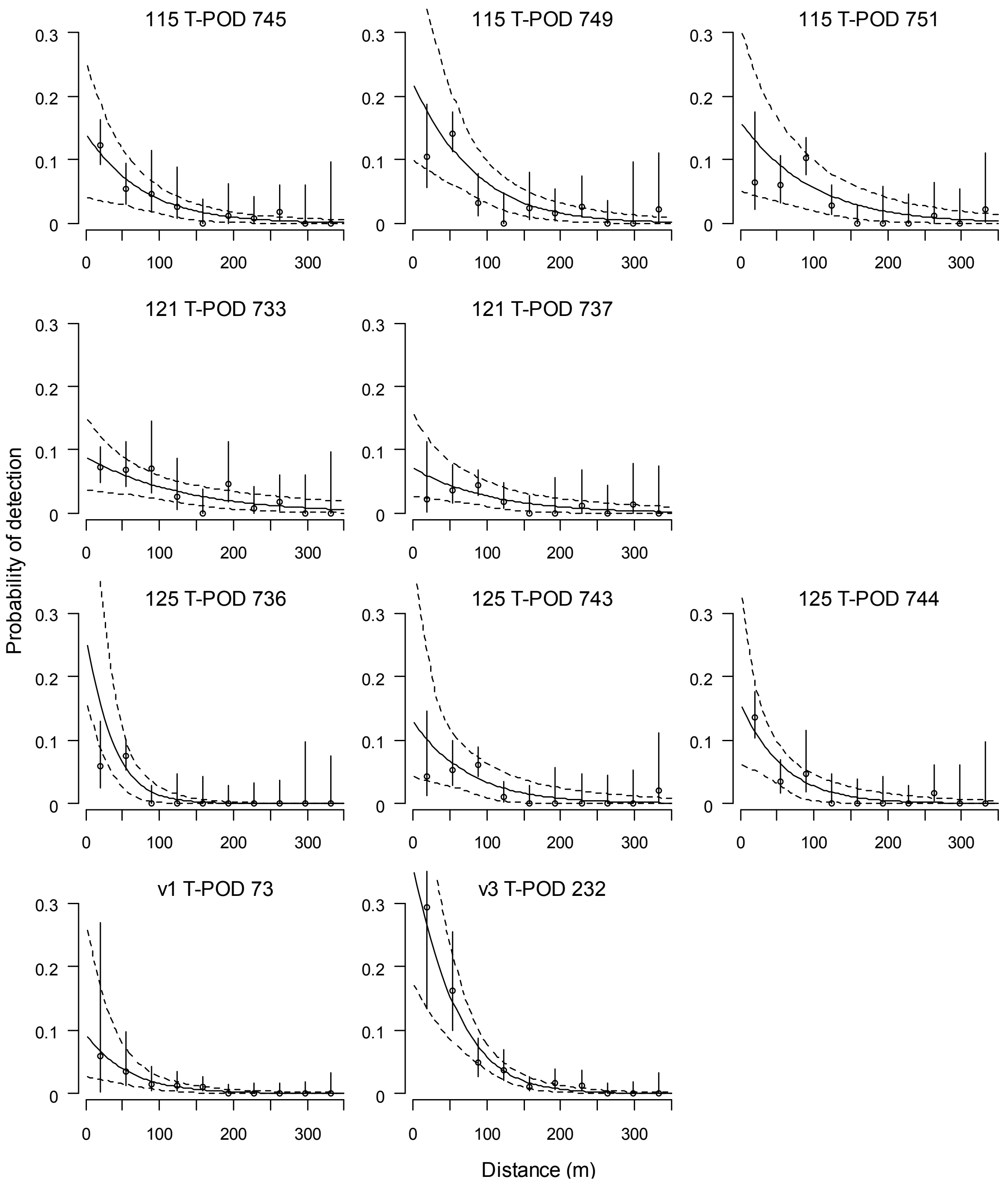


***Figure 4. Estimated probability of detection** (smooth solid lines) and 95% bootstrap confidence intervals (smooth dashed lines) against distance for cues of 15s and data in the category All Trains. Circles show the proportion of positive detections in ten equally-spaced distance bands, and vertical lines show 95% binomial confidence intervals around these proportions. Closeness of the fitted detection line to these proportions indicates goodness-of-fit. The top three panels show estimates for T-PODs belonging to each of the three threshold levels used in 2007; the bottom left and centre panels show estimates for the version 1 and 3 T-PODs used in 2003.*

Table 2. *Effective detection radius (EDR), probability of detection (P), density(confidence interval), D, in porpoises* km^{-2} *for two of the tested cues (15 s & 60 s), T-POD detection thresholds and data categories. 95% confidence intervals on P (in brackets) were derived from a nonparametric bootstrap (see text). The two top most T-PODs are from the 2003 dataset, where T-POD detection threshold were not measured (na).*

T-POD	***Threshold***	***Cue***	***Data category***	ρ***, m.***	***P(±s.d.)***	***D (LCI-UCI)***
73	na	15	All Trains	24.13	0.005 (0.003)	4.19 (1.1-16.2)
			Cet All	17.10	0.002 (0.002)	3.94 (0.8-18.7)
		60	All Trains	50.07	0.020 (0.011)	2.39 (0.7-8.6)
			Cet All	34.54	0.010 (0.009)	2.78 (0.6-13.9)
232	na	15	All Trains	44.96	0.016 (0.002)	3.72 (1.6-8.5)
			Cet All	30.21	0.007 (0.001)	4.36 (1.8-10.5)
		60	All Trains	83.69	0.057 (0.007)	2.55 (1.3-5.1)
			Cet All	64.09	0.034 (0.004)	2.70 (1.4-5.3)
745	115	15	All Trains	38.72	0.012 (0.004)	19.00 (6.6-54.8)
			Cet All	26.50	0.006 (0.002)	5.12 (1.6-16.6)
		60	All Trains	93.13	0.071 (0.022)	5.82 (2.1-16.1)
			Cet All	60.54	0.030 (0.009)	2.38 (0.9-6.6)
749	115	15	All Trains	49.93	0.020 (0.006)	1.75 (0.6-5.1)
			Cet All	39.16	0.013 (0.005)	1.34 (0.4-4.3)
		60	All Trains	103.91	0.088 (0.025)	1.46 (0.5-3.9)
			Cet All	84.82	0.059 (0.021)	0.86 (0.3-2.6)
751	115	15	All Trains	49.31	0.020 (0.009)	2.31 (0.7-7.8)
			Cet All	42.18	0.015 (0.008)	1.69 (0.5-6.3)
		60	All Trains	87.88	0.063 (0.023)	1.57 (0.5-4.7)
			Cet All	76.04	0.047 (0.021)	1.18 (0.4-3.9)
733	121	15	All Trains	47.40	0.018 (0.006)	2.29 (0.8-6.8)
			Cet All	36.07	0.011 (0.005)	0.84 (0.3-2.8)
		60	All Trains	107.84	0.095 (0.027)	1.84 (0.7-4.9)
			Cet All	79.81	0.052 (0.022)	0.70 (0.2-2.2)
737	121	15	All Trains	36.04	0.011 (0.005)	4.18 (1.2-14.6)
			Cet All	32.58	0.009 (0.004)	2.77 (0.8-9.8)
		60	All Trains	80.14	0.052 (0.020)	1.95 (0.6-6.0)
			Cet All	71.85	0.042 (0.019)	1.33 (0.4-4.4)
736	125	15	All Trains	24.61	0.005 (0.002)	2.91 (0.9-9.0)
			Cet All	21.87	0.004 (0.002)	2.22 (0.6-7.6)
		60	All Trains	47.39	0.018 (0.006)	1.75 (0.6-5.2)
			Cet All	39.50	0.013 (0.006)	1.56 (0.5-5.1)
743	125	15	All Trains	35.97	0.011 (0.006)	2.83 (0.8-10.4)
			Cet All	35.20	0.010 (0.006)	1.66 (0.4-6.4)
		60	All Trains	62.69	0.032 (0.012)	1.99 (0.7-6.0)
			Cet All	56.85	0.026 (0.013)	1.42 (0.4-4.9)
744	125	15	All Trains	31.52	0.008 (0.004)	2.82 (0.8-9.7)
			Cet All	22.83	0.004 (0.002)	1.79 (0.5-6.2)
		60	All Trains	66.67	0.036 (0.016)	1.52 (0.5-5.0)
			Cet All	60.90	0.030 (0.015)	0.58 (0.2-2.0)

DENSITY ESTIMATES

Density was estimated for all T-PODs using the detection function for each specific T-POD and was assessed for both data categories ('Cet All' and 'All Clicks'). Results are summarised in Table 2. With one outlier (T-POD 745) the estimated densities fell within one order of magnitude and were evenly distributed, but lower than the visual estimate of density from 2007, which was 8.0±0.84 animals·km^2 calculated for observations within 100 m of each T-POD cluster.

DISCUSSION

This study demonstrates that it is possible to estimate a detection function for a passive acoustic datalogger and in this way derive realistic density estimates for harbour porpoises. This was done by comparing visual tracks with synchronised acoustic detections in a mark-recapture design within the statistical framework of cue counting (Buckland *et al.*, 2001; Marquez *et al.*, 2009). The density estimations gave two very promising results. First of all, the calculated density estimates per cue were similar across all T-PODs, which shows that the differences among T-PODs due to different detection thresholds, and hence number of detected acoustic cues, were levelled out by the derived detection functions, as expected from distance sampling theory. This means that if detection functions are available for individual dataloggers then results can be compared across dataloggers despite differences in thresholds and settings. Secondly, the acoustically derived density estimates were within the same order of magnitude as the visually derived densities.

Density estimation by a passive acoustic method as presented here offers a cheaper alternative to visual surveys since the observer effort and associated costs are greatly reduced. Additional advantages are that data can be collected and density estimated year round and under all weather conditions and data from dataloggers are unaffected by human subjectivity and fatigue during observations. The passive acoustic methodology in combination with cue counting thus provides a viable alternative to visual surveys for density estimations, in particular for low density areas, where reliable visual estimates may be unattainable.

The study was conceived as a feasibility test of the application of cue counting and detection modelling to passive acoustic monitoring data, and as such, succeeded in obtaining a point estimate for density. This is equivalent to obtaining a density estimate based on a single line in a line transect survey and such a point estimate can obviously not be extrapolated to larger areas. To accomplish this and thus derive a population size estimate for a larger study area a robust design must be used, with sufficient number of independent monitoring stations, placed either randomly or systematically with respect to animal distribution.

A critical assumption of cue counting theory is that cues must be instantaneous in time so that a unique distance can be assigned to each cue (Buckland *et al.* 2001). A single echolocation click with a duration of less than one millisecond clearly fulfils this requirement and was used as cue by Marques *et al.* (2009) on beaked whale sounds. Using single porpoise clicks as cues, however, is problematic because the rate of false positives can be very high, due to many other sounds (cavitation noise, echosounders etc) possibly recorded by the datalogger. Such false positives can be difficult to separate from porpoise clicks when treated individually, but can be removed to a large degree by filtering based on properties of click trains. Individual click trains could be used as the acoustic cue, as done by Kimura *et al.* (2010), but this is problematic as there is no common consensus on the definition of a click train and thus how sequences of clicks should be grouped into trains. Furthermore, as the sound beam from a porpoise is highly directional and animals are known to rapidly scan with their head from side to side while swimming (Akamatsu *et al.* 2010) a long continuous train of clicks may artificially break up into many click trains separated by small pauses when detected by the T-POD. This pattern of trains will differ markedly from the trains recorded by a datalogger placed on the dorsal fin of free-swimming porpoises, where one continuous train of clicks is likely to be recorded. The cues (individual trains) measured on the animal are therefore not the same cues as those measured by the stationary datalogger, meaning that measurements on the animal cannot be used directly to estimate cue production rate. As an alternative we decided to use an interval of time with clicks as cue, since cues then can be compared between the two datasets. However, as the cues are no longer instantaneous in time no unambiguous distance can be associated to the cue since the vocalising porpoise will move some distance during the cue interval. Thus, there is a trade off between keeping intervals as short as possible to reduce uncertainty on the distance estimate and increasing the detection rate by increasing interval duration. The repeated analysis with interval sizes of 15 s, 30 s and 60 s clearly showed that higher detection probabilities were attained with the longer intervals, but also that the density estimates in the end were not affected by differences in interval size. The 15 s interval is thus recommended, in order to better comply with the assumption of instantaneous cue production and hence reduce errors on distance estimation.

A second critical assumption in distance sampling theory is that distances are measured exact. In the present study distances were based on theodolite tracks of porpoises. Theodolites are very precise at short distances but the multiplicative error increases with true distance from the theodolite and furthermore is positively biased (i.e. errors on overestimated distances are larger than errors on underestimated distances). For this reason we only used distances within 530 m of the theodolite station and most observations were even closer to the observation point as is evident from fig. 1., so the bias is considered negligible. However, a different uncertainty on distance estimation arises because we interpolated porpoise swimming tracks between surfacings assuming straight lines. This inevitably leads to errors, but these are likely random and independent of true distance to the theodolite as the interpolation was performed in the same fashion for all positions regardless of distance to observers. As small and random errors on distance estimates may still provide reliable density estimates (Gates *et al.*, 1985 in Buckland *et al.*, 2001) we therefore accepted to bend the assumption on measurement precision somewhat. Measurement error should however, be taken very seriously and the assumption here of straight porpoise swimming tracks is likely a limiting factor for precision. Obtaining true distance estimates between surfacings would require detailed knowledge on subsurface movement of porpoises, obtainable either by equipping animals with dataloggers that can accurately track the animals under water, or acoustically by means of a sufficiently large hydrophone array. Furthermore, as the subsurface behaviour of porpoises may likely depend upon site specific factors such as water depth, prey availability and bottom characteristics such data should ideally be obtained within the actual study site in order for the modelling to actually reduce measurement error.

In standard distance sampling applications it is assumed that all cues/animals on the point (datalogger)/trackline are detected ($g(0) = 1$). This assumption does not hold in the present experiment, evident on fig 4., but as the mark-recapture method allows for a direct determination of $g(0)$, there is no need for assuming it. However, it is relevant to consider why $g(0)$ is relatively low, between 0.1 and 0.3 for T-PODs. Harbour porpoises are known to be silent for shorter or longer periods of time (Linnenschmidt, 2007) but the primary reason is probably the directional characteristics of the echolocation sounds. This means that porpoises are only able to effectively ensonify a T-POD part of the time with sound above detection threshold of the T-POD, likely only when looking straight towards the T-POD. Desportes *et al.* (2000) described a behaviour termed ‘bottom grubbing’, also observed at the experimental site, in which porpoises swim in a near vertical position, close to the bottom, the head downwards in search of prey. This behaviour can continue for extended periods of time and during this behaviour clicks from the porpoise will only reach the T-PODs in an erratic fashion, unlikely to be recognised as entire click trains. Prey search behaviour may thus in this study be part of the explanation for the low *g(0)* value.

The probability of detection likely change from area to area, affected by factors such as depth, animal behaviour and mean group size and maybe even with animal density. This means that detection functions ideally should be derived in the same area and at the time in which the population density is being assessed. Future calculations of detection functions in other areas and seasons will show how widely applicably they are. Likewise, for the cue production rate to be appropriate, it should ideally be obtained in the same area as the passive acoustic monitoring takes place, preferably at the same time as the study (Buckland *et al.*, 2001) but by an independent method.

The false detection rate in 2007, where it was assessed, was very low and indicates that the click train algorithm in the T-POD software is efficient and conservative, and when combined with the high abundance of porpoises in this study, it could be ignored.

In a high density area like the present all T-POD click train categories (except boat sonar) may thus be used if data is divided into timed cue intervals. Even if some trains in fact are false positives the rate of false positives to true positives will still be low, especially when a cue is an interval of time with click trains, and false positives are therefore not very important. The situation, however, is essentially different in a low density area, for instance the Baltic Proper. Because the porpoise density is dreadfully low (Hammond *et al.*, 2002) inclusion of false positives will weigh much higher in a density assessment and it is therefore extremely important to be as conservative as possible and to limit the rate of false positives as much as possible, if this rate is unknown. In a low density area only the two highest T-POD click train categories ('*Cet all*') should therefore be used despite the risk of loosing data, in order to keep the density estimate conservative. In this respect one of the T-PODs showed great differences at the level of density depending on whether the estimate was based on '*Cet all*' or '*All trains*' data (Table 2). For '*Cet all*' the density estimates corresponded to those of the other T-PODs, but for '*All trains*' the level was much higher and may have arisen from internal abnormalities within this T-POD, for example overruling of the sensitivity setting, more than being an external problem. Dataloggers should therefore be deployed for field tests to assess such abnormalities before deployment to obtain density estimates, and the decision on which of the data categories to use '*All trains'* or '*Cet all'* should take such results into account.

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Chapter III

Kyhn, L.A., Tougaard, J., Jensen, F., Wahlberg, M., Stone, G., Yoshinaga, A., Beedholm, K. and Madsen, P.T. (2009). Feeding at a high pitch: Source parameters of narrow band, high frequency clicks from echolocating off-shore hourglass dolphins and coastal Hector's dolphins. J. Acoust. Soc. Am. 125(3): 1783–1791
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Hector's dolphin checking out the recording boat, Akaroa Bay, New Zealand, January 2007.

Feeding at a high pitch: Source parameters of narrow band, high-frequency clicks from echolocating off-shore hourglass dolphins and coastal Hector's dolphins

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Toothed whales depend on echolocation for orientation and prey localization, and source parameters of echolocation clicks from free-ranging animals therefore convey valuable information about the acoustic physiology and behavioral ecology of the recorded species. Recordings of wild hourglass (*Lagenorhynchus cruciger*) and Hector's dolphins (*Cephalorhynchus hectori*) were made in the Drake Passage (between Tierra del Fuego and the Antarctic Peninsular) and Banks Peninsular (Akaroa Harbour, New Zealand) with a four element hydrophone array. Analysis of source parameters shows that both species produce narrow band high-frequency (NBHF) echolocation clicks. Coastal Hector's dolphins produce clicks with a mean peak frequency of 129 kHz, 3 dB bandwidth of 20 kHz, 57 μs, 10 dB duration, and mean apparent source level (ASL) of 177 dB re 1 μPa$_{\text{p.-p.}}$. The oceanic hourglass dolphins produce clicks with mean peak frequency of 126 kHz, 3 dB bandwidth of 8 kHz, 116 μs, 10 dB duration, and a mean estimated ASL of 197 dB re 1 μPa$_{\text{p.-p.}}$. Thus, hourglass dolphins apparently produce clicks of higher source level, which should allow them to detect prey at more than twice the distance compared to Hector's dolphins. The observed source parameter differences within these two NBHF species may be an adaptation to a coastal cluttered environment versus a deep water, pelagic habitat.

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I. INTRODUCTION

Toothed whales echolocate to navigate and find prey by processing echoes generated from emission of ultrasonic short clicks of high directionality and source level (Au, 1993). The performance of a toothed whale biosonar system depends on the source parameters of the transmitted echolocation clicks, and analysis of click properties can thus convey valuable information about the acoustic physiology and behavioral ecology of recorded toothed whale species (e.g., Au, 1993; Madsen and Wahlberg, 2007). The variation in habitat and prey type from ice filled fjords, muddy rivers, and deep open oceans provides diverse acoustic environments that may have contributed to the evolutionary shaping of different click types, but little is known about how click

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source parameters may be linked to the physical environment of the different echolocating toothed whale species (Wood and Evans, 1980).

A biosonar is ultimately limited in detection range by either noise or clutter (Urich, 1983). By clutter is meant echoes from irrelevant objects ensonified by the sonar that masks target echo reception when there is temporal overlap in the arrival of target and clutter echoes (Au and Benoit-Bird, 2008). Increasing the source level of the sonar potentially leads to significant ensonification of more unwanted objects in the water meaning that the received echo-to-clutter ratio remains constant or even deteriorates with increasing source level. Instead an improved echo-to-clutter ratio can be achieved by increasing the directionality of the sonar signal as objects outside the sound beam do not add significantly to the clutter, but this gain is at the expense of search width of the sonar beam.

A noise-limited biosonar, on the other hand, is limited by either the ambient noise or the self-noise of the auditory system. For most young and healthy toothed whales (Kastelein *et al.*, 1999; Johnson, 1967) the hearing threshold seems to be close to or below normal ambient noise level in the relevant frequency band, if the current interpretations of how toothed whales integrate noise are correct. Accordingly, an increase in source level increases the echo-to-noise ratio and hence the performance of the biosonar. The echo-to-noise ratio can also be raised by increasing the receiving directionality, which serves to reduce reception of anisotropic noise. Finally, echolocation signals may be shifted to higher frequencies where the ambient noise levels are lower (Møhl and Andersen, 1973; Urich, 1983; Au, 1993) but at the cost of increased sound absorption (Urich, 1983). Thus, different toothed whale species likely have optimized their echolocation capabilities to the specific habitat they have evolved in as seen for bats (Neuweiler and Fenton, 1988), as a trade-off between click source parameters matched to prey properties, sound absorption, ambient noise levels, clutter, and the functional constraints imposed by the morphology and size of their sound generators (Madsen and Wahlberg, 2007; Madsen *et al.*, 2005).

For example, the large sperm whale operates a powerful long range biosonar system to locate mesopelagic prey patches at long ranges by using clicks with high source levels and centroid frequencies between 15 and 20 kHz where absorption is low (Madsen *et al.*, 2002; Møhl *et al.*, 2000, 2003). At the other extreme, several smaller toothed whales have been shown to produce narrow band high-frequency (NBHF) clicks around 130 kHz (Møhl and Andersen, 1973; Dawson, 1988; Madsen *et al.*, 2005; Li *et al.*, 2007). These signals suffer from range-dependent absorption about 40 times higher than sperm whale clicks, so the sonar can only operate at short ranges. The species producing NBHF clicks are found in three different odontocete families and they all produce echolocation clicks at peak frequencies of more than 120 kHz, 3 dB bandwidth of 6–26 kHz and Q-values between 8 and 20 [e.g., *Phocoena phocoena*, *Neophocaena phocaenoides*, *Kogia breviceps*, and *Cephalorhynchus hectori* (Møhl and Andersen, 1973; Au, 1993; Dawson, 1988; Madsen *et al.*, 2005; Li *et al.*, 2007)].

The NBHF clicks are apparently very similar, yet it is not clear what factors may have driven the seemingly convergent evolution of NBHF clicks in species that live in very different habitats. Morisaka and Connor (2007) suggested that the NBHF signal evolved for acoustic camouflage as an anti-predator strategy against killer whales (*Orcinus orca*) whose hearing sensitivity decreases sharply at frequencies above 60 kHz and is practically zero above 100 kHz (Szymanski *et al.*, 1999). For this anti-predator strategy to be effective all energies of the NBHF signal must be emitted at frequencies over 100 kHz, above the upper hearing limit of the killer whale. Since absorption at the same time increases considerable with frequency above 100 kHz, the NBHF species have a small frequency band at their disposal to adapt to their environment. Yet, it seems that the very different habitats from deep water of *Kogia* to the coastal environment of porpoises would face these animals with different echolocation tasks in terms of prey, predation, noise, and clutter levels. Examples of such NBHF species living in different habitats are Hector's dolphin (*Cephalorhynchus hectori*) and the hourglass dolphin (*Lagenorhynchus cruciger*).

Hector's dolphins are coastal and have a body length of about 1.5 m and weigh around 50 kg (Reeves *et al.*, 2002). They are only found in New Zealand and are most often found within 1 km from land (Slooten *et al.*, 1993; Bräger *et al.*, 2002). They feed opportunistically on smaller fish and squid caught at the bottom and at the surface (Slooten and Dawson, 1988). The hourglass dolphins are oceanic and slightly larger than Hector's dolphins, measuring ~1.4–1.9 m and weighing 74–88 kg (Godall *et al.*, 1997). Molecular phylogenies (May-Collado and Agnarsson, 2006) suggest close taxonomic affinity to the *Cephalorhynchus* genus. With its oceanic circumpolar sub-Antarctic distribution knowledge about this species is primarily circumstantial (Godall *et al.*, 1997). The few collected stomachs of hourglass dolphins contained remains of small fish (*Mycophidae*) and squid (*Onychoteuthidae* and *Enoloteuthidae* families) (Godall *et al.*, 1997). So, while NBHF species seemingly produce almost identical clicks, it is possible from their differences in habitat and morphology that they do display differences in source parameters within the NBHF click class, in particular, with respect to source level.

