

Characteristics of biosonar signals from the northern bottlenose whale, *Hyperoodon ampullatus*

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The biosonar pulses from free-ranging northern bottlenose whales (*Hyperoodon ampullatus*) were recorded with a linear hydrophone array. Signals fulfilling criteria for being recorded close to the acoustic axis of the animal (a total of 10 clicks) had a frequency upswEEP from 20 to 55 kHz and durations of 207 to 377 μ s (measured as the time interval containing 95% of the signal energy). The source level of these signals, denoted pulses, was 175–202 dB re 1 μ Pa rms at 1 m. The pulses had a directionality index of at least 18 dB. Interpulse intervals ranged from 73 to 949 ms ($N = 856$). Signals of higher repetition rates had interclick intervals of 5.8–13.1 ms (two sequences, made up of 59 and 410 clicks, respectively). These signals, denoted clicks, had a shorter duration (43–200 μ s) and did not have the frequency upswEEP characterizing the pulses of low repetition rates. The data show that the northern bottlenose whale emits signals similar to three other species of beaked whale. These signals are distinct from the three other types of biosonar signals of toothed whales. It remains unclear why the signals show this grouping, and what consequences it has on echolocation performance. © 2011 Acoustical Society of America. [DOI: 10.1121/1.3641434]

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I. INTRODUCTION

All species of toothed whales with published sound recordings emit ultrasonic pulses, assumed to be used for echolocation. These signals can be grouped into four distinctive types. Most species of dolphins, as well as the narwhal (*Monodon monoceros*) and the beluga (*Delphinapterus leucas*), produce short duration (10–50 μ s) clicks of 2–3 cycles with a spectral range of 20–150 kHz. The source level varies tremendously but is usually less than 220 dB re 1 μ Pa rms (Au, 1993). Another type of clicks is produced by a phylogenetically very heterogeneous group of toothed whales consisting of porpoises, dolphins of the genus *Cephalorhynchus*, and the pygmy sperm whale (*Kogia brevisceps*) as well as probably also the dwarf sperm whale (*K. sinus*). This polyphyletic group is defined as the species that produce signals of 10–15 cycles centered around 120–140 kHz with a source level of up to 195 dB re 1 μ Pa rms (Møhl and Andersen, 1971; Madsen *et al.*, 2005a; Villadsgaard *et al.*, 2007; Kyhn *et al.*, 2009, 2010; Morisaka *et al.*, 2011). The sperm whale (*Physeter catodon*¹), in a group of its own, emits relatively broadband clicks of 2–3 cycles centered

around 15–40 kHz with extremely high source levels (up to 235 dB re 1 μ Pa rms) and acute directionality (Møhl *et al.*, 2000, 2003, 2006). Recordings of three species of beaked whales (Cuvier's beaked whale *Ziphius cavirostris*, Blainville's beaked whale *Mesoplodon densirostris*, and Gervais' beaked whale *M. europaeus*) show that some members of this elusive family emit frequency modulated (up-sweeping) chirps of much longer duration (200–300 μ s) ranging in frequencies from about 25 to 50 kHz (Johnson *et al.*, 2004, 2006; Gillespie *et al.*, 2009). In this paper these longer beaked whale signals are denoted pulses to distinguish them from the transient clicks of dolphins and porpoises. *M. densirostris* also emit unmodulated broadband clicks at higher repetition rates in the so-called buzz phase (Johnson *et al.*, 2006).

As there are about 20 species of beaked whales, recordings are needed from more species before it may be concluded that the use of upswEEP pulses is a common trait within this family. Both the pulse and click signal types of beaked whales are presumably used for echolocation (Johnson *et al.*, 2006). Caution should be used however when using the words echolocation and biosonar signals. Echolocation has been demonstrated experimentally for only a few toothed whales. In this paper we adapt the assumption that signals that are usable for, and used in a context suited for,

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echolocation, are in fact echolocation signals, though experimental proof of this function is still lacking for most species.

Here we present data on the source parameters of echolocation signals from northern bottlenose whales (*Hyperoodon ampullatus*). Previous recordings from this species indicated that the signals differed considerably from other beaked whales (Hooker and Whitehead, 2002). However, the recording gear used by Hooker and Whitehead had a bandwidth of less than 40 kHz, which is below the full bandwidth of the echolocation signals of other species of beaked whales (e.g., Johnson *et al.*, 2006). Therefore the Hooker and Whitehead recordings may not represent the complete frequency range of bottlenose whale signals. In the recordings presented here, signals are recorded with a bandwidth of 80 kHz, and with several recording units to allow the calculation of the source level and directionality properties of the signals. We show that the signals indeed have the same intriguing up-sweep characteristics as those of other species of beaked whales.