Here we show that echolocation clicks of Hector's and hourglass dolphins have different source levels, duration, and bandwidth, possibly due to the different acoustic conditions posed by their respective habitats.

II. MATERIALS AND METHODS

A. Recording chain and field sites

Recordings were made with a linear, vertical array of four Reson TC 4034 spherical hydrophones (Reson A/S, Slangerup, Denmark) with 20 m cable and a measured sensitivity of −222 dB re 1 V/μPa between 100 and 150 kHz. Hydrophones were mounted horizontally in the same direction along a vertical Perspex rod with 1 m hydrophone spacing. The entire array was suspended either 1 m (Hector's) or 2 m (hourglass) below a buoy in the surface and with a 0.5 kg lead weight attached to the other end of the array (*sensu*

Madsen *et al.*, 2004a). Signals were bandpass filtered [100 Hz (one pole) to 200 kHz (four poles)], amplified in a custom-built four-channel amplifier, and digitized [500 kHz, 12 bit NuDAQ pci9812, AdLink, Los Angeles, CA]. The measured frequency response of the entire recording chain was flat (±2 dB) from 200 Hz to 180 kHz and allowed for continuous streaming of data to disk. Clip level of the recording chain was 189 dB re μPa (peak) with 50 dB gain for hourglass dolphins, and either 169 or 189 dB re μPa (peak) for Hector's dolphins (70 or 50 dB gain) set by the max input voltage of ±5 V peak in the analog-to-digital converter.

Recordings were obtained at two field sites. Hector's dolphins were recorded in the coastal habitat around Akaroa Harbour, New Zealand (43°52′9″S; 172°56′16″E) on January 7 and 9, 2007. When dolphins approached the large rigid-hulled inflatable boat (RHIB) to bow ride, the engine was turned off and the recording array lowered in the water. No other marine mammals were in sight or detected acoustically. Recordings were made under very calm weather conditions (low winds, sea state 0–1 Beaufort, sea temperature of 14 °C, and salinity of 34.5‰).

Hourglass dolphins were recorded on January 30, 2007, in the Drake Strait (58°17′50″S; 61°29′39″W) at open sea between Tierra del Fuego and the Antarctic Peninsular. A group of about 20 hourglass dolphins was sighted from the naval vessel HDMS "Vædderen" and identified by their characteristic hourglass-shaped white markings on the flanks and prominent dorsal fin. No other marine mammals were in sight or detected acoustically. The dolphins were approached in a RHIB and when animals were encountered within 100 m of the RHIB the recording array was deployed. Recordings were made under calm weather conditions (low winds, sea state 2 Beaufort, moderate swell, sea temperature of 5.1 °C, and salinity of 33.9‰).

B. Click analysis

Dolphin clicks are very directional and it is thus essential to ensure that clicks used for analysis are recorded as close to on-axis as possible (Au, 1993; Madsen and Wahlberg, 2007). Off-axis clicks are distorted and with much lower apparent source level (ASL) (Au *et al.*, 1986), and the click parameters may be different than on-axis (Au, 1993). For click analysis we applied a set of criteria for on-axis properties following Villadsgaard *et al.* (2007) to ensure that only clicks recorded close to on-axis were used. However, since we did not know whether focal animals were actually pointing their acoustic axis at the array, we used the definition of Møhl *et al.* (2000) of ASL, i.e., the back calculated sound intensity at a distance of 1 m from a directional source recorded in an unknown aspect, for the clicks complying with the following on-axis criteria: (i) recorded on all four channels; (ii) part of a scan, i.e., a series of clicks closely spaced in time normally first increasing then decreasing in amplitude (*sensu* Møhl *et al.*, 2003); (iii) of maximum amplitude on one of the two middle hydrophone channels; and (iv) the direct path of the click had to be stronger than any trailing bottom or surface reflections. Further, we determined that the localization error (see below) could not give rise to a transmission error of more than 2 dB in the source level calculations. Additionally, we visually inspected all on-axis clicks and removed clicks that contained double or triple pulses, since these likely arise from surface reflections and are not source generated (Li *et al.*, 2005).

The source properties were quantified using a series of parameters *sensu* Au (1993) and Madsen and Wahlberg (2007) for each click accepted as on-axis: Duration (defined as between -10 dB points on the envelope, calculated as the absolute value of the analytical waveform. From here on stated as 10 dB duration); peak frequency, centroid frequency (i.e., the frequency dividing the spectrum in two halves of equal energy on a linear scale), 10 dB bandwidth, (i.e., bandwidth at -10 dB points below the spectrum peak), 3 dB bandwidth (i.e., bandwidth at -3 dB points below the spectrum peak), rms bandwidth (i.e., spectral standard deviation around the centroid frequency on a linear scale), and Q-value (centroid frequency divided by the rms bandwidth).

Interclick intervals (ICIs) were found as the interval between the on-axis click and the click preceding the on-axis click in the same click scan. ICI is given in milliseconds. A few clicks were too closely spaced with echoes and clicks from several scans to objectively derive the ICI and these clicks were thus not included in the ICI analysis

The recordings were browsed using ADOBE AUDITION 1.5 (Syntrillium, Adobe, Mountain View, CA) and all analysis and signal processing were performed with custom written scripts in MATLAB (Mathworks).

C. Calibration of localization routines

The array performance was evaluated in Aarhus Harbour, Denmark, by playing out calibrated tone pips with source parameters similar to NBHF clicks at known ranges from the array. The four-hydrophone-array was suspended from a buoy with the top hydrophone 1 m below the surface. The sound source (at 3 m depth) was moved gradually away from the array at measured ranges in 10 m steps. Tone pips (130 kHz sinus pulses of 15 cycles and a 100 μs duration) were transmitted with an omni-directional hydrophone (B&K8105) connected to a sound generator (Agilent, model 33220A). The same recording chain and settings as used for the dolphin recordings were used to record signals transmitted in a range interval from 10 to 80 m from the array. Speed of sound was estimated from the Leroy equation (Urich, 1983) from measured temperature and salinity. A precise localization range was defined as a range within which the rms error (Villadsgaard *et al.*, 2007) with respect to the actual range was within a range jitter corresponding to a variation in transmission loss (TL) (spherical spreading) of <2 dB.

D. Estimation of source level

Synchronized recordings of the same click on four channels allow localization of the clicking dolphin with three hyperbolas calculated from time of arrival differences of the click pair wise among the four hydrophones. Localizations were performed using MATLAB implementing the localization routines of Wahlberg *et al.* (2001) and Madsen and Wahlberg (2007). It proved essential to use a robust measure of the

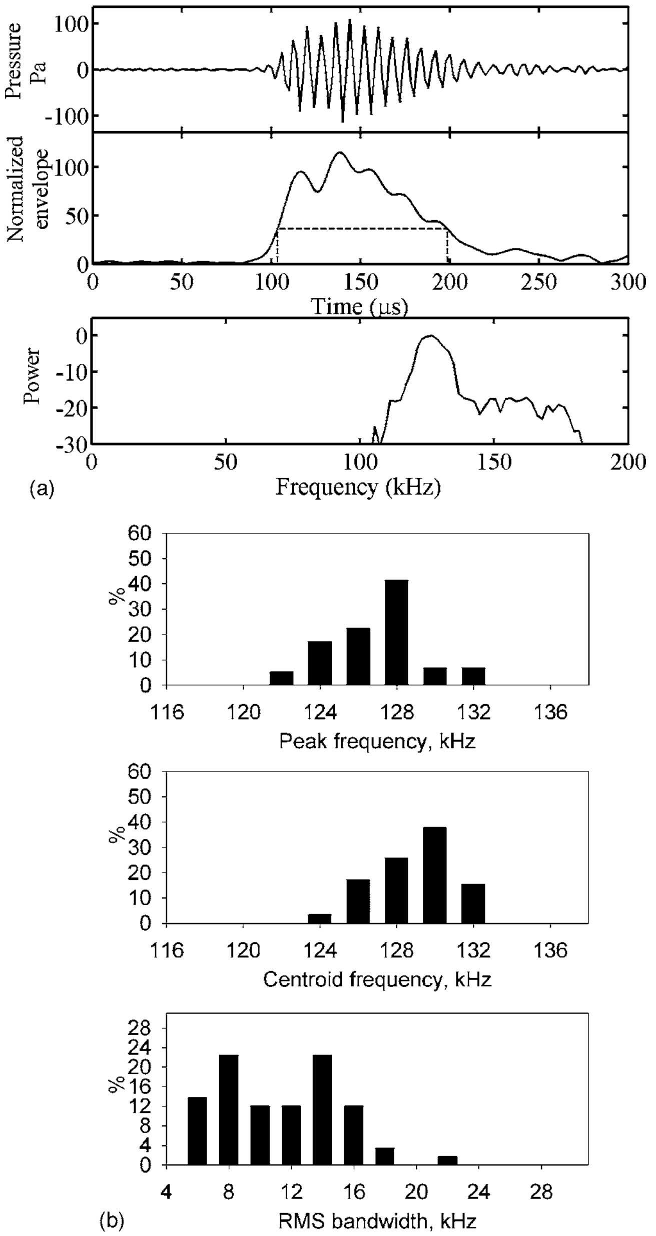

FIG. 1. (a) Time domain, envelope, and power spectrum of a representative hourglass dolphin signal. The dashed square in the envelope denotes the 10 dB duration. [Fast Fourier transform (FFT) size of 256, spectrum interpolated with a factor 100, sampling rate of 500 kHz, and rectangular window.] (b) Histograms of 58 on-axis hourglass dolphins' clicks with peak frequency, centroid frequency, and rms bandwidth. Binwidth is 2 kHz.

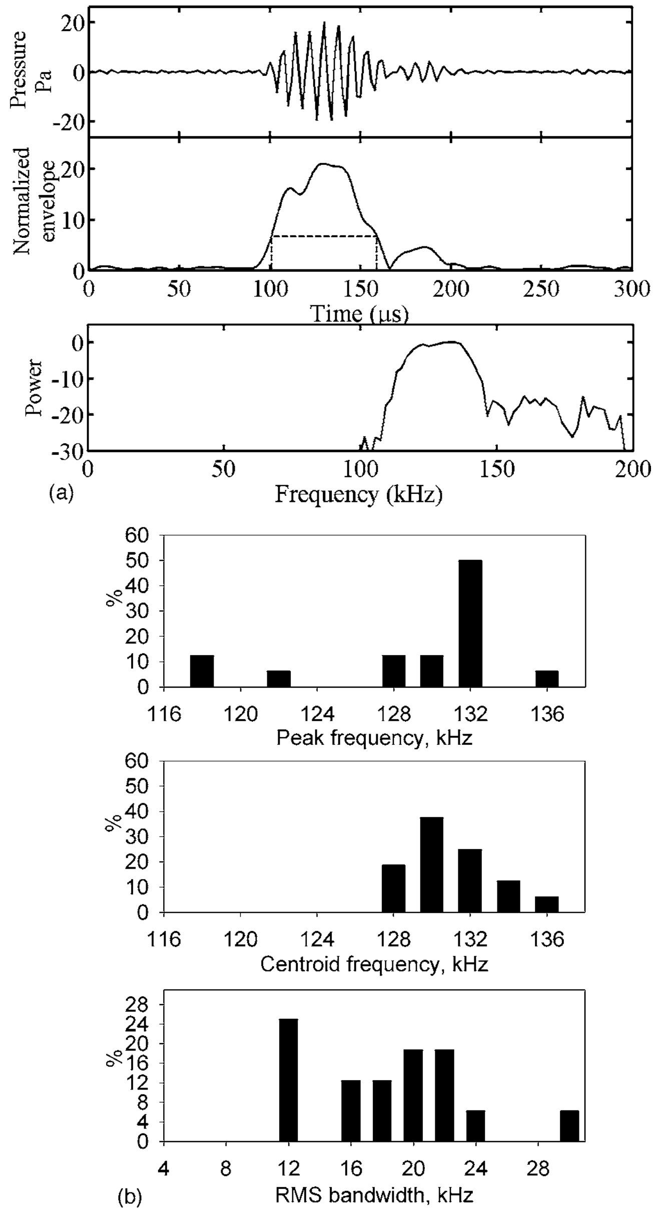

FIG. 2. (a) Time domain, envelope, and power spectrum of a representative Hector's dolphin signal. The dashed square in the envelope denotes the 10 dB duration. (FFT size of 256, spectrum interpolated with a factor 100, sampling rate of 500 kHz, and rectangular window.) (b) Histograms of 16 on-axis Hector's dolphins' clicks with peak frequency, centroid frequency, and rms bandwidth. Binwidth is 2 kHz.

time of arrival differences for the same signal recorded on the four channels. We determined the timing of a click from the first sample exceeding −10 dB of the peak of the click envelope [Figs. 1(a) and 2(a)].

Once the range to the animal has been estimated, TL can be calculated and added to the received level (RL) of a click. Villadsgaard *et al.* (2007) found that propagation loss of 130 kHz porpoise clicks in a shallow water habitat was well approximated by spherical spreading plus the frequency dependent absorption. Given the short distances and good mixing of the water column in the two habitats in the present study, we also assumed that TL could be approximated by spherical spreading plus absorption. ASL of echolocation clicks was thus calculated using the equation

$$\mathrm{ASL} = \mathrm{RL} + \mathrm{TL}(=20 \log r + \alpha r) \quad \text{(Urich, 1983)},$$

where α is the absorption coefficient in dB/m and r is range in m. For the present field sites of 14 and 5.1 °C for Akaroa and the Drake Passage, α was calculated following expressions from Fisher and Simmons (1977) using the centroid frequency of the clicks (α is 0.037 for Hector's dolphin and 0.029 or hourglass dolphin). ASLs are given as peak-peak pressure, rms pressure, and energy flux density (EFD) and were computed as follows. $\mathrm{RL}_{\mathrm{p.-p.}}$ (dB re 1 $\mu\mathrm{Pa}_{\mathrm{p.-p.}}$) was measured directly from the maximum and minimum peak pressures of the waveform. $\mathrm{RL}_{\mathrm{rms}}$ (dB//1 μPa rms) is the rms pressure calculated over the 10 dB duration of the signal. $\mathrm{RL}_{\mathrm{EFD}}$ (dB//1 $\mu\mathrm{Pa}^2$ s) is the signal energy integrated over the 10 dB duration (Madsen, 2005).

TABLE I. Mean (±standard deviation) and range of echolocation click source parameters of hourglass dolphins (*Lagenorhynchus cruciger*) and Hector's dolphins (*Cephalorhynchus hectori*).

	Hector's dolphin *Cephalorhynchus hectori*		Hourglass dolphin *Lagenorhynchus cruciger*	
Parameters	Mean values (stdev)	Range	Mean values (stdev)	Range
10 dB duration (μs)	57(±6)	41–65	115(±24)	79–176
$RL_{p.-p.}$, dB re 1 $\mu Pa_{p.-p.}$	156(±6)	145–166	162(±4)	155–168
$ASL_{p.-p.}$, dB re 1 $\mu Pa_{p.-p.}$ [a]	177(±6)	161–187	197(±4)[a]	190–203[a]
$RL_{-10\ dB}$, dB re 1 μPa rms	145(±6)	133–154	151(±4)	144–158
$ASL_{-10\ dB}$, dB re 1 μPa rms[a]	166(±6)	152–175	186(±4)[a]	179–193[a]
$EFD_{-10\ dB}$, dB re 1 μPa^2 s [a]	121(±4)	110–126	146(±3)[a]	140–152[a]
Peak frequency (kHz)	129(±5)	117–135	126(±2)	122–131
Centroid frequency (kHz)	128(±3)	125–132	128(±2)	124–132
3 dB bandwidth (kHz)	20(±3)	12–26	8(±2)	5–11
10 dB bandwidth (kHz)	30(±10)	24–66	13(±2)	9–18
rms bandwidth (kHz)	18(±5)	11–29	11(±4)	5–22
$Q_{-3\ dB}$	6(±1)	5–11	17(±4)	12–25
Q_{rms}	8(±2)	4–12	13(±5)	6–26
Mean range from array (m)	11(±4)	4–19	50[b]	50[b]
n	16		58	

[a] ASL for hourglass dolphins is calculated from an estimated range.

[b] Estimated minimum range of 50 m, corresponding to a transmission loss of 35 dB.

III. RESULTS

Several hundred Hector's dolphin clicks were recorded over 2 days from 12 groups of between two and eight animals approaching to within 1 m from the hydrophone array. Due to the fission-fusion structure of Hector's dolphins groups (Slooten and Dawson, 1988; Slooten *et al.*, 1993) and their small home range (Bräger *et al.*, 2002) some animals have likely been recorded more than once. The dolphins approached the boat to bow ride.

Around 200 hourglass dolphin clicks were recorded on one occasion from a group of around 20 animals. The clustering of the dolphins and lack of directional movement suggested that they were engaged in feeding activities. Fifty-eight hourglass dolphins' clicks were judged to have been recorded on-axis; however, all were recorded at too great a range (>40 m) from the hydrophone array to allow for accurate localization. We thus based ASL calculations on estimated range. In order to ensure a conservative ASL estimate we used a range of 50 m to calculate TL (see equation above) between the clicking dolphin and the hydrophone array. A TL of 35 dB was therefore added to each RL for this species. No dolphins were recorded closer to the array than 40 m, and we therefore assume that the derived source levels are minimal estimates with the possibility of the estimated source levels to be higher, but very unlikely to be lower.

Source signal parameters of both species are summarized in Table I. Hourglass dolphins and Hector's dolphins both produced clicks with a centroid frequency of 128 kHz with little intraspecific variation and identical maximum values of 132 kHz. Bandwidths were much narrower for hourglass dolphins meaning that the click energy was contained in a smaller frequency band giving a higher Q-value. The RLs of hourglass dolphins ranged from 155 to 168 dB re 1 $\mu Pa_{p.-p.}$ and Hector's dolphins RL ranged from 145 to 166 dB re 1 $\mu Pa_{p.-p.}$. The peak-to-peak source level of hourglass dolphin was thus estimated to be about 20 dB higher than Hector's dolphin clicks, since they were at least 50 m away whereas Hector's dolphins were localized to be <20 m from the array. Hourglass dolphin clicks were on average more than twice as long as Hector's dolphin clicks and appeared to have an EFD at least 25 dB higher due to the higher source level and longer duration. Representative clicks and histograms of click parameters are shown in Figs. 1(a), 1(b), 2(a), and 2(b). We found no correlation for click duration or bandwidth with ICI, for either species (Fig. 5).

For the array calibration 2451 clicks were included in the analysis of the localization routines. 130 kHz clicks could be localized precisely (with a rms error up to 2 dB) out to 40 m from the hydrophone array (Fig. 3). At greater distances the routines underestimated the actual distances to the sound source, giving rise to errors larger than 3 dB in TL.

IV. DISCUSSION

NBHF clicks of porpoises and the *Cephalorhynchus* genus have been described as stereotypical (Au, 1993; Madsen *et al.*, 2005). The source parameters of Hector's and hourglass dolphins recorded in this study, however, displayed some apparent differences. Both species produced NBHF clicks with a centroid frequency of 128 kHz, but clicks of hourglass dolphins were about twice as long, with a narrower bandwidth and therefore higher Q-value, than those of Hector's dolphins. Hourglass dolphins consequently concentrated their energy in a narrower frequency band while the peak frequency and centroid frequency were similar for the two species.

Hourglass dolphins had higher estimated source levels than Hector's dolphin, and the fact that even the highest of the Hector's source levels found in this study did not exceed the lowest of the estimated hourglass dolphin source levels suggests that there is a genuine source level difference be-

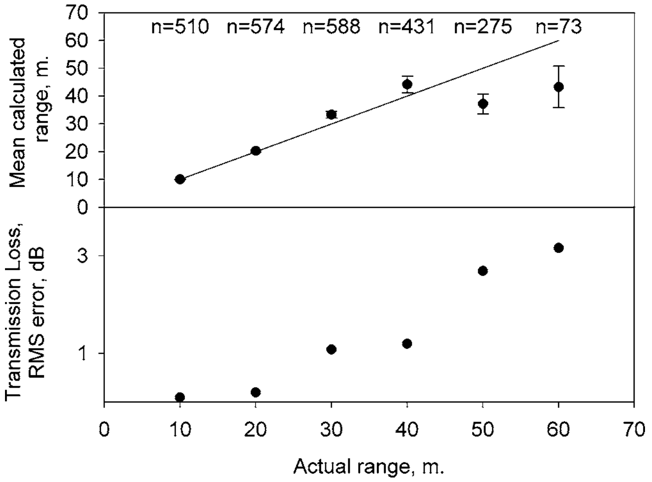

FIG. 3. Calibration of localization precision using a 3 m aperture four element hydrophone array. (a) Mean calculated ranges with standard deviation plotted against actual range. The line denotes the expected localization range from each of the actual ranges. (b) Effect of localization error on TL expressed in rms error, dB. With a 3 m aperture array NBHF species may be localized out to 40 m with ±2 dB precision on source level calculations.

tween the two species. Despite the apparent on-axis approach used in this study we can, however, only ensure that the clicks used for analysis were those recorded closest to on-axis of the clicks in a given scan. Since the ASL decreases with increasing angle to the acoustic axis (Au, 1993), source levels may be underestimated in our analysis compared to true on-axis clicks. Furthermore, the ASL of hourglass dolphins is a rough (but most likely conservative) estimate since the dolphins were too far away to be localized. The estimated range of 50 m for the calculation of TL was based on a visual estimation made at the time of recording and on the fact that 130 kHz clicks can be located accurately out to 40 m from the array. We could not see the animals under water, but the fact that we could not locate any of the recorded clicks leads us to suspect that all dolphins were at greater ranges than 40 m from the array during recording. Further, the hourglass dolphins had a mean RL of 162 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$ and was ~50 m away, whereas Hector's dolphins were <20 m away and had a mean RL of 156 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$. A mean ASL of 197 ± 4 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$ at 1 m and unknown aspect is thus a conservative best estimate for the hourglass dolphin (a range increase from 50 to 100 m would increase mean SL to 204 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$), whereas the estimate of ASL for Hector's dolphins was 177 ± 6 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$ at 1 m (Table I).

Hector's dolphins came to bow ride, and as they were very close to the boat and the hydrophone array at the time of recording their source levels may likely have been lower than during natural foraging, which the hourglass dolphins were engaged in. However, Dawson and Thorpe (1990) also found low ASLs of ~150 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$ for Hector's dolphins foraging at the surface within 5 m from their boat. They also recorded clicks of up to 163 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$, but could not discern the vocalizing animal and thus estimate distance to the hydrophone.

If the source parameters measured in this study are representative for the two species, the ASLs of hourglass dolphins are an order of magnitude higher than those of Hector's dolphins. Hourglass dolphins have been found up to around 40 cm longer and 40 kg heavier than Hector's dolphin and it is possible that the higher ASL of hourglass dolphins can be ascribed to this size difference. However, Villadsgaard *et al.* (2007) reported that ASLs clicks of wild harbor porpoises, similar in size to Hector's dolphins, vary considerable between different recording sites (178–205 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$), possibly depending on background noise level and behavioral states of the animals. The variation in ASL of harbor porpoises thus spans both Hector's and hourglass dolphins, also spanning the size differences between the two. Hector's and hourglass dolphins likely also have a large dynamic range within which they produce clicks since we cannot ascertain that the full source level repertoire was sampled during these recordings.

Source level influences heavily on the range at which a dolphin can detect prey and the source level differences found here may thus provide a hint to the ranges at which the dolphins have adapted their sonars to search for prey. Detection range can only be estimated knowing the echo level threshold (DT) of a dolphin for a prey object with known target strength (TS). Kastelein *et al.* (1999) measured the psychophysical target detection threshold (expressed as echo energy flux density, EE) for a captive harbor porpoise echolocating at two water-filled stain-less steel spheres to be ~27 dB re 1 μPa^2 s (between 22.4 and 27.4 dB re 1 μPa^2 s); however, these calculations were based on too low source level (Au *et al.*, 2007) and the present best estimate of harbor porpoise detection threshold is 44–45 dB re 1 μPa^2 s (Au, personal communication). To calculate detection range Kastelein *et al.* (1999) used the active sonar equation ($\text{EE}=\text{SE}-2\times\text{TL}+\text{TS}_E=\text{DT}$) solved for EE at maximum range of detection, where SE is source EFD, TL is transmission loss, and TS_E is target strength energy. The non-noise-limited form of the sonar equation was used due to the low background noise usually found around 130 kHz (Kastelein *et al.*, 1999; Au *et al.*, 2007). Au *et al.* (2007) found that a 30 cm cod has a broadside target strength of −25 dB emitting artificial NBHF clicks with a centroid frequency of 130 kHz. Assuming that Hector's dolphin and hourglass dolphin have detection thresholds comparable to that of the harbor porpoise of 45 dB re 1 μPa^2 s and using the porpoise as a model we can thus estimate detection ranges of these two species. Under the assumption that both species were recorded with representative maximum source levels, Hector's dolphin is predicted to be able to detect a 25 cm cod broadside up to 10–24 m away, while hourglass dolphins are predicted to detect the same fish out to about 52–96 m, using minimum and maximum EFD source levels of 110 and 126 dB re 1 μPa^2 s and 140 and 152 dB re 1 μPa^2 s and respective absorption values (α, see above) (Fig. 4). Using the same assumptions wild harbor porpoises are predicted to detect the same cod 20–84 m away using minimum and maximum EFDs of 123 and 150 dB re 1 μPa^2 s and α of 0.04 (Villadsgaard *et al.*, 2007). The 25 dB lower EFD of Hector's dolphin clicks thus more than halves the detection range compared to the hourglass dolphin.

Hector's dolphins live within the coastal zone. Shallow coastal areas generally have a higher productivity and thus

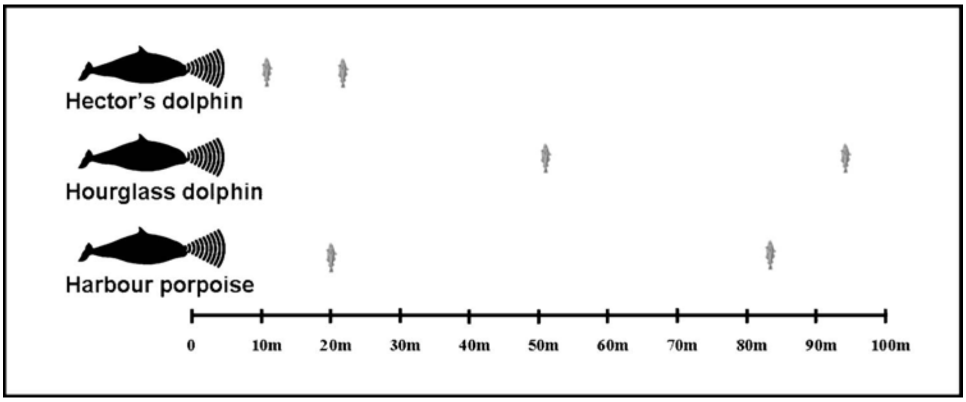

FIG. 4. Estimated detection ranges of hourglass dolphin and Hector's dolphin calculated for minimum and maximum EFD source levels using the harbor porpoise as model (Kastelein *et al.*, 1999, see text for further explanation) and target strength of a 25 cm cod measured broad side (Au *et al.*, 2007). Minimum and maximum detection ranges of harbor porpoise are shown for comparison, build on data from Villadsgaard *et al.* (2007) and Au (personal communication).

greater prey availability, but clutter and reverberation levels are also higher. Since an increase in source level also increases clutter this may explain why Hector's dolphins use a comparatively low source level. Increased transmission and receiving directivity will increase detection range in a cluttered environment since a more directional beam or sound reception will result in fewer unwanted echoes. Transmission directivity depends on size of the sound transducer relative to the emitted wavelength. If the sound production apparatus scales with head diameter of the animal (Au *et al.*, 1999), transmission directivity likely compares among the similar sized Hector's and hourglass dolphins presenting no special adaptation of Hector's dolphin to a cluttered environment. However, if prey density is also higher in the coastal environment, Hector's dolphin may not need high source levels to locate prey there. Future studies may uncover whether Hector's dolphins are capable of producing higher source levels at other behavioral states as observed for harbor porpoises (Villadsgaard *et al.*, 2007).

The higher source levels of hourglass dolphins oppositely suggest that they forage in an environment with lower prey density or with longer distances between prey patches. Since their click duration is also about twice that of Hector's dolphins, the energy content is increased two-ways compared to Hector's dolphin: higher source level (20 dB) and longer duration (doubling of energy content, 3 dB). If there is a size restricted maximum output for NBHF species, as suggested by Au (1993), the longer click duration suggests that hourglass dolphins may be noise limited and that they maximize energy content by making longer clicks to facilitate a longer detection range. The source parameters of hourglass' clicks may be the result of selection for increased target range in a noise-limited sonar situation.

For odontocete clicks, duration and bandwidth are inversely related (Wiersma, 1988; Au, 1993; Beedholm, 2008) so that a change in one parameter will change the other as well. It is therefore not surprising to find that bandwidth of hourglass dolphin clicks is about half that of Hector's clicks. However, it is interesting to note that despite differences in bandwidth both species have all click energy above 100 kHz [Figs. 1(a) and 2(a)] and the differences in source parameters observed between these two NBHF species are thus not in disagreement with the NBHF anti-predator hypothesis of Morisaka and Connor (2007).

The duration of Hector's dolphins' clicks of ~ 60 μs found in this study is lower than in previous published studies of 80–800 μs (Dawson, 1988; Dawson and Thorpe, 1990; Dawson, 1991; Thorpe *et al.*, 1991; Thorpe and Dawson, 1991). These differences in duration likely arise from the fact that previous studies included so-called double, triple, and quadruple pulsed clicks in their analysis, which we omitted here as they are most likely the result of surface and bottom reflections (Li *et al.*, 2005) and possibly off-axis distortions. In addition, previous studies measured duration by hand, whereas we used a definition of -10 dB from maximum amplitude of the signal envelope. The durations of Hector's clicks measured here correspond to that of another NBHF species the finless porpoise (*Neophocaena phocaenoides*) of $\sim 30-60$ μs (unknown recording aspect and definition of duration) (Akamatsu *et al.*, 1998) and are among the shortest of NBHF clicks. Villadsgaard *et al.* (2007), however, reported a range in 10 dB duration of harbor porpoise clicks from 44 to 113 μs thus spanning the range of both Hector's and hourglass dolphin clicks. It is possible that some click source parameters change with behavior and thus that the variation in duration between Hector's and hourglass' clicks could be caused by differences in behavior at the time of recording. Since ICIs change during, e.g., approach and capture phases of prey in other toothed whales (Johnson *et al.*, 2007), we used ICI as a proxy for behavior, and to test whether Hector's dolphins and hourglass dolphins changed their click duration and/or bandwidth with ICI we thus plotted each ICI preceding an on-axis click against its 10 dB duration and rms bandwidth for both species in Fig. 5. ICIs were generally longer for hourglass dolphins, but where the two species overlapped in ICI, the click duration and bandwidth were distinctly different (Fig. 5). Although it is possible that more recordings of the species measured here engaged in different behaviors may show a greater dynamic range in click duration resulting from changes in the context of sonar use, and not only from differences in habitat, this study suggests a genuine difference in click duration between Hector's dolphin and hourglass dolphin.

So far ASLs have only been measured for three free-ranging NBHF species: the harbor porpoise (Villadsgaard *et al.*, 2007) and the two present species (this study and Dawson and Thorpe, 1990). The highest levels were found for hourglass dolphins with a range 190–203 dB re 1 $\mu\mathrm{Pa}_{\text{p.-p.}}$

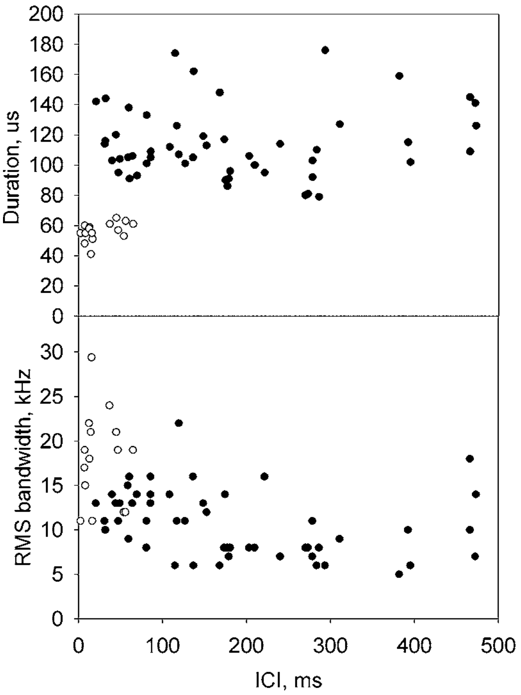

FIG. 5. rms bandwidth and 10 dB duration as a function of ICI. ICI is the one preceding the on-axis click for which bandwidth and duration was measured. Closed circles are hourglass dolphins and open circles are Hector's dolphins.

(Table I) and harbor porpoises with a range from 178 to 205 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$ (Villadsgaard *et al.*, 2007) and Hector's dolphins with a range 161–187 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$ (Table I). These levels are 10–30 times lower than in general for broadband dolphin clicks that have source levels of up to ~220 dB re 1 $\mu\text{Pa}_{\text{p.-p.}}$ (Au, 1993; Rasmussen *et al.*, 2002; Madsen *et al.*, 2004b), which again is reflected in the much longer detection range. It is precarious to generalize from only two species, especially with a very limited sample size in terms of behavior; but at least for *Cephalorhynchus* dolphins and the hourglass dolphin, offshore NBHF dolphins seem to produce clicks with higher source level than coastal dolphins do. To gain a better insight into the evolution and plasticity of the NBHF clicks this hypothesis should be tested by recording clicks from other *Cephalorhynchus* and porpoise species engaged in different behaviors. On the basis of the present findings we hypothesize that the oceanic Dall's porpoise will have a greater source level than coastal-offshore species such as the harbor porpoise and that riverine and very coastal species will have the lowest source levels.

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Chapter IV

Kyhn, L.A., Jensen, F. H., Beedholm, K., Tougaard, J. Hansen, M. and Madsen, P.T. (2010). Echolocation in sympatric Peale's dolphins (Lagenorhynchus australis) and Commerson's dolphins (Cephalorhynchus commersonii) producing narrow-band high-frequency clicks. The Journal of Experimental Biology 213:1940-1949.

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Commerson's dolphins playing in the surf very close to shore, Falkland Islands, March 2008.

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Echolocation in sympatric Peale's dolphins (*Lagenorhynchus australis*) and Commerson's dolphins (*Cephalorhynchus commersonii*) producing narrow-band high-frequency clicks

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SUMMARY

An increasing number of smaller odontocetes have recently been shown to produce stereotyped narrow-band high-frequency (NBHF) echolocation clicks. Click source parameters of NBHF clicks are very similar, and it is unclear whether the sonars of individual NBHF species are adapted to specific habitats or the presence of other NBHF species. Here, we test whether sympatric NBHF species sharing the same habitat show similar adaptations in their echolocation clicks and whether their clicks display signs of character displacement. Wide-band sound recordings were obtained with a six-element hydrophone array from wild Peale's (*Lagenorhynchus australis*) and Commerson's (*Cephalorhynchus commersonii*) dolphins off the Falkland Islands. The centroid frequency was different between Commerson's (133±2 kHz) and Peale's (129±3 kHz) dolphins. The r.m.s. bandwidth was 12±3 kHz for both species. The source level was higher for Peale's dolphin (185±6 dB re 1 μPa p.–p.) than for Commerson's (177±5 dB re 1 μPa p.–p.). The mean directivity indexes were 25 dB for both species. The relatively low source levels in combination with the high directivity index may be an adaptation to reduce clutter when foraging in a coastal environment. We conclude that the small species-specific shifts in distribution of centroid frequencies around 130 kHz may reflect character displacement in otherwise-stereotyped NBHF clicks.

Key words: acoustic species separation, acoustics, character displacement, clutter adaptation, static acoustic monitoring, sympatric species.

INTRODUCTION

Toothed whales, with more than 70 species, cover a large range of sizes and habitats, from shallow rivers to deep mesopelagic ocean water. They presumably all use echolocation to find and capture prey, but little is known about the evolutionary forces shaping the speciation and biosonar source parameters of toothed whales (Wood et al., 1980). In three phylogenetically different groups of toothed whales [Phoconoidea, *Cephalorhynchid* dolphins and the pygmy sperm whale (*Kogia breviceps*)], the same narrow-band high-frequency (NBHF) echolocation signal has evolved, likely as an adaptation to avoid predation from killer whales (*Orcinus orca*) (Andersen and Amundin, 1976; Morisaka and Connor, 2007). However, it is unclear whether these different species have special adaptations within the NBHF signal and, if so, which selective pressures have affected their acoustic signal and foraging strategy within each specific habitat.

Target strength, background noise and clutter are all properties of the acoustic environment of echolocating species, and this means that, regardless of animal adaptations, a sonar will ultimately be limited by either noise or clutter (Au, 1993). For all sonar systems, the limiting factor deciding whether a returning echo is detected is either the echo-to-noise ratio (ENR) of the returning echo or the echo-to-clutter level. The ENR is given by the emitted source level (SL) plus the target strength, minus the two-way transmission loss (absorption and spreading) and the received noise (Urick, 1983). We may thus expect the source parameters of a given animal sonar to be adapted either to maximize range under noise-limited conditions or to reduce clutter, depending on the habitat to which the species has adapted.

Besides noise, clutter in the form of unwanted echoes may also interfere with detection of the returning echo. The influence of clutter is reduced by the directionality of the transmitter: the greater the directionality, the smaller the area ensonified by the animal, and a greater directionality will thus reduce the number of unwanted echoes. By contrast, an increased receiving directionality will decrease amount of received noise. An animal may thus adapt to echo detection in noise by increasing the source level and/or the receiving directionality, whereas an increased transmitting directivity will facilitate echo detection in clutter and increase the SL for the same output power.

Examples of such sonar adaptation are found among bats. The terrestrial environment of echolocating bats offers a range of different types of foraging niches and habitats, facing the animals with different prey types, clutter and noise levels. Accordingly, the sonar signals of different Microchiropteran bats show adaptations to different clutter and noise levels, and several eco-types of bat sonar have been proposed based on how close the bats forage to reflective surfaces such as the foliage, the ground or water surfaces, which all create clutter (Neuweiler, 1989; Neuweiler, 2000; Denzinger et al., 2004; Jung et al., 2007). Open-space foragers have, for example, adapted to noise by making their echolocation signals and cry patterns suitable to long-range navigation by producing high source level, narrow-band signals of lower centroid frequency and with shallow frequency modulation emitted with relatively large inter-pulse intervals, whereas bats foraging in dense forest use clicks of lower SL to avoid clutter (Neuweiler, 1989; Neuweiler, 2000; Denzinger et al., 2004; Jung et al., 2007).

The same type of links between habitat and sonar properties has not been established for toothed whales, despite an increasing number of studies of animals in the wild as well as in captivity. Based on data from only a few odontocetes, there is a tendency for smaller animals to have lower directionality and source level than larger animals without regard to habitat (Au, 1993; Au et al., 1995; Au et al., 1999). That raises the question whether inter-specific differences can be explained by the size of the species alone or whether more-biological shaping factors such as habitat, prey and predation also play important roles in shaping the signals of toothed whale biosonar systems.

As introduced above, three phylogenetically distinct groups of small (<2.5 m) odontocetes have evolved the same type of sonar signal: an NBHF click with a peak frequency around 130 kHz and a half-power bandwidth around 15 kHz. The groups producing these strikingly similar NBHF clicks include the *Phocoenidea* family (Møhl and Andersen, 1973; Akamatsu et al., 1998; Villadsgaard et al., 2007), the *Cephalorhynchus* genus (Kamminga and Wiersma, 1982; Dawson and Thorpe, 1990; Kyhn et al., 2009) within the dolphin family [including the hourglass dolphin (*Lagenorhynchus cruciger*)] and the pygmy sperm whale (Madsen et al., 2005). Furthermore, the Francicana river dolphin (*Pontoporia blainvillei*) (von Fersen et al., 2000) is proposed to use NBHF clicks, but only the peak frequency and –3 dB bandwidth was stated by the investigators (von Fersen et al., 2000).

Peale's dolphin (*Lagenorhynchus australis*) is expected to use the NBHF signal as its sister species, the hourglass dolphin, uses NBHF signals, and both species are here considered to be part of a phylogenetic group consisting of these two species and the *Cephalorhynchus* genus (May-Collado and Agnarsson, 2006; Tougaard and Kyhn, 2010). All together, at least 14 species produce NBHF echolocation clicks, and they mostly inhabit shallow water, but with a few oceanic (such as the hourglass dolphin) and even deep-diving (the pygmy sperm whale) species.

All these species likely use the NBHF signal as a result of evolutionary convergence under the possibly shared selection forces of a small body size and predation from killer whales (Andersen and Amundin, 1976; Madsen et al., 2005; Morisaka and Connor, 2007) that hear frequencies above 100 kHz very poorly (Szymanski et al., 1999). Not all small toothed whales, however, are NBHF species, and, as discussed by Morisaka and Connor (Morisaka and Connor, 2007), there are general differences in both behaviour and group size between NBHF species and non-NBHF species. Although the risk of predation may have driven the evolution of the four phylogenetically different types of NBHF sonar systems to be narrow band and with a peak frequency around 130 kHz to keep all energy above 100 kHz (Andersen and Amundin, 1976; Morisaka and Connor, 2007), the increased absorption and masking noise with increasing frequency have likely restrained the peak frequency upwards to around 130 kHz (Madsen et al., 2005). Within those constraints, however, it is unclear to what degree each species has adapted to its specific habitat in relation to noise and clutter as well as to competition from sympatric NBHF species.

Similar habitats may provide similar selective forces on biosonar systems to favour the same signals, but complete overlap in signal structure may pose disadvantages for sympatric species exploiting the same foraging niche as it may confound communication and possibly interfere with echolocation if echoes from other individuals/species cannot be separated from own echoes – so-called jamming. Some families of sympatric Microchiropteran bats overlap in size, range and foraging niche and have shown inter-specific acoustic specializations. For example, ten sympatric species of Emballonurid bats display inter-specific variation in echolocation signal parameters such as peak frequency, call duration, pulse interval and direction of modulation of the frequency sweep, which cannot readily be explained by habitat specialization (Jung et al., 2007). Such species-specific differences may instead serve to avoid jamming of echolocation signals and/or serve communication in order to provide a basis for species recognition, as it is suggested that the same type of sonar signals may serve both communication and echolocation (Fenton, 1986), depending on the situation. Such specializations have not been examined in toothed whales.

In an attempt to address this deficiency, we recorded two NBHF species in the wild – Peale's dolphin and the smaller Commerson's dolphin (*Cephalorhynchus commersonii*) that are closely related and live sympatrically off the Falkland Islands (Islas Malvinas). As such, they offer a suitable experimental platform for elucidating whether similar trade-offs are at play among the toothed whales between meeting biophysical demands for a given body size, food niche and predation scheme versus the negative effects of not being able to tell each other apart acoustically. The two species overlap in distribution at the Falklands Islands and are both associated with kelp beds. However, whereas Commerson's dolphins are found strictly within 10 km from land, Peale's dolphins range over the continental shelf and may thus be found all the way between the Falklands Islands and Argentina (White et al., 2002).

Based on the knowledge from Microchiropteran bats, we wanted to test the hypotheses that these sympatric NBHF dolphins: (i) may show similar adaptations in source parameters owing to their shared habitat, or (ii) demonstrate scaling with size or character displacement that has led to different distributions of source parameters in these sympatric species.

MATERIALS AND METHODS

Recording chain and field sites

Recordings were made with a linear array of six Reson TC 4034 spherical hydrophones (Reson A/S, Slangerup, Denmark) with a 20 m cable and a measured sensitivity of –222 dB re 1 V/μPa between 100 and 150 kHz. The hydrophones were calibrated in an anechoic tank both prior to and following the field recordings. Hydrophones were mounted horizontally in the same direction along a vertical Perspex rod with 0.75 m hydrophone spacing, except between the two topmost hydrophones that were spaced 1.5 m apart. The 41 mm diameter Perspex rod was hollow and water filled when submersed and very stiff to avoid bending of the array during deployment. The hydrophones were mounted in fixed holes spaced with sub-millimetre accuracy in all dimensions. This is crucial as time-of-arrival differences of the same click between the different hydrophones are used to compute the distance to the animal, which again is a prerequisite for the source level and beam pattern estimations.

The array was suspended vertically below a buoy, with the top hydrophone 2 m below the surface and the bottom hydrophone 6.50 m below the surface. A 0.5 kg weight in the bottom kept the array vertical in the water. Signals were bandpass filtered at 1 kHz (1 pole) to 180 kHz (4 poles) and amplified either 50 or 60 dB by custom-made amplifiers. Signals were digitized in three synchronized National Instruments A/D converters (USB-6251) at a sampling rate of 500 kHz per channel and a resolution of 16 bits. The measured frequency response of the entire recording chain was within ±2 dB in the range from 2 kHz to180 kHz. The clip level of the recording chain was 186 dB re μPa (peak) for Peale's dolphins (*Lagenorhynchus australis*, Peale 1848), and either 186 or 176 dB re μPa (peak) for Commerson's dolphins (*Cephalorhynchus commersonii*, Lacépède 1804), depending on gain settings.

Recordings were obtained at two different field sites at the Falkland Islands (Fig. 1) on six occasions in the period 25 February to 11 March 2008. Peale's dolphins were recorded outside Stanley Harbour (51°39′29.31″S, 57°48′10.04″W) at Gypsy Cove and Tussac Point, and Commerson's dolphins were recorded at Mare Harbour (51°54′39.30″S, 58°25′45.54″W). Both field sites were close to shore, with an estimated water depth of 10–20 m. The dolphins were recorded from six different vessels (four different RHIBs, an engine-going sailing yacht and a military landing craft). When the dolphin groups approached the boat to bow ride, the engine was turned off and the hydrophone array lowered into the water. Only one species was observed at a time, and no other marine mammals were observed or detected acoustically. Recordings were made under very calm weather conditions (low winds, sea state 1), and the surface behaviour and whereabouts of the dolphins were noted.

Click analysis

To minimize the risk of including distorted off-axis clicks in the analysis (Madsen and Wahlberg, 2007) we applied a set of criteria to determine clicks as being on-axis by following the methods of Villadsgaard and colleagues (Villadsgaard et al., 2007) and Kyhn et al. (Kyhn et al., 2009): On-axis clicks should be: (i) recorded on all six channels; (ii) part of a scan – that is, a series of clicks closely spaced in time, normally first increasing then decreasing in amplitude (*sensu* Møhl et al., 2003); (iii) of maximum amplitude in the scan; (iv) of maximum amplitude on one of the four middle hydrophone channels; and (iv) such that the direct path of the click had to be stronger than any trailing bottom or surface reflections. Furthermore, the localization error (Villadsgaard et al., 2007) could not give rise to an r.m.s. transmission error of more than 3 dB in the source-level calculations. Additionally, we visually inspected all on-axis clicks and removed clicks that contained double or triple pulses, as these likely arise from surface reflections and are not source generated (Li et al., 2005). Owing to the one-dimensional vertical configuration of the array, the on-axis definition pertains only to the vertical plane, and we have assumed that the clicks are on-axis in the horizontal plane as well.

The source properties were quantified using a series of parameters *sensu* Au (Au, 1993) and Madsen and Wahlberg (Madsen and Wahlberg, 2007) for each click accepted as on-axis: duration$_{-10\,\mathrm{dB}}$ given by the –10 dB points of the signal envelope (the absolute value of the analytical waveform); peak frequency (F_{Peak}), centroid frequency (F_{C}) defined as the frequency dividing the spectrum in two halves of equal energy, –10 dB bandwidth defined as the bandwidth at –10 dB points below the spectrum peak, –3 dB bandwidth defined as the bandwidth at –3 dB points below the spectrum peak), r.m.s. bandwidth defined as the spectral standard deviation around the centroid frequency on a linear scale, $Q_{\mathrm{r.m.s.}}$ defined as the centroid frequency divided by the r.m.s. bandwidth, and $Q_{-3\,\mathrm{dB}}$ defined as the peak frequency divided by the –3 dB bandwidth.