II. MATERIALS AND METHODS

Recordings were made on 21 of July 2006, from r/v Narhvalen, a 45 feet steel ketch equipped for bioacoustic research. The recording location was approximately 100 nm north of the Faeroe Islands centered at the location $N63^{\circ}36.7' W6^{\circ}07.0'$. The water depth at the recording location varied between 1 and 2 km. The Sea State was 1 to 2. Heavy fog reduced visibility to within 100–200 m. A group of approximately five northern bottlenose whales approached the vessel and were observed for about 3 h. This species is known to be very curious and often approaches boats. No other species of whales were observed during the recordings.

The recording equipment consisted of 5 recording units synchronized with fiberoptics (see Heerfordt *et al.*, 2008, for details). Each unit consisted of a model nr. 4034 (RESON) omnidirectional hydrophone connected with a 137–176 cm hydrophone cable to a cylindrical pressure-housing (canister) containing the electronics. The hydrophone cable was kept stretched downwards and separated approximately 10 cm from the fiberoptic cable by a metallic wire. The individual distance between each canister was measured with a standard measuring tape prior to field work and varied between 42.8 and 49.4 m. The recording started as the array was still being deployed, so it was not possible to obtain data on absolute depths of the recording units during the various recordings. The top canister depth ranged from right under the water surface to a depth of a few 100 m during the recordings.

Each canister contained a preamplifier and filter unit (preamplifier gain of 20 or 40 dB, custom-built fourth-order high-pass filter with -3 dB cutoff frequency at 500 Hz, and a fourth-order low-pass antialiasing filter with a -3 dB cutoff frequency at 40 kHz for recording unit 2 and 4, and 80 kHz for recording unit 1, 3, and 5), a 16 bit AD-converter (maximum input voltage ± 10 V), and a multiplexer. The multiplexer fed the bits from the AD-converter into the bit-stream from the other units into the optical fiber. The system has a sampling rate of 96 kHz. Three of the recording units (1, 3, and 5) allowed for combining two parallel channels

separated in time by half a sample interval (with a precision within 5%) achieving a doubled sampling rate. The multiplexed signals were stored on a computer onboard the boat.

The sensitivity of each unit of the hydrophone array was calibrated at 250 Hz with a pistonphone calibrator (model 4223, Bruel & Kjaer), using a custom-built cavity, calibrated for the used hydrophone model. Calibration of all hydrophones was made both before and after the deployment of the array, without any significant change in hydrophone sensitivity (-211 ± 0.9 dB re 1 V/ μ Pa). Also, prior and after field work, insert-voltage calibration was made with a pure tone varied in 1–10 kHz steps within the frequency range 1–40 kHz. The recording units differed in their sensitivity by no more than 2 dB, and the difference in sensitivity for each unit before and after field work was no more than 0.9 dB. The variation in sensitivity between individual recording units was taken into account in the calculation of the received level of the signals. The receiver directionality pattern of the hydrophones was obtained from the manufacturer (RESON) and varied with less than 1 dB except for recording directions close to the direction of the hydrophone cable (in our case the vertical upward direction).

A salinity and temperature profile of the recording site was obtained for depths from 0 to 1000 m with a data logger (DSTCTD, Star-Oddi) attached to the lowest canister in the array. From this the sound speed profile was calculated using the equation of Medwin (1975).

The recordings were screened for echolocation clicks with Adobe Audition (ver. 1.5, Adobe). Selected clicks were imported in Matlab (ver. 6.5, MathWorks). Here the recordings of receiver 1, 3, and 5 were reconstructed from two sets of data-series, spaced 0.5 clock pulse apart. In this way an effective doubled bandwidth (80 kHz) was obtained. The source parameters were measured from the double bandwidth recordings. The peak-to-peak source level is the difference between the maximum and the minimum pressure of each signal, compensated for the transmission loss. The duration of the signal was measured by creating the cumulative energy function, and defining the start and end of the click as when the cumulative energy reached 2.5% and 97.5%, respectively, of all energy within the pulse. The root-mean-square intensity and the energy density of the signal were calculated within this time window, and compensated for transmission loss. The centroid frequency was calculated as the average of the spectrum (in linear energy units), and the rms bandwidth as the standard deviation of the spectrum (in linear energy units) around the centroid frequency. These measurements are more thoroughly explained in Madsen and Wahlberg (2007).