Inter-click intervals (ICIs) were defined as the pause between an on-axis click and the previous click. If click trains overlapped, ICIs were found for several preceding pauses to find the correct interval to include in the analysis. All analysis and signal processing were performed with custom-written scripts in Matlab 6.5 (Mathworks).

Calibration of localization routines

The array localization performance was evaluated in Aarhus Harbour, Denmark, by playing out calibrated tone pips with duration and spectral properties similar to NBHF clicks at known ranges from the array. The six-element hydrophone array was suspended from a buoy, with the top hydrophone 1 m below the surface. Tone pips (130 kHz sinus pulses of 15 cycles and a 100 μsec duration) were transmitted with an omni-directional hydrophone (B&K8105, depth 3 m below surface) connected to a sound generator (Agilent, model 33220A). The same recording chain and settings used for the field recordings were used to record signals transmitted in a range interval from 10 to 80 m from the array. The speed of sound was estimated from the Leroy equation (Urick, 1983) from the measured temperature and salinity.

Fig. 1. Field sites for making recordings of Peale's and Commerson's dolphins. Red cross: recordings of Peale's dolphins at the Stanley Harbour area (51°39′29.31″S, 57°48′10.04″W). Red circle: recordings of Commerson's dolphins at Mare's Harbour (51°54′39.30″S, 58°25′45.54″W).

Estimation of source level

To obtain the range to the vocalising animal, we used the linear array of six hydrophones to generate an over-determined localization setup whereby the localization error can be assessed for each click (Wahlberg et al., 2001; Madsen and Wahlberg, 2007). The six hydrophones yield a localization calculated from time-of-arrival differences of the click pair-wise among the six hydrophones. Localisations were performed using Matlab implementing the localization routines of Wahlberg and colleagues (Wahlberg et al., 2001) and Madsen and Wahlberg (Madsen and Wahlberg, 2007). It proved essential to use a robust measure of the time-of-arrival differences for the same signal recorded on the six channels. We determined the timing of a click from the first sample (using an interpolation factor of 10) exceeding –10 dB of the peak of the click envelope. All localizations were evaluated visually, and, based on results from the array calibration, all localizations giving rise to an r.m.s. error (translated to transmission loss) larger than 3 dB were omitted from the data set. Furthermore, only clicks recorded at a distance of less than 65 m were included in the analysis.

Once the range to the animal has been estimated, transmission loss (TL) can be estimated and added to the received level (RL) of a click. Villadsgaard and colleagues (Villadsgaard et al., 2007) found that the propagation loss of 130 kHz porpoise clicks in a shallow-water habitat was well approximated by spherical spreading plus the frequency-dependent absorption. Given the short distances and good mixing of the shallow water column in the two habitats in the present study, we also assumed that transmission loss could be approximated well by spherical spreading plus absorption. The apparent source level (ASL) of echolocation clicks was thus calculated using the equation (Urick, 1983):

$$\mathrm{ASL} = \mathrm{RL} + \mathrm{TL}\ (\mathrm{TL} = 20\log r + \alpha r)\ , \tag{1}$$

where α is the absorption coefficient in dB/m and r is the range in meters. A value of α of 0.039 dB/m was used, based on the equations of Fisher and Simmons (Fisher and Simmons, 1977) for 130 kHz and a water temperature of 9°C. SL is given as peak–peak (p.–p.) pressure, r.m.s. pressure and energy flux density (EFD) computed as follows: $\mathrm{SL}_{\mathrm{p.\text{–}p.}}$ (dB//1 μPa p.–p.) was measured from the maximum and minimum peak pressure of the waveform. $\mathrm{SL}_{\mathrm{r.m.s.}}$ (dB//1 μPa r.m.s.) is the r.m.s. pressure calculated over the $\mathrm{duration}_{-10\mathrm{dB}}$ of the signal. $\mathrm{SL}_{\mathrm{EFD}}$ (dB//1 $\mu\mathrm{Pa}^2$s) is the signal energy over the $\mathrm{duration}_{-10\mathrm{dB}}$ (Madsen, 2005; Madsen and Wahlberg, 2007). We used the term apparent source level (ASL) to denote the sound pressure back-calculated to one meter off the acoustic axis.

Estimation of beam pattern

The apparent source level as a function of the angle to the acoustic axis – the source beam pattern – can be estimated when it can be assured that the same click has been recorded simultaneously both on and off the acoustic axis at known angles (Au, 1993). A linear array does not provide any information on animal orientation relative to the array, and the beam pattern must therefore be assumed to be rotationally symmetrical around the acoustic axis – that is, assuming that the beam pattern in the horizontal plane is the same as in the vertical plane (Madsen and Wahlberg, 2007).

Radiation plots were created by plotting the apparent source-level values against the angle relative to the assumed on-axis at which they were recorded. The peak amplitude and zero angle were subsequently adjusted in order to approach on-axis by interpolating between the highest recorded source level and the values from the two neighbouring hydrophones using a Lagrange interpolation polynomial. Unfortunately, for NBHF clicks, it is not always possible to tell whether a click was indeed recorded on-axis, and the actual aspect angle may therefore be underestimated when making such a plot. To address that problem and compare with the present data, we therefore carried out a Monte Carlo simulation of the process to estimate the theoretical distribution as it would have looked if the whales were indeed theoretical piston transducers with a 4 cm diameter [as is found using values from Au and colleagues (Au et al., 1999) and the circular piston model of Au et al. (Au et al., 1987)]. In the Monte Carlo simulation, a theoretical 4 cm diameter piston transducer transmitted clicks at angles up to 50 degrees off the acoustic beam and at ranges of 2–15 meters from the array, matching the distances to the recorded animals. Using the same on-axis criteria and algorithms as for our recorded data, we then fitted the resulting collection of click power versus estimated angle to the piston model by means of a non-linear least-squares method. Only in extreme cases with angles up to 30 degrees off the array did the model fail and consistently underestimate the parametric piston diameter.

Having asserted that the Lagrange approach was indeed sound, we then proceeded to fit the collection of real data points from the two dolphins in the same way to arrive at the least-square fit of the diameter of the piston that matched the data of each species best.

The use of the flat piston model over other geometries has mostly consequences for the side lobes. Side lobes are much more pronounced for tonal signals, which is not the situation for the more broad-band echolocation clicks. For describing the echolocating performance of dolphins, the side lobes are therefore less relevant, and, as argued by Morse (Morse, 1948), we therefore used the piston model to describe the beam pattern of the two target species.

Species separation

To test whether the two species could be separated based on the observed differences in mean centroid frequency, we made a Monte Carlo simulation with a classification criterion of 130.5 kHz. The criterion of 130.5 kHz was the centroid frequency resulting in the highest number of correct classifications for both species. Clicks with a centroid frequency below this value were classified as Peale's dolphin and clicks with a centroid frequency at or above 130.5 kHz were classified as Commerson's dolphin. For each species, clicks were drawn at random from clicks recorded from the species and the proportion of clicks correctly classified was noted. The random clicks drawn consisted of the on-axis clicks from the analysis above as well as the corresponding off-axis clicks for the same recordings – that is, a 1:5 on-axis to off-axis values. One hundred clicks were drawn 10 times for each species, and the mean percentage correct as well as standard deviation of the mean were calculated. The entire procedure was then repeated with sets of clicks, such that the mean centroid frequency of 2, 4, 8, 16 and 32 random clicks was compared with the threshold criterion.

RESULTS

130 kHz clicks could be localized with a precision corresponding to an r.m.s. error on source level of less than 3 dB out to 65 m from the six-element hydrophone array (Fig. 2). At greater distances, the routines underestimated the actual distances to the sound source, giving rise to combined errors larger than 3 dB in transmission loss.

Signals from Commerson's dolphins were recorded on two occasions at the same field site in the harbour of the Falkland Royal Air Force (RAF), Mare's Harbour (Fig. 1). According to the military personnel at the RAF base, Commerson's dolphins are always present in the area and, on the days of recording, approximately 30–40 dolphins were present in the area. On both occasions, the dolphins were engaged in foraging in a kelp bed before coming to bow ride. Some dolphins remained foraging while 10–15 dolphins came to bow ride in front of the boat. The dolphins stayed around the boat some time after the engine was turned off, ensonifying the hydrophone array. However, they quickly lost interest and returned to the kelp bed. Only Commerson's dolphins were seen at the time of recording. More than 1000 clicks were recorded, and, of these, 94 met the on-axis criteria, and had source ranges within 65 m from the hydrophone array. The waveform and power spectrum of a representative click are shown in Fig. 3. The source parameters of Commerson's clicks are summarized in Table 1.

Signals from Peale's dolphins were recorded on four occasions, and no other odontocetes were observed during the recordings (Fig. 1). Recordings were made of several different groups, ranging in size from three to more than ten animals, likely up to 20. We did not observe the dolphins until they were fast approaching to bow ride, but, when they left, we saw them forage in near-shore kelp beds. On one occasion, a group containing two calves was observed,

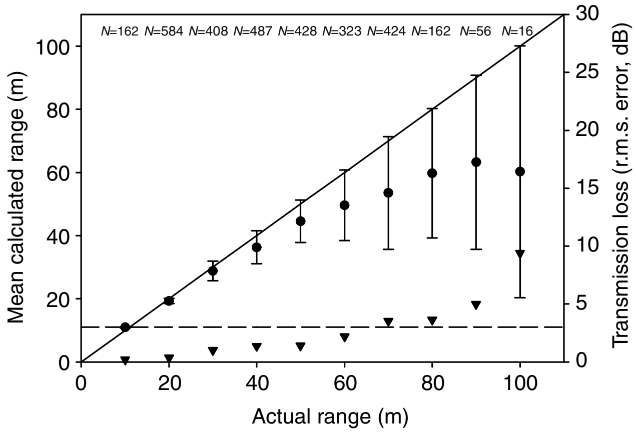

Fig. 2. Localization performance of a 4.5 m aperture six-element hydrophone array. Closed circles are mean calculated ranges (with standard deviation) plotted against the actual range. The solid line denotes the expected localization range from each of the actual ranges. The effect of localization error on transmission loss is expressed in r.m.s. error dB, and plotted as triangles while utilizing the separate right *y*-axis. The broken line signifies that, with a 4.5 m aperture array, NBHF species may be localized out to 65 m with less than 3 dB r.m.s. error on source-level calculations. The number of measurements (*N*) made at each range is shown along the top of the graph.

but data from this group were omitted from the analysis. Of more than 1000 clicks recorded, 87 clicks were defined as on-axis according to the listed criteria and subsequently included in the analysis. All these clicks were recorded at ranges of less than 65 m. The waveform and power spectrum of a representative click are shown in Fig. 3. The source signal parameters of both species are summarized in Table 1. ICIs for both species are plotted against range in Fig. 4.

Fig. 5 depicts the results of the non-linear least-squares method used to validate the use of the method for estimating the directionality of the two species. Directional characteristics generated by the piston model together with the real data for both species are shown in Fig. 6. The piston diameter for which the directional characteristics fitted the data best was 6.5 cm for Commerson's dolphins and 7 cm for Peale's dolphin.

The centroid frequencies of both species had a normal distribution [Kolmogorov–Smirnov (two-tailed): P=0.00, N=87 (Peale's), N=94 (Commerson's)]. Source levels of Peale's dolphins were significantly higher than source levels of Commerson's dolphins (Mann–Whitney U-test = 8178, χ^2=134.8, P<0.001, N=181) (Tables 1 and 2; Fig. 4). Centroid frequency was significantly higher for Peale's dolphin (U=7034.5, χ^2=69.95, P<0.001, N=181) (Table 1).

Commerson's dolphin could be classified with higher certainty and using fewer clicks than Peale's dolphins could (Fig. 7). Based on the mean centroid frequency of 16 clicks, almost all click series were classified correctly. Clicks from Peale's dolphin, by contrast, proved more difficult, and, even with a click series of 32 clicks, the percentage of misclassifications was 10.2%.

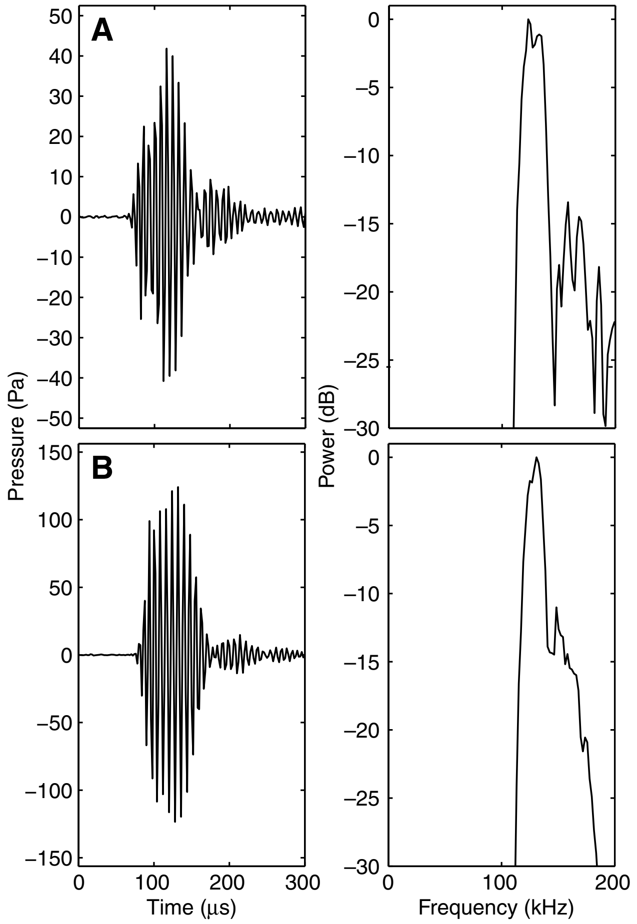

Fig. 3. Time domain signal and power spectrum of a representative click of (A) Commerson's dolphin and (B) Peale's dolphin. (Fast Fourier transform size of 256, spectrum interpolated with a factor 10, sampling rate 500 kHz, rectangular window.) The difference in pressure on the *y*-axis is caused by different received levels.

DISCUSSION

We present the first wide-band recordings of Peale's dolphins and show that they produce NBHF clicks, with the main energy centred around 130 kHz. No tonal sounds or clicks of lower frequency were heard or recorded from Peale's or from Commerson's dolphins. The NBHF properties are in contrast to the only previously published recordings from Peale's dolphins; Schevill and Watkins (Schevill and Watkins, 1971) recorded sounds from Peale's dolphins with dominant frequencies below 5 kHz. However, their analog recording apparatus was band-limited at around 30 kHz and would thus not have picked up the NBHF sounds. In line with what has been shown for harbour porpoise signals (Hansen et al., 2008), it is very likely that most of the low-frequency sounds recorded by Schevill and Watkins (Schevill and Watkins, 1971) were in fact distortion products of the NBHF signals, created by clipping the analog tape recorder/amplifier. The present results are consistent with the recent finding that the sister species of the Peale's dolphin, the hourglass dolphin, also produces NBHF signals (Kyhn et al., 2009), supporting the suggested close phylogenetic affinity of these two species to the dolphin genus *Cephalorhynchus* (May-Collado and Agnarsson, 2006; Tougaard and Kyhn, 2010).

The source parameters of Peale's and Commerson's clicks are very similar (Table 1). However, there are small, but consistent, differences with relevance for the two stated hypotheses: Peale's dolphins produce clicks of lower centroid frequency than Commerson's dolphins. Furthermore, Peale's dolphins produce clicks of higher source level than Commerson's dolphins. However, the source levels of both species were lower than for offshore species of similar size.

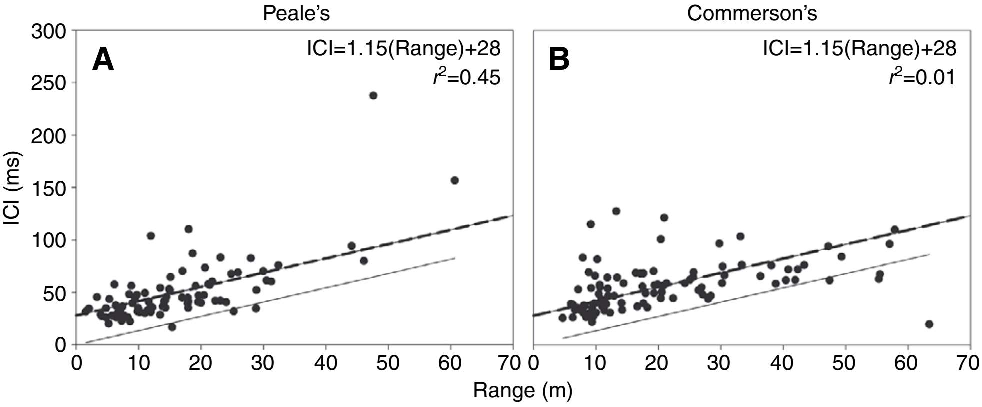

Fig. 4. Relationship between inter-click intervals (ICIs) and recording range. Plots show Peale's (A) and Commerson's (B) dolphin ICIs as a function of range from array. The thin solid line is the expected two-way travel time (TWT) if the dolphins were focusing at the array. The bold regression line was plotted with a fixed slope given by: 2*TWT*(speed of sound in water)$^{-1}$ (1470 ms^{-1})=1.15 ms. The interception of the regression line with the *y*-axis may thus be interpreted as the lag time of the dolphins – that is, the time between reception of an echo and emission of a new click.

The scaling hypothesis predicts that the larger Peale's dolphins would produce the lowest frequencies if normal scaling of sound production was the primary evolutionary driving force (Bradbury and Vehrencamp, 1998). We found that the mean centroid frequency of clicks of Peale's dolphins was 4 kHz lower than that of Commerson's, and this was significant (Table 1). However, their distributions of centroid frequencies are overlapping, and, with a mean difference of only 3%, it seems that such a small difference is less than that implied by the size difference of the two species. Second, Morisaka and Connor (Morisaka and Connor, 2007) did not find a correlation between body size and frequency for NBHF species. The small shift in centroid frequency between Peale's and Commerson's dolphins (Table 1) may instead be an adaptation to the sympatric living around the Falkland Islands. We hypothesized that these two sympatric NBHF dolphins would show some degree of character displacements in their frequency content to allow species recognition. For the two species to tease apart their clicks with mean differences of only 4 kHz demands high-frequency resolution and sampling of several clicks to get a sufficiently large sample to identify a click source as conspecific. We found, however, that the significant difference in mean centroid frequencies alone is sufficiently large to form the basis for species classification in, for example, static acoustic monitoring (SAM) (Fig. 7). We based the discrimination on a random mix of on- and off-axis clicks recorded at various angles and from various animals, thus with some variation in centroid frequency. An animal itself, by contrast, will evaluate incoming clicks over entire click trains, with less variation in centroid frequency over the click train. It is highly likely, therefore, that the found mean difference in centroid frequency is big enough for the animals to do the same. To base species recognition accurately on centroid frequency in SAM, however, requires that the SAM data logger has a frequency resolution sufficiently high to resolve the small difference in centroid frequency between the species. Furthermore, the centroid frequency threshold should be evaluated carefully, and it may prove useful to use several thresholds to find the highest percentage of correctly classified clicks for entire click

Table 1. Mean (±s.d.) and range of echolocation click source parameters of Peale's (*Lagenorhynchus australis*) and Commerson's (*Cephalorhynchus commersonii*) dolphins

	Commerson's dolphin *Cephalorhynchus commersonii*		Peale's dolphin *Lagenorhynchus australis*	
	Mean ± s.d.	Range	Mean ± s.d.	Range
10 dB duration (µs)	78±1	52–138	92±2	65–153
Source level (dB re 1 µPa p.–p.)	177±5	165–190	185±6	169–196
Source level$_{-10\mathrm{dB}}$ (dB re 1 µPa r.m.s.)	166±5	153–180	173±6	156–185
Energy flux density$_{-10\mathrm{\,dB}}$ (dB re 1 µPa2 s)	125±5	111–137	133±6	117–144
Peak frequency (kHz)	132±6	119–139	126±3	120–133
Centroid frequency (kHz)	133±2	123–137	129±3	123–138
3 dB bandwidth (kHz)	21±3	16–31	15±4	9–34
r.m.s. bandwidth (kHz)	12±3	7–19	12±3	5–23
$Q_{-3\mathrm{\,dB}}$	6±1	4–8	9±2	4–14
$Q_{\mathrm{r.m.s.}}$	12±3	7–18	12±3	6–23
Directivity index (dB)*	25		25	
Equivalent aperture diameter (cm)*	6.4		7.0	
Sample size, *N*	94		87	

*Only 45 clicks from Commerson's and 49 clicks from Peale's dolphins were recorded at a range of less than 15 m and included in the beam pattern and directivity calculations.

p.–p., peak–peak; r.m.s., root mean square.

Table 2. Body sizes and source levels of five NBHF dolphin species

	Source level (dB re 1 μPa p.–p.)		Body length (m)	
	Range	Mean ± s.d.	Mean	Max.
Hector's dolphin *Cephalorhynchus hectori*	161–187	177±6	n.a.	145
Commerson's dolphin *Cephalorhynchus commersonii*	165–190	177±5	n.a.	146
Harbour porpoise *Phocoena phocoena*	178–205	191	145–160	168 (>200)
Hourglass dolphin *Lagenorhynchus cruciger*	190–203	197±4	142–187	187
Peale's dolphin *Lagenorhynchus australis*	169–196	186±6	193	218

Tabulated data derived from various sources (see Godall et al., 1997a; Godall et al., 1997b; Reeves et al., 2002; Villadsgaard et al., 2007; Kyhn et al., 2008). p.–p., peak–peak.

trains. Additionally, a combination of several criteria – for example both centroid frequency and r.m.s. bandwidth – may improve the probability of species identification.

The hypothesis of acoustic character displacement is thus supported here and could be tested further by recording the same species where there is no overlap with other NBHF species. Character displacement is 'the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone' (Brown and Wilson, 1956). Therefore, the possibility that Peale's and Commerson's dolphins are subject to character displacements in their echolocation clicks may be investigated further by performing wideband sound recordings of Commerson's dolphins at the Kerguelen Islands, where the species do not overlap with other NBHF species. The existing recordings from Kerguelen (Dziedzic and Buffrenil, 1989), however, do not allow for such detailed analysis.

Along the same line, it is interesting that, within the porpoise family and the *Cephalorhynchus* genus, for species overlapping with other NBHF species, there is a tendency for greater diversity in coloration than for species with no overlap with other NBHF species. Noteworthy is, for example, the striking difference in coloration between sympatric Dall's and harbour porpoises, between sympatric Commerson's and Peale's dolphins and between sympatric Commerson's and Chilean dolphins, contrary to the inconspicuous colour patterns of the isolated NBHF Vaquita and finless porpoise. Colour patterns may thus be an important short-range cue for species recognition in these acoustically very similar species if other evolutionary selection forces limit the acoustic differences in NBHF clicks across species.

Kyhn and colleagues (Kyhn et al., 2009) showed that offshore hourglass dolphins produce clicks of higher source levels than the coastal Hector's dolphins. Hourglass dolphins are oceanic and may thus have evolved to generate a higher source level than coastal NBHF species as prey patches are more widely distributed in the open sea as opposed to shallow coastal habitats where the inter-prey distances are smaller, and where clutter levels likely are higher. For the present study, with the differences in overall habitat between Peale's and Commerson's dolphins (White et al., 2002), we thus hypothesized that Peale's dolphins would have the highest source level of the two species and that the source levels of both species would be lower than the source levels of the offshore hourglass dolphin. The collected data do indeed show that source levels of the shelf-living Peale's dolphins are significantly higher than the source levels of the coastal Commerson's dolphins (Table 1 and Fig. 4). The higher source level of Peale's dolphin could also be caused by the larger size of this species; however, among all the five NBHF species recorded to date, there is no apparent relationship between body size and source levels (source levels and body sizes are listed in Table 2) (Villadsgaard et al., 2007; Kyhn et al., 2009) (this study). Many factors may influence the measured source levels of biosonar systems (Madsen and Wahlberg, 2007), but here we recorded the two species in the same habitat in the same behavioural states with the same recording system, which should reduce many of the factors that can be attributed to other things than actual species differences. In Fig. 4,

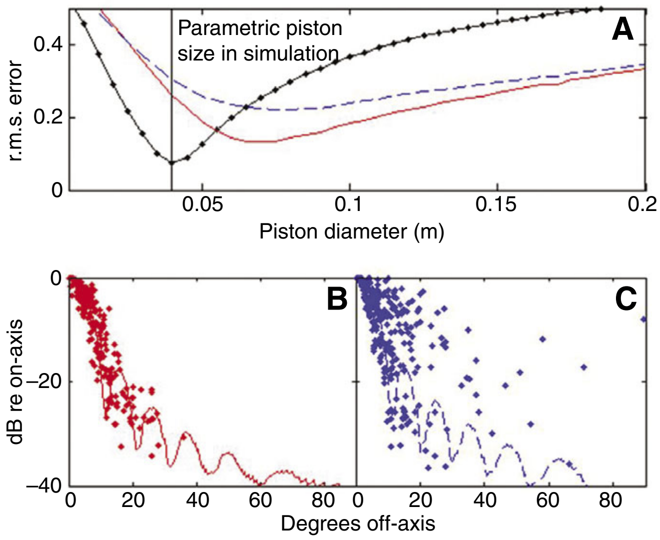

Fig. 5. Fits to the piston model (A) and transmission beam patterns of Commerson's dolphin (B) and Peale's dolphin (C). In (A), the dash-dot black line shows the r.m.s. error of a fit to simulated data from a piston of 4 cm aperture transmitting a Commerson's dolphin click as a function of piston diameter. The vertical line is at the correct 4 cm diameter. The real data from the two species (Commerson's solid red, and Peale's broken blue line) were likewise fitted to piston models of varying diameters to find the best match. The diameter giving the best fit – that is, with the least r.m.s. error for each species – was taken to be the best estimate of the diameter of the transmitting aperture. The radiation patterns for the piston diameter with the least r.m.s. error for each animal found in (A) are plotted in (B) and (C) as lines on top of the data points. The points are field data: on-axis clicks (45 Commerson's and 49 Peale's clicks), each with five off-axis versions recorded on the other hydrophones simultaneously. All used clicks were recorded within 15 m of the array.

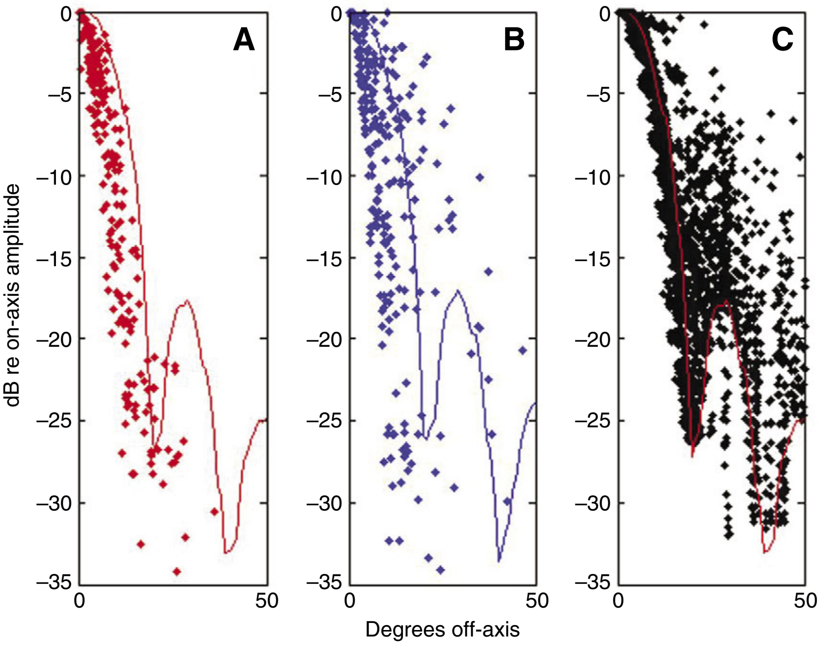

Fig. 6. Transmission beam pattern data from Commerson's (A) and Peale's dolphin (B) together with theoretical 4 cm piston data (C). Lines denote the beam pattern of a 4 cm piston transmitting a click of the respective species (Commerson's dolphin in C). Black dots in (C) show the theoretical 4 cm diameter piston transmitting a Commerson's dolphin click and recorded at varying degrees off angle in a Monte Carlo simulation to test the applicability of the piston model.

ICIs are plotted as a function of range, showing a positive relationship with a constant lag-time, suggesting that, in this study, both dolphin species were focusing at the array (*sensu* Au, 1993) at the time of recording. As the array calibration showed that only ranges of less than 65 m would render source-level estimates with errors of less than 3 dB (Fig. 2), we only included clicks recorded within this range. Within these 65 m, Commerson's dolphins were recorded at a mean and median range of 20.7 m and 16.9 m, and Peale's were recorded somewhat closer, with a mean of 16.2 m and median of 14.1 m, thus a rather small difference in range. This means that the observed source-level differences cannot relate to differences in recording range. We thus consider the observed higher source levels of Peale's dolphin to be genuine.

For the five NBHF species detailed in Table 2, the oceanic and shelf-living species (harbour porpoise, Peale's and hourglass dolphins) produce the highest source levels (Table 2). Close to shore, prey ranges may decrease, but the clutter level likely increases owing to echoes from the nearby sea floor and kelp beds. We observed both species foraging in kelp beds, and the few scientific records available on both species report that among other species closely associated with the kelp (Schiavini et al., 1997; Viddi and Lescrauwaet, 2005) they prey on cephalopods (Clarke and Goodall, 1994; Schiavini et al., 1997). This means that they forage in an environment expected to be highly cluttered. Bats living in cluttered environments have evolved different strategies to reduce the problems of clutter. One general adaptation is that bat species in cluttered habitats use lower source levels than open-space foragers (Neuweiler, 2000) because a higher source level will not improve the performance of a clutter-limited sonar. The low source levels found for our two studied NBHF species may reflect a similar adaptation among odontocetes to operate a biosonar system in a highly cluttered habitat: a high source level will not improve biosonar performance in shallow water. The lower source level of the Commerson's dolphins may in that light reflect their closer affiliation with very shallow water compared with that of the Peale's dolphins. If this hypothesis is correct, we predict that Kogias that forage on mesopelagic prey produce higher source levels than observed for any of the coastal NBHF species.

If high clutter levels of shallow water are a primary driving force for those of the NBHF species that inhabit them, it is also relevant to address other means by which biosonars can reduce clutter. As the problem of clutter is the reception of unwanted echoes interfering with target signals, another way to reduce clutter would be to increase transmission directionality to reduce the width of the sound cone emitted from the animal and thus reducing the ensonified area

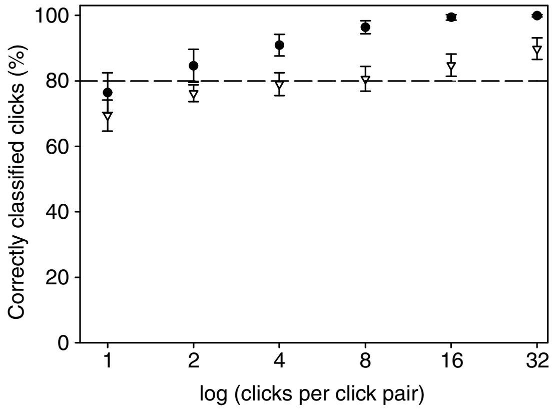

Fig. 7. Acoustic species discrimination. Peale's and Commerson's dolphins may be separated by means of differences in centroid frequency using a criterion of 130.5 kHz, even using off-axis values. Commerson's dolphins (circles) can be determined with higher certainty than Peale's dolphins (triangles); however, the more clicks included in a click pair, the better the discrimination. The dashed line indicates 80% correctly classified clicks. Dolphins will have entire click trains available arriving from more-or-less fixed angles, thus with lower variation between clicks, and it therefore seems very likely that the mean difference in centroid frequency is sufficient for accurate species recognition by the dolphins. Such species recognition may prove useful in static acoustic monitoring, provided there is fine-scale frequency resolution in the recordings. The percentage correct (*y*-axis) for each click pair is the mean of ten rounds of randomly drawing 100 click pairs consisting of *N* clicks per pair (*x*-axis), and the values are shown with the standard error of the mean. The clicks included are 1:5 on-axis to off-axis clicks.

ahead of the animal. In line with Au and colleagues (Au et al., 1999), we hypothesized that the larger Peale's dolphin would have a more directional sound beam owing to a larger aperture transmitting clicks of almost the same centroid frequency as Commerson's clicks (Table 1).

The radiation diagrams shown in Figs 5 and 6 indicate that both Commerson's and Peale's dolphins are more directional than what has been reported for porpoises. The piston for which the radiation diagram fitted the data best had a diameter of 6.5 and 7 cm for Commerson's and Peale's dolphins, respectively, and the corresponding transmitting directionality indices (DIs) were 25 dB for both species. These estimated DIs are less prone to the type of errors typically relevant when estimating the beam pattern from recordings of wild odontocetes (Møhl et al., 2003; Rasmussen et al., 2004). The most important error in the previous studies is that the supposed on-axis clicks may in fact not be recorded on-axis despite the conservative on-axis selection regime. Here, we used a novel method interpolating between the channel deemed on-axis and its two neighbour channels to find the acoustic axis, and the method was further verified using a Monte Carlo simulation (Fig. 6). We used a one-dimensional vertical hydrophone array and have thus assumed rotational symmetry around the acoustic axis, which may not be the case for these species, even though it has been found for harbour porpoises, bottlenose and white-beaked dolphins as well as the beluga (Au et al., 1999; Rasmussen et al., 2004). Both species were more directional than found for the similar-sized harbour porpoise (DI=22 dB) and match the larger bottlenose dolphin better (DI=25.8 dB) (Au et al., 1999). Despite the controlled setup of Au and colleagues (Au et al., 1999), the array for those measurements was also one-dimensional, and the clicks were not corrected for slight off-axis values, as done here with the Lagrange method. Accordingly, it may be that the DI of porpoises is indeed higher than 22 dB and is thus comparable to the values found here and for bottlenose dolphins. The effect of a higher directionality is a reduced ensonified area in front of the animal. This high directionality will in combination with the low source levels reduce the number of returning echoes for each click emitted. The high directionality may thus be the result of similar adaptations by the two species to solve the biosonar challenges faced in a coastal cluttered environment.

The exact number of animals, and their body sizes, sampled in this study is not known as the dolphins were free ranging and not filmed under water. Although this is a shortcoming when quantifying and comparing the acoustic source parameters of two species, NBHF species in general are known to produce very stereotyped clicks within the same species (Au, 1993; Madsen et al., 2005; Villadsgaard et al., 2007; Akamatsu et al., 1998). The centroid frequency of both species was normally distributed. This implies that either these species produce stereotyped clicks or that a large number of animals were recorded. If only a low number of animals with non-stereotyped clicks were recorded, the distribution of centroid frequencies would not likely have been normal. Also $BW_{-3\mathrm{dB}}$, $BW_{\mathrm{r.m.s.}}$ and $Q_{-3\mathrm{dB}}$ were normally distributed for both species. As these different source parameters show normal distributions, we argue that the present data set actually represents the two species.

In conclusion, Peale's and Commerson's dolphins both use very similar NBHF clicks, and no other types of sounds were recorded, suggesting that these closely related dolphins evolved to operate their sonars under similar selection pressures. The two species have overlapping distributions of centroid frequency around 130 kHz, but with means that differ by 4 kHz. That difference may be caused by character displacement to allow species recognition among these sympatric NBHF dolphins within the constraints of operating an NBHF sonar above the hearing range of killer whales and at the same time avoiding too high absorption at higher frequencies. As the two species are observed to forage predominantly in non-overlapping groups and, as they use very narrow beams, there may not have been strong selection for further acoustic specialization to avoid jamming, and there is no indication of strong acoustic niche segregation, as is observed for sympatric Microchiropteran bats. Peale's dolphins produced clicks of higher source levels than Commerson's dolphins, but the levels of both species were lower than observed in general for both NBHF and non-NBHF off-shore dolphins. Both species produced clicks of higher directionality than previously found for similar-sized species. In combination, the relatively low source levels and high directionality of these two small NBHF species may be adaptations to echolocate for prey in a cluttered coastal environment.

LIST OF ABBREVIATIONS

ASL	apparent source level
BBT	broad-band transient
$BW_{-3\mathrm{dB}}$	bandwidth measured at –3dB from the peak
BW_{rms}	r.m.s. bandwidth
DI	directivity index
EFD	energy flux density
ENR	echo-to-noise ratio
F_{C}	centroid frequency
FM	frequency modulation
F_{Peak}	peak frequency
ICI	inter-click interval
n.a.	not available
NBHF	narrow-band high-frequency
p.–p.	peak–peak level
$Q_{-3\mathrm{dB}}$	peak frequency / –3dB bandwidth
Q_{rms}	centroid frequency / r.m.s. bandwidth
r	range
r.m.s.	root mean square
RAF	Royal Air Force
RL	received level
s.d.	standard deviation
SL	source level
TL	transmission loss
TWT	two-way travel time
α	absorption coefficient

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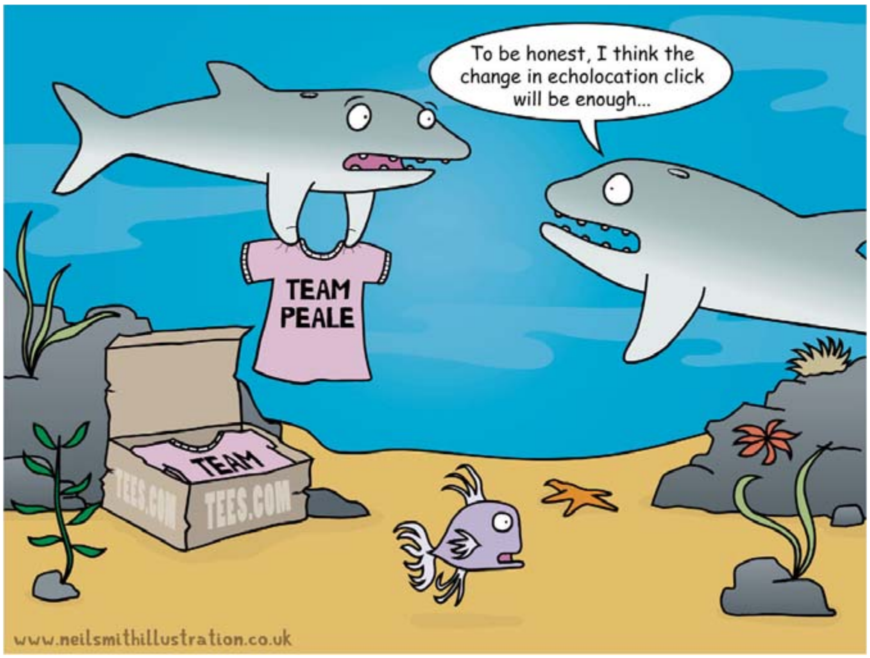

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Chapter V

Tougaard, J. and Kyhn, L.A. (2009). Echolocation sounds of hourglass dolphins (Lagenorhynchus cruciger) are similar to the narrow band high-frequency echolocation sounds of the dolphin genus Cephalorhynchus. Marine Mammal Science 26: 239-245.

Peale's dolphin displaying in front of sailing yacht. Looks pregnant or fat, Falkland Islands, March 2008.

Marine Mammal Science

MARINE MAMMAL SCIENCE, 26(1): 239–245 (January 2010)

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Echolocation sounds of hourglass dolphins (*Lagenorhynchus cruciger*) are similar to the narrow band high-frequency echolocation sounds of the dolphin genus *Cephalorhynchus*

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The dolphin genus *Lagenorhynchus* Gray, 1828 is currently placed in the subfamily of true dolphins (Delphininae), but the systematics of the genus are currently under revision (LeDuc *et al.* 1999, Pichler *et al.* 2001, Harlin-Cognato and Honeycutt 2006, May-Collado and Agnarsson 2006). Molecular data unequivocally indicate that four species of the genus are more closely related to the Lissodelphininae subfamily, a sister group to Delphininae (LeDuc *et al.* 1999, Pichler *et al.* 2001, Harlin-Cognato and Honeycutt 2006, May-Collado and Agnarsson 2006). The four species are Peale's dolphin, *Lagenorhynchus australis* (Peale 1848); hourglass dolphin, *Lagenorhynchus cruciger* (Quoi and Gaimard 1824); Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (Gill 1865); and dusky dolphin, *Lagenorhynchus obscurus* Gray 1828.

Lissodelphininae currently contains the two genera *Cephalorhynchus* Gray, 1846 and *Lissodelphis* Gloger, 1841 (Rice 1998). How the four species of *Lagenorhynchus* should be placed within Lissodelphininae is debated, especially how closely they relate to the genus *Cephalorhynchus*. One set of molecular data (cytochrome *b*) suggests that *L. australis* and *L. cruciger* are nested within the genus *Cephalorhynchus* (May-Collado and Agnarsson 2006) and consequently the authors advocate that the two species should be moved to *Cephalorhynchus*. Other data sets suggest that *L. cruciger* and *L. australis* form a sister group to *Cephalorhynchus*, either on their own (Harlin-Cognato and Honeycutt 2006; mitochondrial DNA control region and cytochrome *b* and two nuclear DNA sequences, Actin and RAG2) or together with *L. obliquidens* and *L. obscurus* (Pichler *et al.* 2001; mitochondrial DNA control region). In both cases, this has led the authors to suggest the transfer of *L. cruciger* and *L. australis* to a new genus *Sagmatias* Cope, 1866.

The genus *Cephalorhynchus* presently contains four species: Commerson's dolphin, *C. commersonii* (Lacépède 1804); Chilean dolphin, *C. eutropia* (Gray 1846); Hector's dolphin, *C. hectori* (P.-J. van Bénéden 1881); and Heaviside's dolphin, *C. heavisidii* (Gray 1828). These four dolphins are among the smallest cetaceans and are anatomically and ecologically well separated from other dolphins and deviate from other dolphins in the sounds they use for echolocation. All known echolocation sounds from dolphins are short ultrasonic pulses (Au 1993). The "normal" echolocation pulse of dolphins is a very short click (below 50 μs) which has energy distributed over a broad frequency range, from below 20 kHz to above 200 kHz (Au 1993). This type of echolocation signal is referred to as a broadband click (Au 1993). In contrast to this are the echolocation signals used by the *Cephalorhynchus* species. They use signals that are longer and of higher frequency with all energy concentrated in a narrow band between 100 and 150 kHz, so-called Narrow Band High Frequency signals (NBHF, Madsen *et al.* 2005). In addition, *Cephalorhynchus* dolphins are not known to produce tonal sound (Kamminga and Wiersma 1982, Evans *et al.* 1988, Dawson 1988) unlike most delphinids.

Sounds of *L. cruciger* and *L. australis* could offer information to help determine their phylogenetic relationships to other dolphins within Lissodelphininae, but their sounds have not yet been described. As all four species currently in *Cephalorhynchus* use NBHF signals it would be reasonable to expect that also *L. cruciger* and *L. australis* use NBHF signals, if the molecular phylogeny of (May-Collado and Agnarsson 2006) is correct.

Recordings from *L. cruciger* were obtained on 30 January 2007 in the Drake Passage between Tierra del Fuego and the Antarctic Peninsula (58°17′50"S, 61°29′39"W). A small group (about 20 individuals) of hourglass dolphins were observed from the Danish naval vessel HDMS *Vædderen* and easily identified by their characteristic hourglass-shaped white markings on the flanks and prominent dorsal fin. The dolphins, presumably engaged in foraging, were approached in a 6 m rigid-hull inflatable boat (RHIB) and when they were within 100 m of the RHIB the recording array was deployed. Recordings were obtained under calm weather conditions (low winds, sea state Beaufort 2, moderate swell) and with the boat engine stopped.

Recordings were done with four spherical hydrophones (TC4034, Reson A/S, Slangerup, Denmark) mounted along a vertical Perspex rod and suspended below a small buoy, with the topmost hydrophone about 2 m below the surface. Signals were band-pass filtered (100 Hz to 200 kHz), amplified by a custom-built 4-channel amplifier and fed into a 4-channel 12-bit analog-to-digital converter operating at 500 ksamples/s. The analog-to-digital converter (NuDAQ pci9812, AdLink, Los Angeles, CA) was connected to a laptop by a PCI-extension box (Magma Mobility Electronics Inc., Scottsdale, AZ) and allowed for continuous streaming of sound recordings to the hard disc of the laptop. The frequency response of the entire system was flat (±1 dB) in the range 100–200 kHz.

In total, 5 min of recordings were obtained on two occasions from the same group of dolphins. The signals were analyzed and signal parameters extracted by means of custom-made software (SigPro and Matlab routines). Only clicks likely to have been recorded directly in front of the animal (on-axis) were used for analysis. Likely

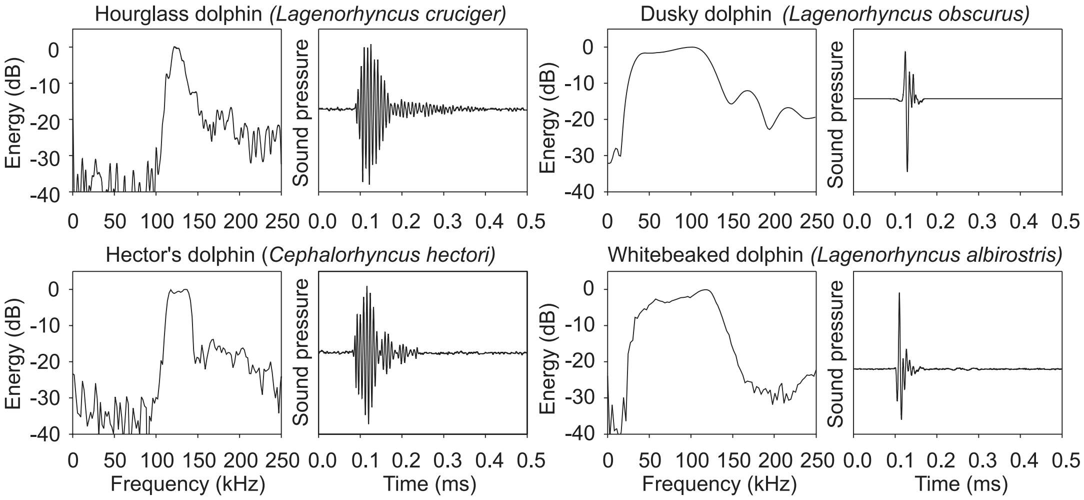

Figure 1. Echolocation signals of *Lagenorhynchus* and *Cephalorhynchus*. Representative echolocation signals and frequency spectra of three species of the genus *Lagenorhynchus* and one species of the genus *Cephalorhynchus*. *L. obscurus* and *L. albirostris* signals courtesy of W. W. L. Au and M. H. Rasmussen, respectively. *C. hectori* signal recorded at Akaroa Bay, New Zealand, January 2007 (Kyhn *et al.* 2009).

on-axis clicks fulfilled the criteria of Villadsgaard *et al.* (2007): (1) the click had to be recorded on all four channels, (2) the click had maximum amplitude on one of the two middle hydrophones, (3) the click had maximum amplitude in a series of clicks closely spaced in time, and (4) the amplitude of the directly transmitted click had to be larger than any trailing bottom or surface reflections.

Although a large number of signals were recorded (around 200), the low number of dolphins from which recordings were obtained means that conclusions are limited to some degree by pseudoreplication. However, common experience with echolocation signals, especially of the NBHF type, is that these signals are extremely stereotypic, both within and among individuals. Consequently, the signals presented here are considered to be representative of *L. cruciger* signals in general.