To obtain apparent source levels (defined as the sound intensity 1 m from the sound source, in any direction from it; see Möhl *et al.*, 2000), pulse source locations were determined and intensity back-calculated to 1 m from of the source, assuming spherical spreading and an acoustic attenuation of 10 dB/km. The acoustic localization routine measured the time-of-arrival differences for the same pulse recorded on the five receivers by cross-correlating each input signals with the signal recorded at the top receiver. For this the 40 kHz bandwidth recordings were used to obtain

comparable data from all channels. The sound velocity used for acoustic localization was the average of the measured sound velocity profile. The receivers were assumed to be placed in a linear array with an interreceiver distance given by the measured individual fiber-optic and hydrophone cable lengths. The acoustic localization routine both calculated the hyperbola intersects and a least-square regression to obtain the source coordinates (see Madsen and Wahlberg, 2007). Only cases where the average hyperbola intersect and the least-square solution differed by no more than 20 m were used for further analysis.

Toothed whale echolocation signals are highly directional. Two criteria were used to find clicks that were regarded as being recorded close to the acoustic axis. First, the apparent source level was calculated for receiver 1, 3 and 5 using the 80 kHz bandwidth recordings. A pulse was regarded as being recorded on-axis at the central receiver 3 if the peripheral receivers 1 and 5 recorded the same click at a lower or equal apparent source level, and if the previous and subsequent click in the central channel was of lower intensity (as expected in a scan of equal intensity pulses). By calculating the relative source level as a function of the angle to the sound source, assuming that the assigned on-axis click was recorded at 0° , it was possible to estimate the acoustic beam pattern. For each pulse, the beam pattern established by energy measurements on the 80 kHz bandwidth receivers 1, 3, and 5 normalized so that receiver 3 had a level of 0 dB. The peak direction and level was thereafter determined by a second-order Lagrange interpolation to reach an angular resolution of 0.1° . The angle at which the interpolation function peaked was identified. This was defined as the acoustic axis for all clicks. A computer model (implemented in Matlab, Mathworks) calculated the beam pattern of a circular piston emitting one of the recorded bottlenose whale (presumably on-axis) pulses. The diameter of the piston was varied, and the beam pattern having the smallest least square error between model and data was chosen as the piston beam pattern best fitting the data. The directionality index was calculated using the formula in Møhl *et al.* (2003) on this piston beam pattern. A flat circular piston has been used previously to describe the beam patterns of both bats (Mogensen and Møhl, 1979; Jakobsen and Surlykke, 2010) and toothed whales (Au, 1993; Beedholm and Møhl, 2006; Kyhn *et al.*, 2010; Møhl *et al.*, 2003). Even though none of these animals have a sound generator mechanism even remotely resembling a flat piston, the beam patterns calculated from the piston model have been useful when comparing transmission beam patterns between species.

III. RESULTS

The sound velocity profile derived from temperature and salinity measurements followed the pattern seen in temperate waters during the summer. The constant decrease of sound velocity from the surface and down to about 400 m follows the temperature gradient. At greater depths the sound velocity increases with the ambient pressure. The salinity varied between 32 and 35 ppt, and the temperature from 9.5°C at the surface to a minimum of 0°C at a depth of 450 m. Ray trace

modeling showed that the ray paths were almost straight and curving had no significant effect on acoustic localizations or sound level measurements (using methods described in Wahlberg *et al.*, 2001).

Approximately 1 h of recordings were made during the 3 h the animals were observed. An example of a recorded click sequence is seen in Fig. 1(a), and the hyperbola plot for the derivation of the location of a pulse source is seen in Fig. 1(b). Of the recorded pulses 5 sound files with a total duration of 3 min 20 s had pulses recorded on 5 channels. From two of the 5-channel files, 10 pulses complying with on-axis criteria were extracted for source level and directionality calculations. In addition, 856 interpulse intervals were measured from more than 20 pulse trains recorded on 1–5 channels, and two buzz sequences (click trains of fast repetition rates) were extracted from the recordings. The on-axis clicks were localized to horizontal distances of 123–294 m, vertical depths of 170–342 m and straight-line ranges of 256–416 m, all relative the top receiver.