The recorded signals all shared the same characteristics of narrow bandwidth and virtually no energy below 100 kHz. No other sounds, such as tonal whistles or burst-pulse type calls were heard or recorded. Figure 1 shows a representative signal together with its frequency spectrum and representative signals from *C. hectori*, *L. obscurus*, as well as white-beaked dolphin, *L. albirostris*, for comparison. Average signal parameters for the four species are shown in Table 1.

It is immediately evident that the signals of *L. cruciger* deviate substantially from the signals of the two other *Lagenorhynchus* species and at the same time closely resemble the NBHF signals of *C. hectori*. They are longer than normal Delphinoidea-type clicks (exemplified by the two other *Lagenorhynchus* species in Fig. 1) and their bandwidth is smaller (Table 1). For further details on the acoustics of the signals, see Kyhn *et al.* (2009).

The nature of the newly recorded sounds is consistent with the hypothesis of a close taxonomic affinity of *L. cruciger* to the genus *Cephalorhynchus*. The narrowband clicks are strikingly similar to *Cephalorhynchus* NBHF clicks and markedly different from

Table 1. Key acoustic parameters for echolocation sounds of the four species in Figure 1.

Species	Mean (SD) peak frequency (kHz)	Mean (SD) −3 dB bandwidth (kHz)	Mean (SD) duration (ms)	Source
Hector's dolphin *(Cephalorhynchus hectori)*	112–130	~14	~140	Dawson (1988), Au (1993)
Hourglass dolphin (*Lagenorhynchus cruciger)*	125 (2)	15	150	This study
Dusky dolphin (*Lagenorhynchus obscurus)*	74 (27)	67 (27)	~20	Au and Würsig (2004)
White-beaked dolphin (*Lagenorhynchus albirostris)*	115 (3)	70 (12)	15 (3)	Rasmussen and Miller (2002)

sounds of other *Lagenorhynchus* species. Phylogenies suggested for Lissodelphininae are shown in Figure 2 with indication of the type of echolocation sounds used by the individual species. Good recordings are available from *L. obliquidens* (Evans 1973), *L. obscurus* (Au and Würsig 2004), *C. hectori,* (Dawson 1988), and *C. commersonii* (Kamminga and Wiersma 1982, Evans *et al.* 1988). Recent, unpublished recordings of sounds from *C. eutropia* describe these as "porpoise like," consistent with a NBHF signal (Götz *et al*. 2005). The only published recordings of *L. australis* and *C. heavisidii* (Schevill and Watkins 1971, Watkins *et al.* 1977) do not contain any signals normally considered suitable for echolocation but only faint pulsed signals of frequencies below 5–10 kHz. However, the recording apparatus used was bandwidth limited at about 30 kHz, which means that virtually nothing would be recorded of a typical NBHF

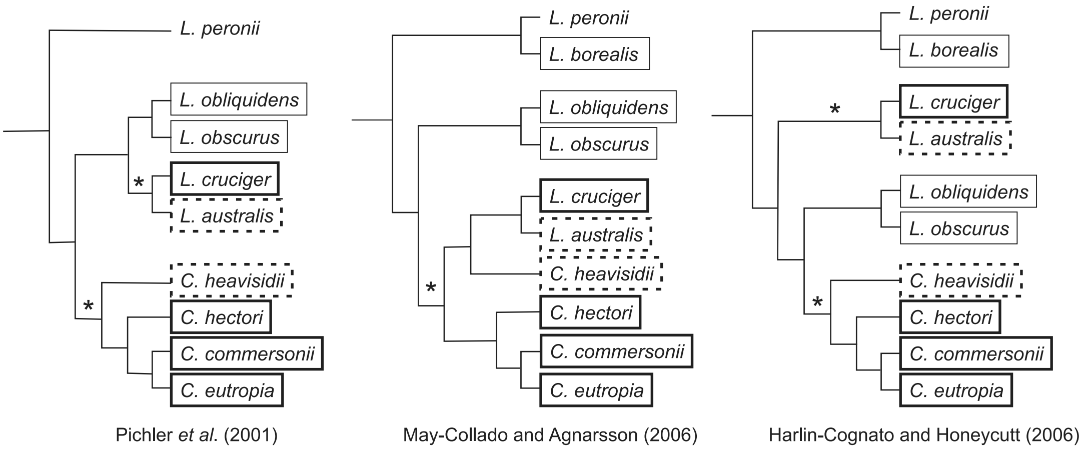

Figure 2. Lissodelphininae cladograms. Suggested cladograms of the Lissodelphininae subfamily based on molecular phylogeny with indication of types of echolocation sounds used by the different species. Thin outline indicates broadband clicks typical of dolphins in general; thick outline indicates narrowband signals typical of the *Cephalorhynchus* species. Broken outline indicates indirect evidence. Points where the narrowband sound appears in the phylogenetic history are indicated by *. Cladograms from (Pichler *et al.* 2001, Harlin-Cognato and Honeycutt 2006, May-Collado and Agnarsson 2006); information on sounds from (Schevill and Watkins 1971, Evans 1973, Kamminga and Wiersma 1982, Dawson 1988, Au and Würsig 2004, Götz *et al.* 2005, Rankin *et al.* 2007) and present study.

signal. The low-frequency sounds recorded by Schevill and Watkins (1971) and Watkins *et al.* (1977) are likely to be artifacts caused by overdriving the analog tape recorder, as has been shown to be the case for earlier recordings of harbor porpoise signals (Hansen *et al.* 2008). Broadband signals of the normal Delphinoidea type on the other hand are easily recorded by bandwidth-limited equipment (although greatly distorted), as they contain considerable energy at low frequencies (Au 1993). This is likely the case for the only available recording of sounds from the northern right whale dolphin, *Lissodelphis borealis* Peale, 1848 (Rankin *et al.* 2007), which indicate a normal Delphinoidea signal. No recordings are available from the Southern right whale dolphin *Lissodelphis peronii* (Lacépède 1804).

The acoustic data as a whole are consistent with formation of a clade containing the four present *Cephalorhynchus* species together with *L. cruciger* and *L. australis* as suggested by May-Collado and Agnarsson (2006). Under this scenario the NBHF signal appears to be a synapomorphy of the clade and suggests that the signal evolved only once within delphinids. The taxonomic consequences of this conclusion depend on the exact position of the *L. cruciger/L. australis* group in relation to the four existing *Cephalorhynchus* species. If they are nested within the group, as the cladogram of May-Collado and Agnarsson (2006) indicates, they should be transferred to the *Cephalorhynchus* genus. Alternatively, if the four existing *Cephalorhynchus* species form a monophyletic clade with *L. cruciger/L. australis* as a sister clade, then the latter two species could be put into the genus *Sagmatias*, or they could be included in *Cephalorhynchus*, depending on how much weight is put on anatomical and ecological similarities and differences from the four small *Cephalorhynchus* species.

The acoustic data cannot be used to disprove the two alternative phylogenetic hypotheses (Pichler *et al.* 2001, Harlin-Cognato and Honeycutt 2006) but in both cases an additional hypothesis is required to explain the data of Figure 2. Either the NBHF signal originated independently twice within the Lissodelphininae or a reversion to the broadband dolphin signal occurred in *L. obliquidens* and *L. obscurus*. However, as the NBHF signal evolved independently at least three times within the evolutionary history of toothed whales: in Lissodelphininae (Kamminga and Wiersma 1982), Phocoenidae (Møhl and Andersen 1973) and Kogidae (Madsen *et al.* 2005), the possibility of convergent evolution of the NBHF signal within Lissodelphininae should not be dismissed and further tests of the three suggested phylogenies are needed.

It is not known in detail how the NBHF signals are produced by any of the three groups of odontocetes known to use the signals. However, the anatomical structures responsible for sound production clearly differ among the three groups (Amundin and Cranford 1990, Cranford *et al.* 1996). This indicates that whatever drives the selection for this particular type of signal (see Morisaka and Connor 2007 for a discussion of this), the endpoint can be achieved in different ways. This suggests that further tests of the hypothesis of close relatedness of *L. cruciger/L. australis* to *Cephalorhynchus* could be found in anatomical studies of the sound-producing structures in these species. If the NBHF sounds share a common origin, the sound production mechanism and hence the anatomy of the sound-producing structures associated with the nasal complex would be expected to be similar. Conversely, if significant differences in the sound production mechanisms are found, this would support independent origin and convergent evolution of the signals and thus speak against a closer connection between the two groups of dolphins.

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Chapter VI

Kyhn, L.A., Tougaard, J., Beedholm, K., Ash, E., Williams, R. Jensen, F.H. and Madsen, P.T. Clicking in killer country: Is evolution of echolocation click parameters driven by predation or habitat? (Drafted for Behavioural Ecology and Sociobiology).

Blainville's beaked whale, male, tagged with Dtag seconds earlier, El Hierro, May 2008.

Drafted for Behavioural Ecology and Sociobiology

Clicking in killer country:
Is evolution of echolocation click parameters driven by predation or habitat?

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Abstract

Acoustic adaptations to reduce predation are common among Microchiropteran bats. For odontocetes it is hypothesized that narrow band high frequency (NBHF) echolocation clicks evolved to reduce predation by killer whales that hear frequencies above 100 kHz very poorly. The NBHF click arose by convergent evolution four times, yet species from these four evolutionary groups produce strikingly similar clicks. Microchiropteran bats have adapted their echolocation to specific habitats, but the same has only been indicated for odontocetes. Since NBHF species are found in all marine niches it is expected that their clicks show adaptations to different foraging niches. Here we used a six-element hydrophone array to examine plasticity of NBHF porpoise clicks by recording harbour porpoises in two different habitats (Denmark and British Columbia) and harbour porpoise and Dall's porpoise in the same BC habitat to test if there are differences pertaining to habitat and if there are species differences between sympatric porpoises allowing acoustic species separation. The BC harbour and Dall's porpoise produced lower source levels than Danish harbour porpoises which may be a consequence of decreased/relaxed selection for high-amplitude clicks in areas with more clutter. BC harbour porpoises produced clicks of higher centroid frequency than Dall's (and Danish harbour) porpoises. Clicks were filtered with the harbour porpoise audiogram to simulate porpoise sound reception and based on centroid frequency alone the two BC porpoises could be separated using eight random clicks in a Monte Carlo simulation. The centroid differences thus conform to acoustic character displacement theory to allow species separation.

Keywords: Porpoise, source level, adaptation, acoustic camouflage, anti-predation strategy, Static acoustic monitoring, passive acoustic monitoring.

Introduction

A range of field studies have shown that echolocation clicks of Microchiropteran bats show differences in signal peak frequency, bandwidth, duration and repetition rate related to their habitat (Neuweiler, 1989; Neuweiler, 2000; Denzinger *et al.*, 2004; Jung *et al.*, 2007). The knowledge on similar adaptations among marine echolocators, the toothed whales, is less detailed and very little is still known about how each species have adapted acoustically to their specific habitats.

It has, however, been suggested that both echolocation clicks and acoustic behaviour of several odontocetes have been adapted to reduce the risk of predation from killer whales (*Orcinus orca*) of which some ecotypes prey on a range of different cetaceans (Jefferson, Stacey and Baird, 1991) that in British Columbia are termed *transients* (sensu Ford et al. 1998). The group of odontocetes in focus of the present paper is the narrow band high frequency (NBHF) species comprised of four different groups of smaller odontocetes (six species of porpoises (Au, 1993; Silber, 1991; Li *et al.*, 2007; Villadsgaard *et al.*, 2007), six dolphin species in the Lissodelphininae subfamily (Kyhn *et al.*, 2009, ; Götz *et al.*, 2010; Kyhn *et al.*, 2010), the pygmy sperm whale (*Kogia simus*) (Madsen *et al.*, 2005) and likely the Blainville river dolphin (*Pontoporia blainvillei*) (von Versen *et al.*, 1999), the only river dolphin also found coastally). The NBHF echolocation click is produced with essentially no energy (Madsen *et al.*, 2010) below the upper effective hearing range of killer whales, of about 100 kHz (Szymanski *et al.*, 1999). This mismatch between the spectrum of NBHF clicks and killer whale hearing is the main argument for inferring that the clicks are adapted to obtain acoustic camouflage allowing the NBHF species to echolocate and communicate without being heard by killer whales (Andersen and Amundin, 1976; Madsen *et al.*, 2005; Morisaka and Connor, 2007). Similar sized non-NBHF species produce clicks of equally high frequency, but energy is contained over a much wider frequency band including frequencies below 100 kHz (Au, 1993).

All other odontocetes echolocate and communicate with different types of signals all audible to killer whales, i.e. with energy at frequencies below 100 kHz, but they have evolved different means of reducing the risk of predation from killer whales behaviourally (see for example Norris and Schilt, 1988; Tyack *et al.*, 2006; May-Collado *et al.* 2007; Morisaka and Connor, 2007).

Thus apparently enforced as an anti-predation strategy the NBHF species have an extremely restricted acoustic frequency span within the hearing range of animals and even a reduced vocal behaviour and repertoire compared to other odontocetes. Yet, within this confined range they have to overcome the same physical constraints enforced by the environment from for example clutter and noise. A functional biosonar system requires clicks of high source level to detect and recognise prey and obstacles at ranges that allow the animal to find sufficient food. The high source level is obtained by high directionality, which is a function of the ratio of the size of the transmitting organ and the wavelength of the projected sound (Urich 1983; Au, 1993). Therefore small echolocating animals must use higher frequencies compared to bigger ones. The sharp anti-predation high-pass filtering may have pushed the centroid frequency up in correspondence with NBHF body size but may further have restricted the frequency content to a narrow band of frequencies by cutting off sharply all frequencies below 100 kHz (Madsen et al., 2010). Yet, this confined bandwidth should allow target discrimination for the echolocating animal. Furthermore, cetaceans spend the majority of their time in periods or areas of limited light. Since most NBHF species live in small, loosely segregated units of 2-3 individuals, searching for a mate of the right species may benefit from acoustic species detection and recognition. It is likely that biosonar clicks from NBHF species therefore contain acoustic cues that allow sympatric species to not only detect but also recognize a conspecific animal. Thus requirements on top of the variety of different niches NBHF species are found in from deep seas to shallow water. The question then is whether each NBHF species has retained plasticity to accommodate adaptations to different acoustic habitats or whether the risk of predation has restrained them to a single set of click source parameters that are stereotypical for the species regardless of which habitat it is found in?

Au (1993) found that non-NBHF dolphins decrease source level, centroid frequency and bandwidth in a cluttered environment and Au and co-authors (Au *et al.*, 1974; Au *et al.*, 1985) found that source level and bandwidth increases in noisy environment. Similarly there are evidence that individual NBHF species may have responded similarly to different environments since Kyhn and co-authors (Kyhn *et al.*, 2010) found that two NBHF dolphins, Commerson's (*Cephalorhynchus commersoni*) and Peale's dolphin (*Lagenorhynchus australis*), both had relatively low source levels, very narrow bandwidth and high directionality favourable in the coastal cluttered habitat of these animals and since Li and co-authors (Li *et al.*, 2007) found significant differences in peak frequency, bandwidth and duration between riverine and coastal subpopulations of the finless porpoise (*Neophocaena phocaenoides*, G.Cuvier 1829) in China. Galatius and co-authors (In press) have further demonstrated significant differences in porpoise skull shapes that correlate with habitat for the six porpoise species, indicating that the acoustic source parameters also could be adapted to the general habitat of each species or be the result of founder effects. They further conjectured that the skull shape of the offshore Dall's (*Phocoenoides dalli*, True 1885) and spectacled porpoise (*Phocoena dioptrica*, Lahille 1912) had room for a larger melon, which may be consistent with a higher directionality and source level. The habitat may thus affect the echolocation click source parameters of a given species provided that the click parameters are sufficiently plastic.

In the Falkland Islands Kyhn and co-authors (Kyhn *et al*. 2010) found acoustic species differences among sympatric NBHF dolphins congruent with the theory of character displacement (Brown and Wilson, 1956) stating that closely related sympatric species will develop differences to avoid hybridization. The acoustic differences were small, but the species could be separated based on centroid frequency alone in a Monte Carlo simulation. It may however be very difficult to determine whether species specific differences relate to founder effects or are actual character displacements. One way to test this is by recording the same species both in a habitat with sympatric species and in a single species habitat. Thus besides adaptations to a specific habitat sympatrically living species may also show acoustic differences pertaining to species differentiation.

Here, we used a six-element linear hydrophone array to examine the degree of plasticity in source parameters of NBHF porpoise clicks by recording the harbour porpoise (*Phocoena phocoena*, L 1758) in two different habitats (Denmark and British Columbia (BC)) and harbour porpoise and Dall's porpoise in the same habitat (British Columbia) with overlapping distribution (Williams & Thomas, 2007). More specifically we test if there are 1) differences pertaining to habitat, i.e. differences between the two harbour porpoise populations and similarities between Dall's and BC harbour porpoises, and 2) species-specific differences between sympatric porpoises allowing acoustic species separation. We discuss the findings in light of the anti-predation theory, habitat specializations and character displacement and conclude that the two BC porpoises likely have conformed to a coastal cluttered habitat producing clicks of lower source levels than Danish harbour porpoises found in a more open and deeper, likely less cluttered, habitat. BC harbour porpoises produce clicks of higher centroid frequency than Dall's and Danish harbour porpoises. This may be the result of character displacement since the two BC porpoises may easily be separated in a Monte Carlo simulation after having filtered clicks with the harbour porpoise audiogram simulating clicks as perceived by the porpoises. The results are not consistent with a reduced level of predation in the Danish habitat.

Materials and methods

Recording chain and field sites

Recordings were made with a linear array of six Reson TC 4034 spherical hydrophones (Reson A/S, Slangerup, Denmark) with 20 m cable and a measured sensitivity of –221 dB re 1V/µPa (-/+ 2 dB) between 100 and 150 kHz. The hydrophones were calibrated in an anechoic tank both prior to and following the field recordings. Hydrophones were mounted horizontally in the same direction along a vertical acrylic rod with 0.75 m hydrophone spacing, except between the two topmost hydrophones that were spaced 1.5 m. Half-way through the field recordings in Canada, hydrophone 3 malfunctioned and provided no data for the remainder of the recordings. The 41 mm diameter acrylic rod was hollow and water-filled when submersed and very stiff to avoid flexing of the array during deployment.

The array was suspended vertically below a buoy with the top hydrophone 2 m below the surface and the bottom hydrophone 6.5 m below the surface in Canada. In Denmark, the topmost hydrophone was 4 m below the surface. A 0.5 kg weight in the bottom kept the array vertical in the water. Signals were bandpass filtered at 1 kHz (1 pole) to 180 kHz (4 poles) and the recordings were amplified by 60 dB using custom made amplifiers. Signals were digitized in three National Instruments multifunction devices (USB-6251) at a sampling rate of 500 kHz at 16 bits, using a common clock for triggering AD conversions in all devices.

Recordings were made in Denmark and in British Columbia, Canada. At all locations recordings were made from a small outboard boat. Porpoises were approached at low speed and the array lowered when the engine was stopped. Recordings were made over some minutes and the procedure repeated with the same or a new group. In Canada, recordings were obtained at several different sites near the Broughton Archipelago (50º36’N, 126º40’W) in July 2009. Here the bottom is hard made of rocks covered with kelp. Harbour porpoises were primarily encountered in Beware and Retreat Passages. Dall’s porpoises were consistently found in tidal eddies in Blackfish Sound west of Hanson Island. On one occasion both porpoise species were observed in the same general area (recordings not used), but otherwise only one species was observed at a time and no other marine mammals were observed or detected acoustically at times of recordings. Killer whales were observed close to the recording sites several times, most likely the fish eating eco type, *residents*. Recordings were made under calm weather conditions (low winds, sea state 1), but at times of Dall’s recordings there were heavy tidal currents in the water. In Denmark, porpoises were encountered in the narrowest part of Little Belt (55º33’N, 9º45’E), outside Fredericia harbour and between the highway and railway bridges in June 2010. The water is very deep for Danish waters with depths up to 80 m. The bottom is soft made of mud and sand with no kelp. The Belt is heavily trafficked, which may have increased the ambient noise level. Killer whales are sighted very infrequent in Denmark and there is only one documented event in Danish Waters from 1861, where a stranded killer whale had remains of not less than 13 porpoises and 14 harbour seals in the stomach (Kinze, 2007).

Click analysis

To minimize the risk of including distorted off-axis clicks in the analysis (Madsen and Wahlberg, 2007) we applied a set of criteria to determine clicks as being on-axis following Villadsgaard *et al.* (2007), Kyhn *et al.* (2009) and Kyhn *et al*. (2010): On-axis clicks should be i) recorded on all six (five) channels; ii) part of a scan, i.e. a series of clicks closely spaced in time (sensu Møhl *et al.*, 2003); iii) of maximum amplitude in the scan; iv) of maximum amplitude on one of the four (three) middle hydrophone channels; v) the direct path of the click had to be stronger than any trailing bottom or surface reflections, and last vi) only one click per scan could be on-axis and included. We did not include clicks from buzzes, i.e. click trains emitted at attempts of prey capture where click repetition rate increases to some hundred clicks per second.

The source properties were quantified using a series of parameters sensu Au (1993) and Madsen and Wahlberg (2007). All analysis and signal processing was performed with custom written scripts in Matlab 6.5 (*Mathworks*).

Estimation of source level

Range to the vocalising animal was estimated from the time-of-arrival differences between the six hydrophones of the array, by the algorithms devised by Wahlberg *et al.* (2001). Due to the over-determined design of the array a localization error could be assessed for each positioning (Wahlberg *et al*., 2001). Transmission loss (TL) was estimated from the distance assuming spherical spreading loss plus frequency dependent absorption (DeRuiter *et al.* 2010). Source level (SL) was calculated with unknown recording angle (i.e. apparent source level), which means that source levels likely may be higher. Source level can then be estimated as

$$SL = RL + 20 \log r + \alpha r$$

where α is the absorption coefficient in dB/m and r is range in meters. Alpha was found for each species using its mean centroid frequency based on the equations of Fisher and Simmons (1977) for the specific water temperature of 9.2° C for BC and 15° C for Denmark. SLs are given as peak-peak (pp) pressure, RMS pressure and energy flux density (EFD) computed as follows: SL_{pp} (dB//1µPa pp) was measured from the maximum and minimum peak pressure of the waveform. SL_{RMS} (dB//1µPa RMS) is the rms pressure calculated over the $duration_{-10dB}$ of the signal. SL_{EFD} (dB//1µPa^2s) is the signal energy integrated over the $duration_{-10dB}$ (Madsen and Wahlberg, 2007). The accuracy of the array localization has previously been evaluated (Kyhn *et al*., 2010) and based on this only clicks from animals localized within 65 m of the array were used where the rms-error on the transmission loss is < 3 dB.

Estimation of beam pattern

By recording a click at the six hydrophones at a known distance to the animals and with a defined on-axis hydrophone, a porpoise' beam pattern may be estimated from the six representations of the click by the differences in received level between the on-axis hydrophone and each of the off-axis hydrophones as a function of angle to the animal from each hydrophone. Beam patterns were calculated for on-axis clicks recorded within 20 m from the array for each species (see Kyhn *et al*. 2010).

Species separation based on echolocation click parameters

We used a canonical discriminant analysis in Systat 10 (SPSS Inc.) to examine the differences in source parameters among the three porpoise groups. We used the spectral properties centroid frequency and rms bandwidth along with duration as variables. To test whether porpoises from British Columbia may distinguish each other based on the differences in click source parameters, we made a new data set for each of the two species where we filtered all on-axis clicks and the clicks recorded simultaneously on the five other hydrophones with the audiogram of a harbour porpoise (Kastelein *et al*., 2002) in order to make the clicks resemble what the porpoises hear. We thus assumed that Dall's porpoise would have the same audiogram as harbour porpoises. After the filtering we calculated all click source parameters again for both on- and off-axis clicks and we then performed a Monte Carlo simulation where we randomly selected 100 sets of 1, 2, 4, 8, 16 or 32 clicks for each species for the new data sets containing 1:5 on:off-axis clicks. Based on the mean centroid frequency of each of the 100 click sets and a separation criterion found by means of a receiver operation characteristics (ROC) plot (click sets with mean centroid frequency below 139 kHz classified as Dall's porpoise, above 139 kHz as harbour porpoise) the total proportion of correct classifications were calculated. The procedure was repeated ten times, allowing for calculation of standard deviations on the performance.

Results

Canadian porpoises

Porpoises were encountered in small groups of 3-8 animals and a total of 4.7 hours and 4.5 hours of recordings were obtained from groups of Dall's and harbour porpoises, respectively. Of the thousands of clicks recorded 98 clicks from Dall's porpoise were accepted as on-axis clicks according to the five criteria and 78 of the BC harbour porpoise clicks were classified as on-axis.

Danish harbour porpoises

Harbour porpoises were recorded in Little Belt, Denmark, over three days. Animals were found in groups of sometimes more than 10 animals, actively foraging and observed together with gulls diving vigorously where the porpoises were surfacing. In total 4.1 hours of recordings were obtained and 247 clicks accepted as on-axis were derived.

Table 1. Echolocation click source parameters *of on-axis clicks from Danish and British Columbian (BC) harbour porpoises (*Phocoena phocoena*) and BC Dall's porpoise (*Phocoenoides dalli*) recorded with a six element hydrophone array.* All clicks used for beam pattern estimations were recorded within 20 m from the array resulting in 5 BC and 19 Danish harbour porpoise clicks and 15 Dall's porpoise clicks.*

	Dall's porpoise ***Phocoenoides dalli***		**Pacific Harbour porpoise** ***Phocoena phocoena***		**Atlantic Harbour porpoise** ***Phocoena phocoena***	
Parameters	Mean values (±st.d)	Range	Mean values(±st.d)	Range	Mean values(±st.d)	Range
10dB duration, μs	104±37	53-251	88±29	48-189	54±8	35-98
Source level, dB re 1 μPa (p.-p.)	183±7	153-203	178±4	170-189	189±5	169-199
Source level$_{-10dB}$, dB re 1 μPa (rms)	172±7	141-192	166±4	158-178	178±5	158-188
Energy Flux Density$_{-10dB}$, dB re 1μPa^{2}s	132±7	104-150	125±4	116-137	135±5	114-144
Peak frequency, kHz	137±4	119-143	139±2	137-143	137±6	112-145
Centroid frequency, kHz	137±3	121-147	141±2	138-148	136±3	126-144
3dB bandwidth, kHz	11±7	3-23	8±3	3-19	17±5	5-36
RMS bandwidth, kHz	8±2	5-14	8±2	5-14	10±2	6-17
Q_{-3dB}	15±8	6-45	21±7	7-42	9±3	3-30
Q_{RMS}	17±5	10-29	18±4	9-28	14±3	8-25
*Directivity index, dB**	25.2		24.3		25.6	
*Equivalent aperture,diameter, cm.**	10		12		10	
n	98		77		246	

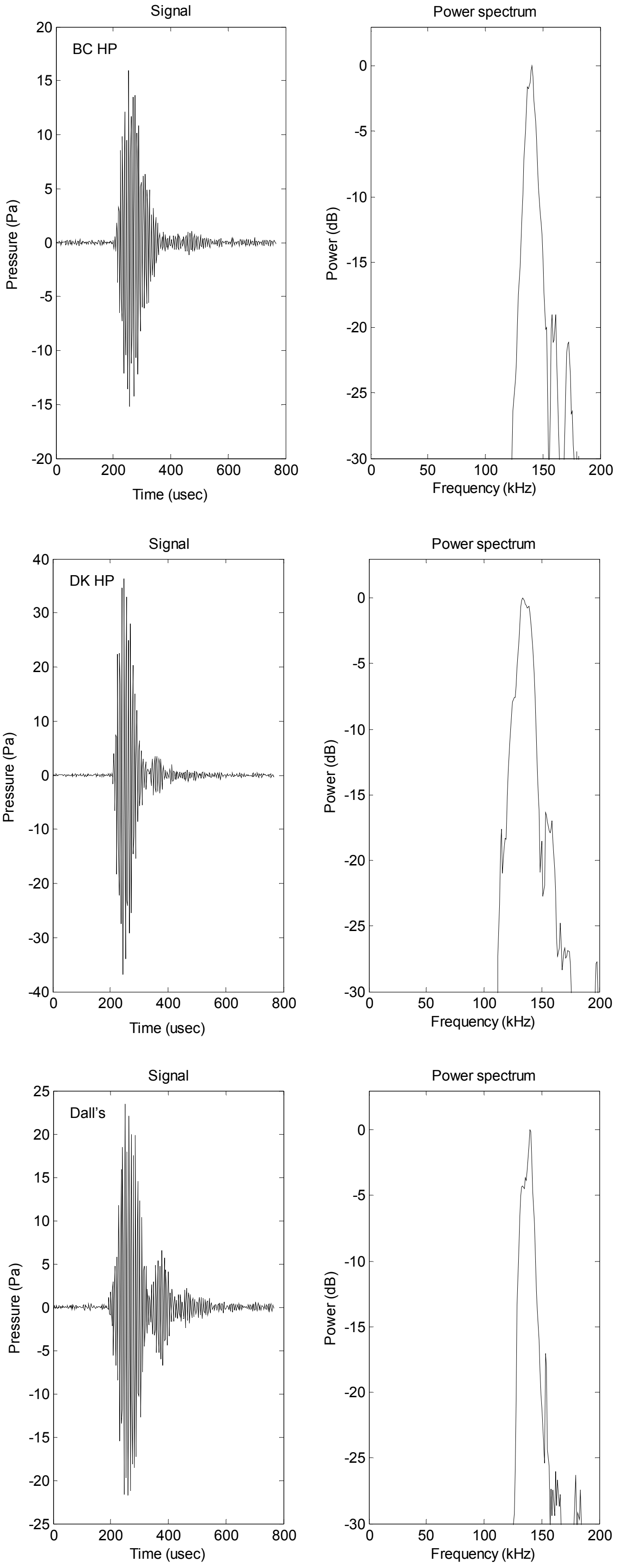


***Figure 1. Representative clicks** from a) British Columbia harbour porpoise, b) Danish harbour porpoise and c) Dall's porpoise. (Fast Fourier transform size of 512, spectrum interpolated with a factor 10, sampling rate 500 kHz, rectangular window). Note that the scale of the Y-axis in the first panel varies due to differences in received level.*

Source parameters are summarised (for all three porpoise groups) in table 1 and representative clicks are shown in figure 1. Centroid frequency, rms-bandwidth and source level was compared among the four data sets with Kruskall-Wallis One-Way Analysis of Variance on ranks. The source level of Danish harbour porpoises were significantly higher than source levels of Dall's and BC harbour porpoises (n= 421, p<0.001) and BC harbour porpoises produced clicks of the lowest source levels (n= 421, p<0.001) among the porpoises. Clicks of BC harbour porpoises had the highest centroid frequency (p <0.001, n = 421) among the porpoises and Dall's porpoise had the narrowest bandwidth (p <0.001, n = 421). Mann-Whitney Rank Sum Test showed that BC harbour porpoises produced clicks with energy concentrated in a narrower and higher placed frequency band than Danish harbour porpoises: Centroid frequency was significantly higher (p <0.001) and bandwidth significantly narrower (p <0.001) than for Danish harbour porpoises.

Table 2. Classification matrix *(cases in rows, categories classified into columns) of the canonical discriminant analysis for the three porpoise groups. Included variables are Duration*$_{-3dB}$*, Centroid frequency and RMS-bandwidth.*

	BC HP	DK HP	Dall's	% correct
BC harbour porpoise	65	8	4	84
DK harbour porpoise	28	215	3	87
Dall's porpoise	5	20	73	74
Total	98	243	80	84

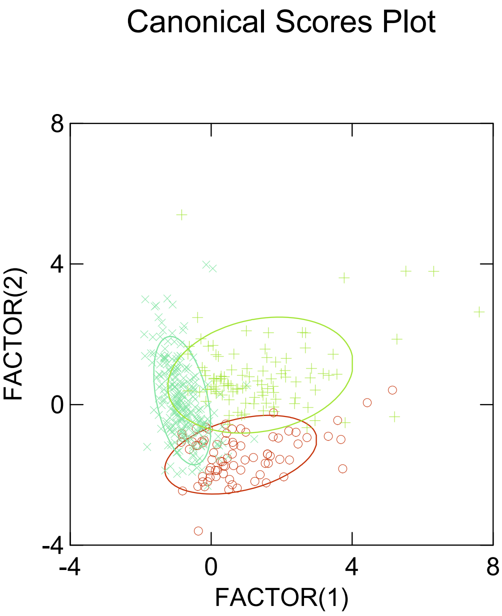


Figure 2. Discriminant analysis*. Centroid frequency, bandwidth (rms) and duration were used to separate BC harbour porpoises, Danish harbour porpoises and Dall's porpoises. All parameters were significantly different across populations. The three species could be separated 84 % correct**ly.*

Species separation based on click parameters

The canonical discriminant analysis showed that all source parameters were significantly different among the three porpoise populations and that they may be separated with overall 84 % correct classifications based on on-axis values (Table 2) for single clicks. Dall's porpoise were equally likely to be misclassified as either BC harbour porpoise or Danish harbour porpoise. BC harbour porpoises were more often misclassified as Danish harbour porpoises than as Dall's porpoise, while Danish harbour porpoises were more often mis-classified as Dall's porpoises (table 2, figure 2). The Monte Carlo simulation based on clicks filtered with the harbour porpoise audiogram showed that Dall's and BC harbour porpoises could be separated based on mean centroid frequency of eight randomly drawn clicks from a mixture of on-and off-axis origin with more than 95 % correctly classified click pairs (figure 3).

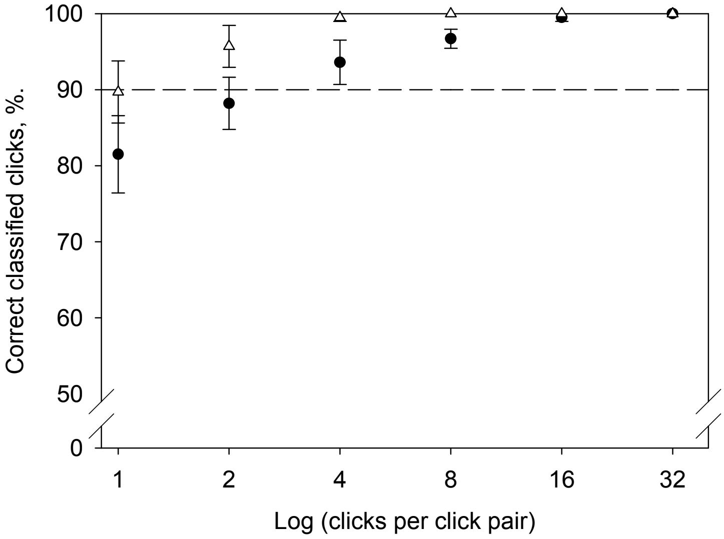


Figure 3. Acoustic species discrimination*. Dall's (circles) and BC-harbour porpoises (triangles) can be separated by means of differences in centroid frequency using a criterion of 139 kHz in a Monte Carlo simulation. The clicks were first filtered with the harbour porpoise' audiogram (see text) to simulate porpoise reception. The dashed line indicates 90 % correctly classified clicks. Such differences may also be useful in passive acoustic monitoring, provided there is fine-scale frequency resolution in the PAM dataloggers. The percentage correct (y-axis) for each click pair is the mean of ten rounds of randomly drawing 100 click pairs consisting of N clicks per pair (x-axis), and the values are shown with the standard error of the mean. The clicks included are 1:5 on-axis to off-axis clicks.*

Beam patterns

With only slight differences among the three groups, Danish harbour porpoises had the narrowest transmission beam pattern (figure 4) and highest directionality index (DI) (table 1). The beam patterns were based on clicks recorded within 20 m from the array; five BC harbour porpoise clicks, 19 Danish harbour porpoise clicks and 15 Dall's porpoise clicks.

Source levels

Detection range is plotted against source energy flux density (EFD) for the three groups along with EFDs of four other NBHF species in figure 5. The figure is colour coded to signify three habitat types. From top to bottom along the y-axis the colours signify coastal, intermediate and offshore habitat as explained in the discussion. Source levels of the three porpoise groups are plotted in figure 6a against recording range with regression lines and equation. In figure 6b mean source levels are plotted as a function of ICI bands with standard deviation for each group. The ICI bands were 20-40, 40-60, 60-80, 100-150 & 150-200 ms; the larger outer ICI bands were chosen due to lower sample sizes in these areas. Within each porpoise group the mean source level was not significantly different across the ICI bands (Kruskall Wallis, BC HP: p=0.512; DK HP: p=0.439; Dalls: p=0.681). Between the three groups each ICI band was significantly different for all ICI bands (Kruskall Wallis, p<0.000) except for 150-200 ms (Kruskall Wallis, p=0.084).

Discussion

The three porpoise populations recorded in this study made remarkably similar clicks across the species (table 1) corresponding closely to those previously recorded from other NBHF species (Silber, 1991; Madsen *et al.*, 2005; Li *et al.*, 2007; Villadsgaard *et al.*, 2007; Kyhn *et al.*, 2009; Götz *et al.*, 2010; Kyhn *et al.*, 2010). However there are statistically significant differences in both spectral content (figure 2) and source levels (figure 5 and 6) that we will discuss in light of the posed hypotheses on possible habitat specializations and character displacement in the following discussion.

A first step in evaluating if source parameters are different among populations of NBHF species should involve the level of variability of NBHF clicks within an individual. Studies of harbour porpoises in captivity have shown that the spectral content of clicks changes with click repetition rate and source level (Beedholm, 2010). Within a click train, centroid frequency goes up and bandwidth narrows down as source level increases in amplitude with falling click repetition rate.

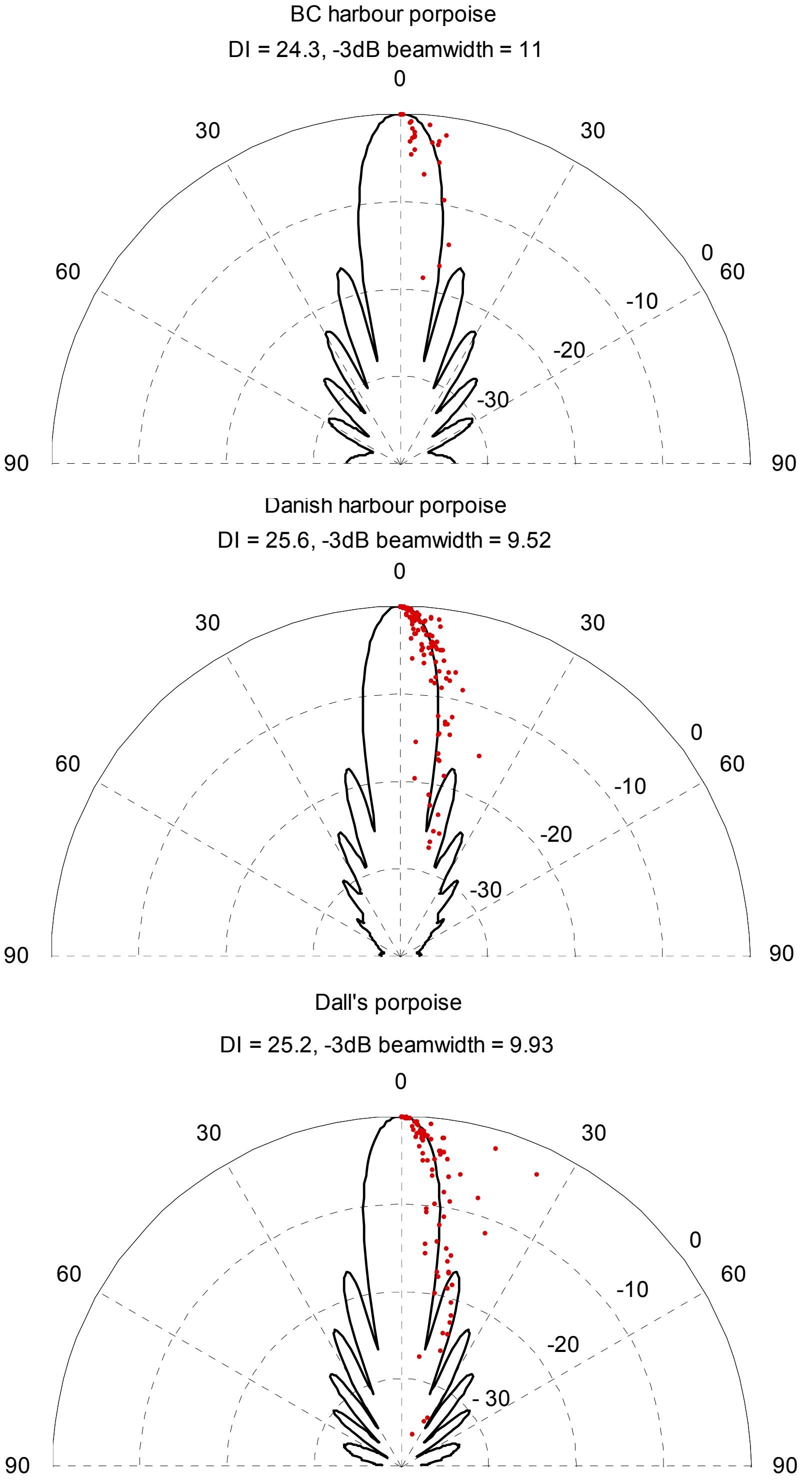


***Figure 4. Transmission beam patterns** of a) BC harbour porpoise, b) Danish harbour porpoise and c) Dall's porpoise. The points are field data. On-axis clicks recorded within 20 m from the array (5 BC harbour porpoise, 19 Danish harbour porpoise, 15 Dall's), each with the five off-axis versions recorded on the other hydrophones simultaneously. O-90 are degrees off-axis re on-axis at 0º. 0 to -30 is dB re on-axis source level. All used clicks were recorded within 20 m of the array.*

The correlation is likely a consequence of the sound production mechanism restricting the high pressure available to produce a high source level when the click repetition rate is high, thus source level fall with increasing click repetition rate. The study was made from a stationed harbour porpoise that echolocated freely. This means that the observed differences in spectral contents and source levels found from the recorded wild porpoises could result from comparing different stages of click trains between the three porpoise groups. Click trains typically vary in repetition rate during prey capture events: In captivity click repetition rate is stable around 50 ms in the search phase, falls gradually as the animal approaches the prey and then falls rapidly ending in a buzz (Verfuss et al., 2009; Deruiter et al., 2010). In this study, we strictly chose clicks for analysis according to five criteria maximising chances that the clicks were recorded on-axis. This means that we purposefully only included the one click of maximum signal to noise ratio in a click train and omitted buzzes that are of lower source levels. Since received signal to noise ratio depends on recording range, most click trains of low source levels are not included unless recorded at very close range. This means that click trains of high source level, and thus low click repetition rates, are overrepresented in the present dataset since the porpoises did not come very close to the recording boat. Thus, in view of our conservative on-axis criteria it seems that at the same time we reduced the possible variation from intra-click train differences and we therefore find the three data sets collected under comparable sound production situations.

We posed the hypothesis that there would be differences in the echolocation click source parameters caused by habitat differences between the BC and Danish porpoises and the discriminant analysis confirmed that there were consistent differences between the three porpoises (figure 2), where the two harbour porpoise populations grouped further from each other than either did to Dall's porpoise. This means that they share more properties with Dall's porpoise than they do with each other. One important habitat difference is the lack of predation in the Danish habitat. Accordingly, it may be predicted that the click source parameters are of less camouflage value in the Danish habitat if the camouflage value, i.e. the high frequency, otherwise has a negative effect in respect of biosonar. The higher the frequency the greater the absorption, and the high centroid frequency of NHBF clicks thus have a negative effect on detection range due to absorption. The observed lower centroid frequency and wider bandwidth of Danish porpoises can thus be said to be congruent with a relaxed protection against predation in the Danish habitat. However, killer whales can likely still not hear clicks of 136 kHz and the difference in absorption caused by this centroid frequency shift

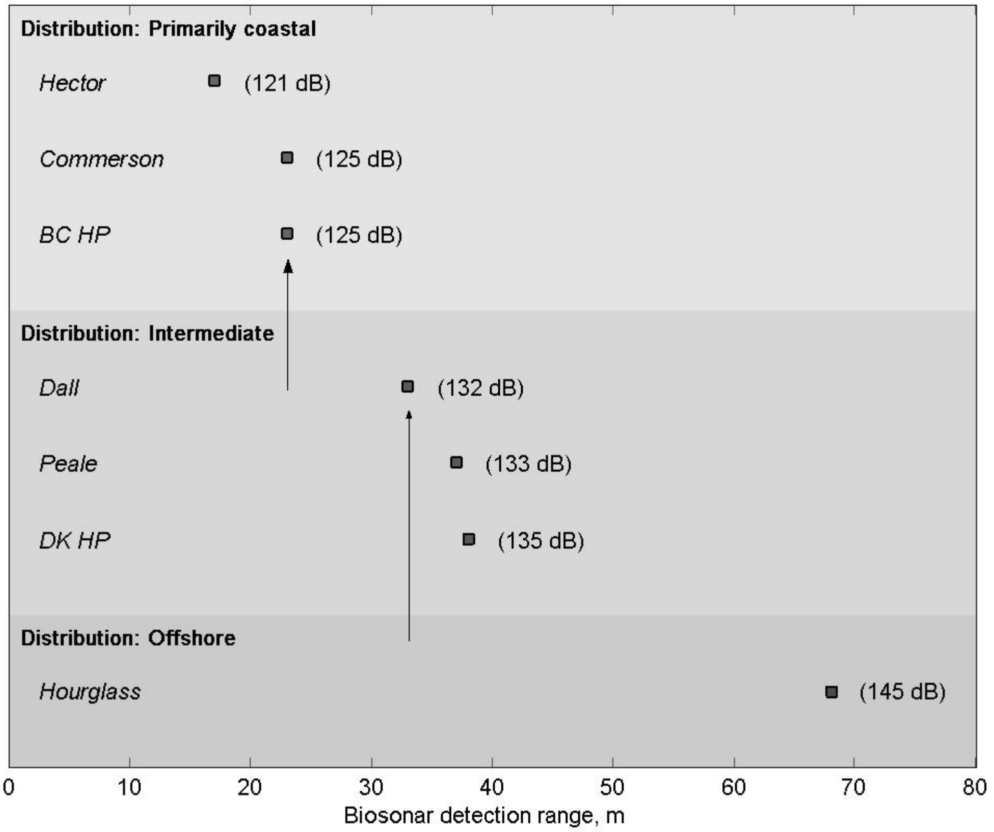
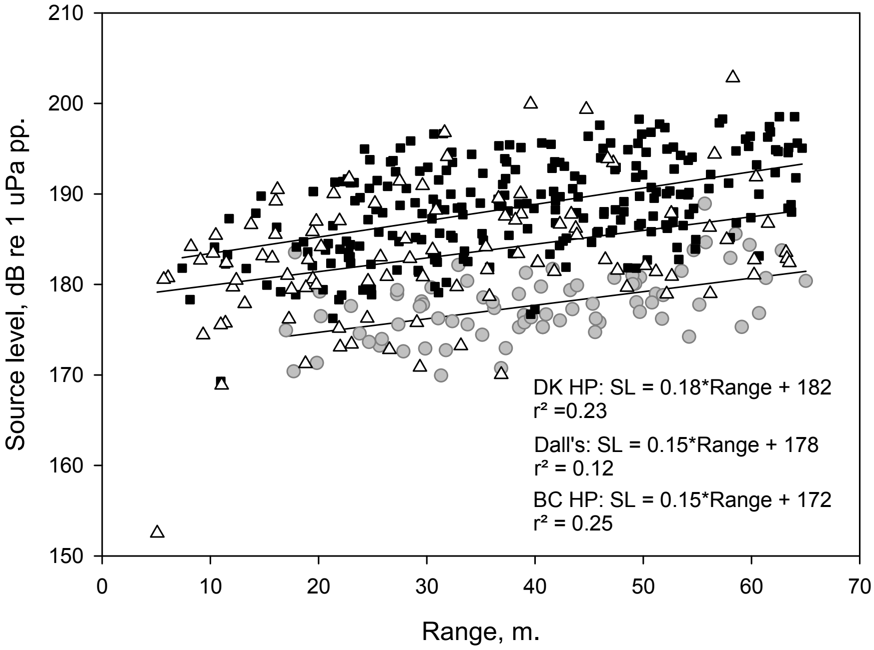


***Figure 5. Mean detection range** plotted as a function of energy flux density source level (dB re 1 μPa^2s) for seven NBHF species (Danish (DK HP) and British Columbia (BC HP) harbour porpoise, Dall's porpoise, Commerson's dolphin, Peale's dolphin, Hector's dolphin and hourglass dolphin). The background colours signify preferred habitat of the species where the top panel is primary coastal habitat close to shore, the middle is intermediate habitat, i.e. species found coastally but with observations far offshore as well, and the bottom panel is offshore habitat. See text for calculation of detection range. The arrows point to the fact that Dall's porpoise has shorter detection range than the other offshore species and BC harbour porpoises have shorter detection range than Danish harbour porpoises.*

is negligible in a biosonar context (Urick, 1983). The hearing of porpoises is however matched to high frequencies with best hearing above 100 kHz (Kastelein *et al*., 2002) (however, see below) and in an evolutionary light the matched hearing, evolved over thousands of years, may thus be a stronger selective force for keeping frequencies above 100 kHz than a few hundred years with a reduced predation level. The lower centroid frequency of Danish harbour porpoises is therefore not likely to be caused by the lack of predation. Recordings of harbour porpoises in the Black Sea (*P.p.*

relicta) could shed more light onto whether centroid frequency may change in response to a lack of predation or not, since there are no killer whales in the Black Sea.

The spectral differences between the BC and Danish porpoises are also congruent with the theory of character displacement; that in areas where two closely related species overlap, characters allowing for species recognition will shift away from each other relative to habitats where a species is found alone. Such characters may well be auditory cues for cetaceans. The BC harbour porpoises may as such have shifted the centroid frequency up in response to the presence of Dall's porpoise by which they also happened to become different from the Danish harbour porpoises. For such differences to be preventive in terms of reducing hybridization, however, requires that the species may make use of the spectral differences, i.e. tell each other apart by received clicks alone. No experiments have been made in captivity to test such fine frequency resolution of porpoises using clicks, but their auditory filters are narrow, approximately 4 kHz (Popov *et al.*, 2006; Kastelein *et al.*, 2009), and their hearing sensitivity is also good at the highest frequencies matching their echolocation clicks. The frequency of best hearing is however around 100 kHz (Kastelein *et al.*, 2002), opposed to the porpoise' click centroid frequency around 130-140 kHz. It is possible that this mismatch between click centroid frequency and frequency of best hearing is an artefact if the animals were clicking during the auditory experiments, thus possibly masking their own hearing. Nevertheless, in order to approach the question of species recognition based on the found differences in centroid frequency of only app. 5 kHz that are based slightly above the frequency of best hearing, we filtered clicks of the two BC species with the audiogram of harbour porpoises (Kastelein *et al.*, 2002) and calculated new centroid frequencies. The two new data sets were then subjected to a Monte Carlo simulation (figure 3) based on both on- and off-axis centroid values, that showed that correct species identification could be obtained by drawing only eight random clicks with a probability of 95% (the same result was obtained with normally filtered clicks), which is consistent with the study of Kyhn and co-authors (Kyhn *et al.*, 2010) that found similar species differences for two sympatric NBHF dolphins. It therefore appears likely that porpoises may do the same since they may also use cues such as duration and bandwidth as well as differences in click repetition rates and likely communicative burst-pulsed calls as have been found in captivity for harbour porpoises (Amundin, 1991; Clausen *et al.*, 2010). We therefore suggest that the observed differences in centroid frequency between the BC harbour porpoise and Dall's porpoise is a result of character displacement to reduce hybridization, despite that hybrids are found in the wild (Baird *et al.*, 1998; Willis *et al.*, 2004).



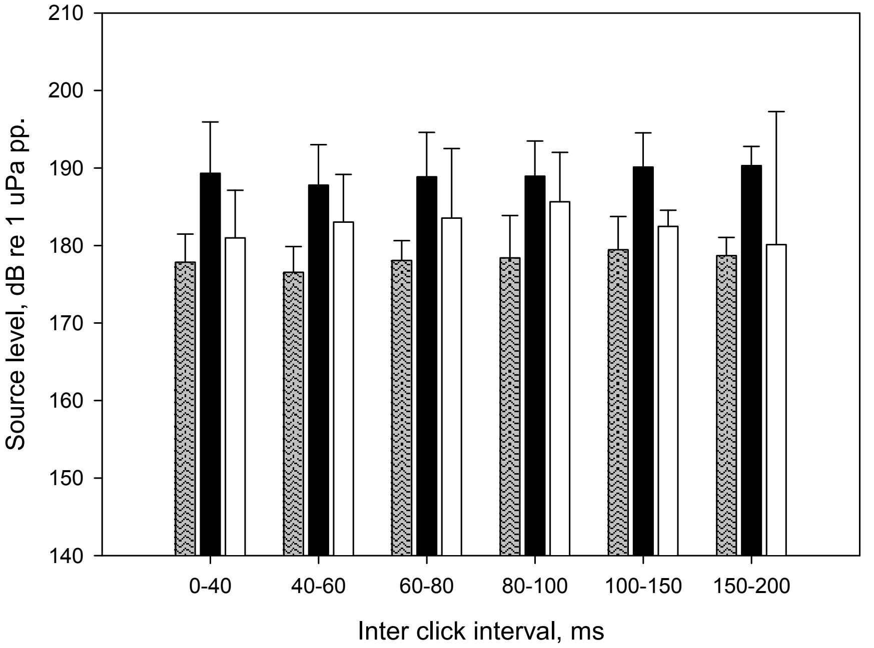


Figure 6*. *Source levels *A) plotted against range to array with linear regressions for British Columbia harbour porpoise (BC-HP, grey circles), Danish harbour porpoise (DK-HP, black squares) and Dall's porpoise (Dall, white triangles). B) Mean source level and standard deviation per Inter-Click-Interval (ICI) band for Danish harbour porpoises (black), BC harbour porpoise (grey) and Dall's porpoise (white). Danish harbour porpoises use clicks of significantly higher source level regardless of range or ICI band than the two other porpoise groups.*

Such species differences also have important implications for passive acoustic monitoring. If dataloggers with good frequency resolution are developed there is basis for acoustically monitoring a range of habitats where several NBHF species are found, provided that similar species differences exist. Since acoustic monitoring is a cheap alternative to visual monitoring, and since many NBHF species are subject to by-catch (e.g. Williams *et al.*, 2008) it is important that this possibility is devoted focused attention in the near future.

There were mean differences in source levels between the three porpoise groups (table 1 and figure 6a). The Danish harbour porpoises used clicks of higher source level than did the two BC porpoises. As explained above, the source level varies with click repetition rate/ICI (Beedholm and Miller, 2007) and with target distance (Atem *et al.*, 2009). Despite that neither source level nor ICI in captivity reach the values we find here in the wild (Verfuss *et al.*, 2005; Atem *et al.*, 2009; Miller, 2010), the same correlation may apply in the wild if it is given by the biosonar operation and/or the physics of sound production. In captivity source level and ICI fall with decreasing range to target (Atem *et al.*, 2009; Verfuss *et al.*, 2009). This means that the observed source level differences could be caused by the porpoises focusing at the array from different mean ranges. Thus to see if the porpoises focused at the array we plotted ICI and corresponding two-way-travel time (TWT) against range (figure 7). In the field we did judge all recorded porpoise groups to be engaged in foraging at the time of recording, however, from figure 7 it appears as though at least some Dall's porpoises focused at the array as seen by the corresponding slopes of ICI and TWT (Au 1993). Since it may require lower source levels to echolocate the array than to find a small fish we tested if the differences in source levels were genuine or caused by context such as click repetition rate or behaviour by comparing mean source level differences across ICI bands (figure 6b). Mean source levels were constant with ICI band within each species and significantly different between the ICI bands across species. Source level therefore did not appear context specific in the present study; regardless of behaviour source level was higher for Danish porpoises. That in turn supports our notion that the estimated source levels are genuine for each species or each habitat.

The Asian corn borer moth (*Ostrinia furnacalis,* Guenée) has evolved a special ant-predation mechanism in which it *whispers* its ultrasonic signals during courtship to reduce the risk of predation by Microchiropteran bats and thereby increases the chance of successful mating. In this light it is tempting to suggest that the lower source levels of porpoises in the BC killer whale habitat could be whispering to reduce the risk of being heard by killer whales that locate prey by means of passive acoustics (Barrett-Lennard *et al.* 1996). Certainly, mammal-eating killer whales modify their vocal behaviour to avoid detection by acoustically sensitive prey, and harbour seals have learned to discriminate between the calls of fish-eating and mammal-eating killer whales in the region (Deecke *et al.* 2002). However, there is no experimental evidence to suggest that killer whales may hear porpoise clicks (Szymanski *et al.*, 1999), but the notion could be tested by playback of NBHF clicks to killer whales in an experimental setup.

The source level differences may instead stem from different biosonar requirements in the two habitats. For successful prey detection the returning echo must exceed the background noise level to be detected. Thus the higher the background noise level the greater the source level for the same required detection range. If ambient noise level is assumed equal at these high frequencies, the source levels of the different species may be used to compare their maximum detection ranges across habitats. Maximum detection range may be estimated if the echo detection threshold, DT, is known for a prey object with known target strength, TS. By assuming that NBHF species have echo detection thresholds corresponding to app. 45 dB re 1 μPa^2s (Au, pers. comm. based on re-evaluations of Kastelein *et al.*, 1999) as found for a captive harbour porpoise measured as the psychophysical target detection threshold (expressed as echo energy flux density, EE) (Kastelein *et al.*, 1999), detection range may be found by solving the active sonar equation for maximum EE ($EE=SE-2*TL+TS_E=DT$). SE is source energy flux density, TL is transmission loss for the species specific centroid frequency based on Fisher and Simmons (Fisher and Simmons, 1977), and TS_E is target strength. To compare maximum detection ranges between NBHF species we assumed equal masking noise for all species and that all species were echolocating for a 30 cm long cod-like fish in a broadside angle, since Au and co-authors (Au *et al.*, 2007) found such prey to have target strength of -25 dB for a 130 kHz signal. With the inherent limitations of a range of assumptions maximum detection ranges are shown in figure 5 as a function of energy flux density source level. The maximum detection ranges fell into three groups (figure 5) correlating with habitat of the species with the shortest detection ranges found for the primarily coastal species, Hector's dolphin and Commerson's dolphin, and the longest for the offshore species, the Hourglass dolphin, moving from top to bottom along the y-axis. The middle group are the species intermediate in habitat, i.e. primarily coastal but with sightings offshore as well (Reeves *et al.* 2002; Sveegaard *et al.* In press). This suggests that source energy flux densities in use by the different species may be related to the habitat in which they forage, where shorter prey ranges may be expected close to shore, whereas prey is more dispersed offshore. However, Dall's porpoise is equally well found far offshore as well as nearer to the coast. Based on its offshore living as well as the large body size we therefore

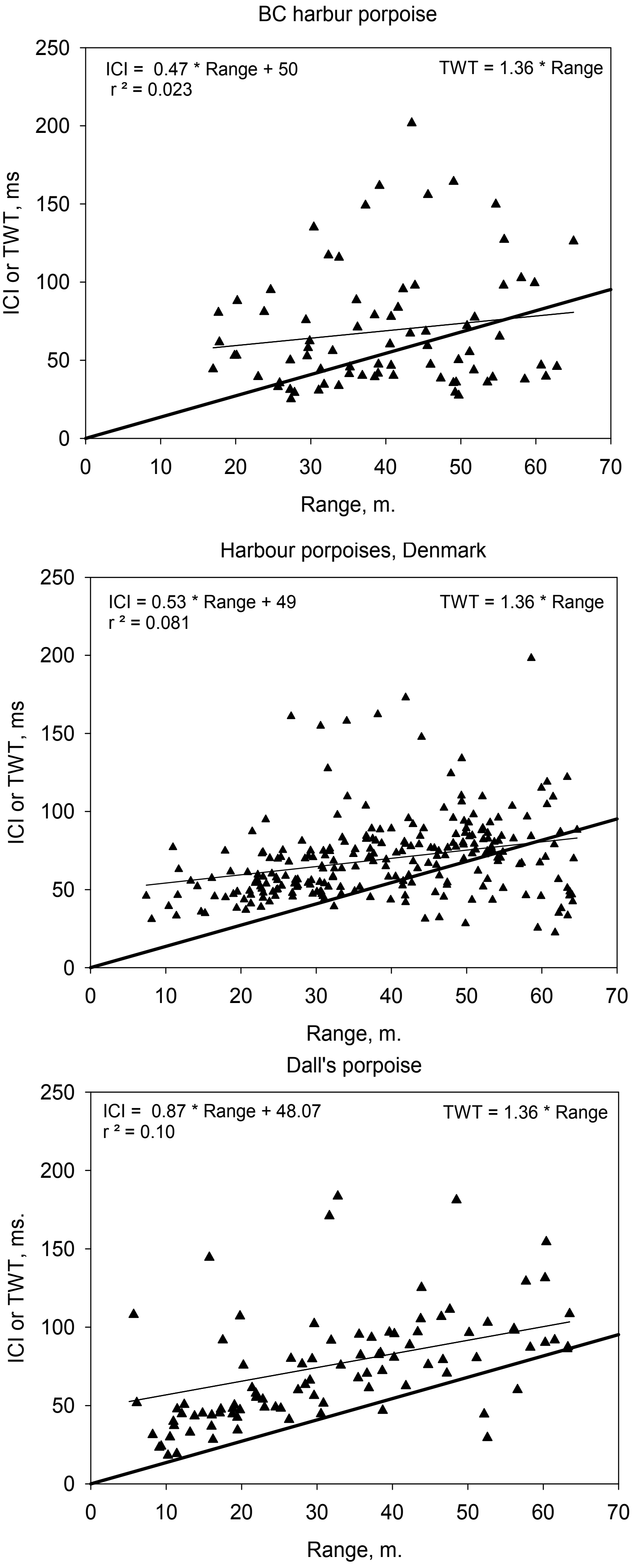


Figure 7. Inter-click-Interval (ICI) *(triangles) and Two-Way Travel (TWT) time (thick line) plotted against range for a) BC harbour porpoises, b) Danish harbour porpoise and c) Dall's porpoise. Linear regressions with equations are given for both plots. Dall's porpoise seem to have devoted some attention to the array whereas the other porpoises only seem echolocating at the hydrophones when very close, this is seen as the correspondence in slopes of the two axes in the Dall's plot.*

expected that it would produce clicks of higher source level grouping as an offshore species, but it did in fact group with the intermediate species such as Peale's dolphin and the Danish harbour porpoise. We similarly expected that the BC harbour porpoise, intermediate in habitat, would group with the Danish harbour porpoise but it grouped with the obligate coastal species such as Hector's dolphin. The two BC porpoises thus form exceptions within the NBHF species with respect to source level and detection range when an equal ambient noise level is assumed.

Another prerequisite of successful biosonar is that the target echo is detectable from non-target echoes from other objects in the environment, i.e. clutter. Clutter can be reduced primarily by increasing directionality of the sound beam. The BC habitat have likely been cluttered for the porpoises since it was a rocky archipelago interspersed with kelp in relatively shallow water, with varying depths (<100m) in the narrow straits and passages between the islands, and clutter is generally expected to be limiting for coastal species (Beedholm and Miller, 2007; Atem *et al*., 2009). The Danish habitat, Little Belt, despite being coastal, is oppositely relatively deep ~ 80 m over muddy and sandy bottom and without kelp, i.e. an open environment. There are thus likely profound differences in clutter levels between the two habitats and the lower source level in the BC habitat may thus be a result of a clutter limited situation where high source levels do not improve detection. This result is consistent with earlier recordings of the same population of harbour porpoises in Denmark finding that source levels in Little Belt were significantly higher than in a more shallow water habitat further north in Denmark (Villadsgaard *et al*. 2007). Li and co-authors (Li *et al*., 2009) oppositely found that the Yangtze finless porpoise (*Neophocoena phocaenoides asiaeorientalis*) produce source levels up to 209 dB re 1 µPa pp., which is even higher than source levels of offshore NBHF hourglass dolphins (*Lagenorhynchus cruciger*, Quoy and Gaimard 1824) (Kyhn *et al*., 2009). Bottlenose dolphins and Belugas have been found to adjust their source levels to differences in ambient noise levels (Au, 1993; Au *et al*., 1985) and the two BC porpoise species may likely also produce clicks of higher source level when found offshore. It thus appears that porpoises may adapt their source levels to prevailing noise and clutter conditions and be as flexible and responsive to immediate changes in noise and clutter as has been found for captive delphinids to obtain successful echolocation.

High source levels and less clutter problems are obtained by focusing the projected sound pulse into a narrow sound beam with high directionality index. The three recorded porpoise groups all had directionality indexes of app. 25 dB, which is higher than found for captive harbour porpoises (Au et al., 1999), but matches the general finding for smaller toothed whales with DIs of

25-30dB (Au, 1993; Au et al., 1986; Au et al., 1995; Rasmussen et al. 2004; Kyhn et al., 2010). The sperm whale (*Physeter macrocephalus*, L. 1758) performs extraordinarily well in terms of DI and may produce clicks with DI up to 36 dB (P.T. Madsen, personal communication), which likely is the result of its enlarged and different sound transmission anatomy. Generally though, DI is the result of the ratio of the size of the sound transmission organ and the prevailing wavelengths of the click. Given the similar DIs across different species, toothed whales have thus solved this equation remarkably similar likely by keeping the frequencies as low as possible to balance absorption against directionality. It therefore appears that for a given size there is a minimum centroid frequency that will yield sufficient directionality for maintaining an efficient biosonar system. The high centroid frequency of NBHF species is thus likely a function of their small body size to obtain high directionality and only the high-pass filtering resulting in the narrow bandwidth, keeping all click energy at frequencies above 100 kHz, is thus caused by the anti-predation strategy to obtain efficient biosonar properties and at the same time acoustic camouflage allowing the NBHF species to echolocate while being inaudible to killer whales.

Conclusion

By recording two populations of harbour porpoises in different habitats as well as Dall's porpoise sympatrically with harbour porpoises we have shown that Dall's and BC harbour porpoises may have adapted to a sympatric living by shifting their centroid frequency away from each other and this difference may be used to separate the species acoustically. These differences may be exploited in passive acoustic monitoring. Harbour porpoises from a predation free environment had not changed their echolocation centroid frequency to levels below that found in killer whale areas despite that a lower absorption in that case could be obtained, and they are thus equally well camouflaged. It is likely that their matched high frequency hearing, evolved over thousands of years, is a more important selective pressure for high centroid frequency clicks than a few hundred years without predation. The emitted source levels varied for the three porpoise groups and could not be correlated with porpoise distance to the hydrophone array; however, the lowest levels were found in the BC habitat that is also expected to be more limiting for the porpoises in terms of clutter. Despite that NBHF species are remarkably similar in source parameters with all energy kept in a narrow band of frequencies above 100 kHz, they still have plasticity to allow species differences and to overcome different requirements from the habitat to obtain successful echolocation.

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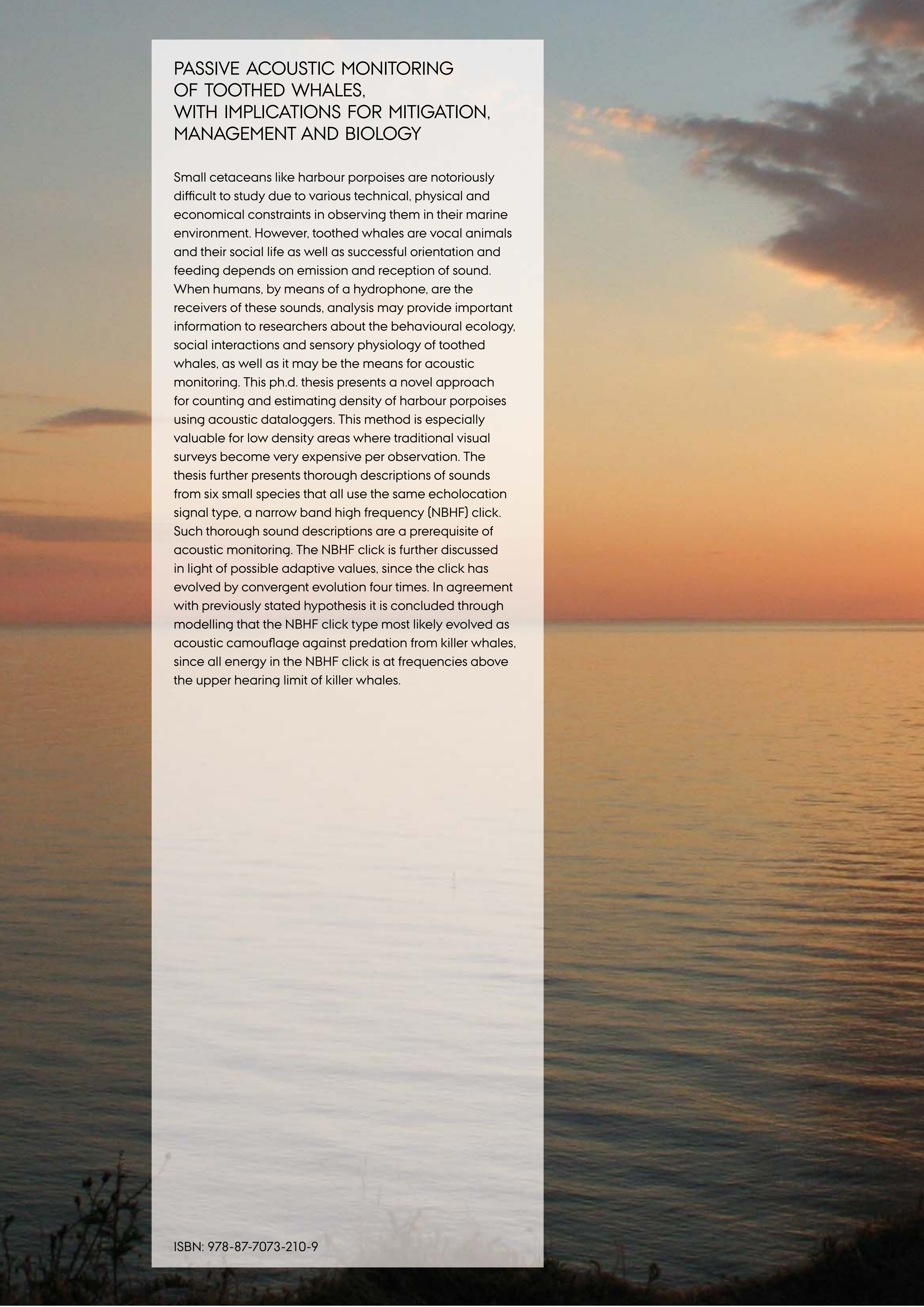

PASSIVE ACOUSTIC MONITORING OF TOOTHED WHALES, WITH IMPLICATIONS FOR MITIGATION, MANAGEMENT AND BIOLOGY

Small cetaceans like harbour porpoises are notoriously difficult to study due to various technical, physical and economical constraints in observing them in their marine environment. However, toothed whales are vocal animals and their social life as well as successful orientation and feeding depends on emission and reception of sound. When humans, by means of a hydrophone, are the receivers of these sounds, analysis may provide important information to researchers about the behavioural ecology, social interactions and sensory physiology of toothed whales, as well as it may be the means for acoustic monitoring. This ph.d. thesis presents a novel approach for counting and estimating density of harbour porpoises using acoustic dataloggers. This method is especially valuable for low density areas where traditional visual surveys become very expensive per observation. The thesis further presents thorough descriptions of sounds from six small species that all use the same echolocation signal type, a narrow band high frequency (NBHF) click. Such thorough sound descriptions are a prerequisite of acoustic monitoring. The NBHF click is further discussed in light of possible adaptive values, since the click has evolved by convergent evolution four times. In agreement with previously stated hypothesis it is concluded through modelling that the NBHF click type most likely evolved as acoustic camouflage against predation from killer whales, since all energy in the NBHF click is at frequencies above the upper hearing limit of killer whales.

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