In Table I the source parameters of the on-axis pulses are described. An example of an upsweep pulse and its spectrum is seen in Figs. 2(a) and 2(b). The spectrogram representation using the Wigner-Ville transform (Cohen 1989)

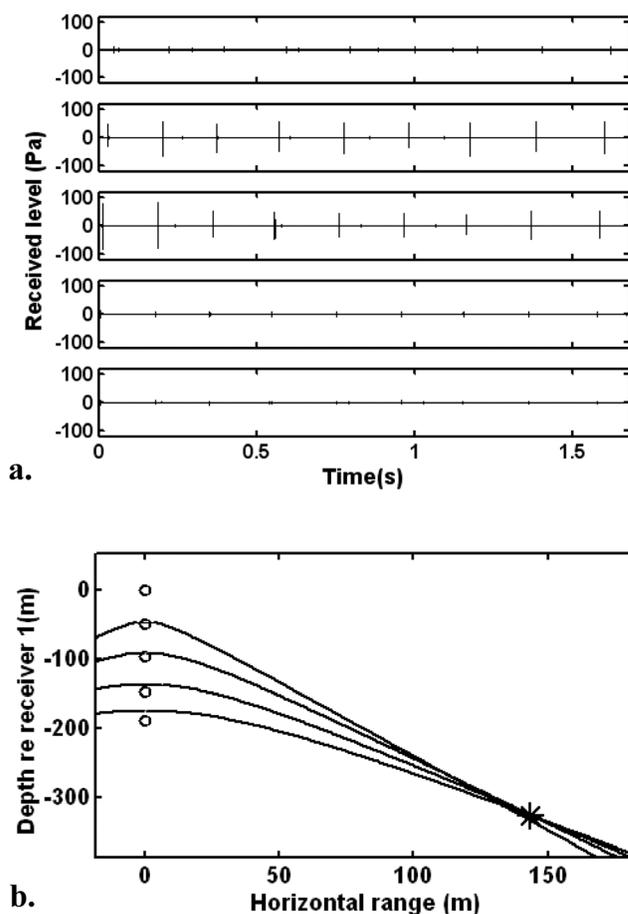


FIG. 1. (a) Example of recording series from five recording units, spaced 50 m apart. The signals are from northern bottlenosed whales (*Hyperoodon ampullatus*) and have been high-passed filtered with a 1 kHz -3 dB cutoff four-pole Butterworth filter. (b) Hyperbola plot used to acoustically localizing a northern bottlenose whale. Circles indicate receiver locations, and the analytically derived source location is indicated with an asterisk (*).

TABLE I. Source parameters of 10 on-axis biosonar pulses from the northern bottlenose whale (*Hyperoodon ampullatus*). RMS (root-mean square) and pp (peak-to-peak) source level, energy density and duration are calculated over a time window defined by the 95% content of the signal energy. The directionality index (DI) and beam width is estimated from a calculated beam pattern of an on axis bottlenose whale pulse emitted through a piston of a diameter of 12.2 cm which gives the smallest least square error between model and data on the ten pulses, aligned using the peak in a Lagrange interpolation function through the data points.

Parameter	Unit	Mean \pm 1 s.d.	Range
RMS Source level	dB re 1 μ Pa rms at 1 m	186 \pm 9	175–202
pp Source level	dB re 1 μ Pa pp at 1 m	203 \pm 9	194–220
Energy density	dB re 1 μ Pa ² s at 1 m	169 \pm 10	156–186
95% duration	μ s	276 \pm 58	207–377
Centroid frequency	kHz	43 \pm 7	32–51
RMS bandwidth	kHz	17 \pm 5	10–24
–3 dB beam width		19.8°	
–10 dB beam width		25.7°	
DI (dB)		18.3	

shows the characteristic upsweep of the pulse [Fig. 2(c)]. Buzz clicks which were emitted with a higher repetition rate (see below) were of much shorter duration, and had a broader spectrum than the lower repetition rate regular pulses [Figs. 3(a) and 3(b)].

The directionality pattern of the low-repetition rate pulses is seen in Fig. 4. The solid line depicts the radiation pattern of a *Hyperoodon* pulse emitted from a radiating piston with a diameter of 12.2 cm, which is the diameter best matching the *Hyperoodon* beam pattern. The Directionality index of this piston radiation pattern is 18.3 dB.

Interpulse intervals ranged from 73 to 949 ms ($N = 856$) for regular pulses [mean 306 ms, SD 118 ms; Figs. 5(a) and 5(b)]. Buzz interclick intervals were measured from 2 sequences, with a total of 469 clicks having a minimum interclick interval of 5.8 ms and a maximum of 13.1 ms [mean 8.4 ms, SD 1.3 ms; Fig. 5(c)]. The buzz clicks were only detected on one or two receivers simultaneously and the source level of these signals could therefore not be calculated.

IV. DISCUSSION

No other whales were observed during these recordings, but the visibility was restricted so it cannot be ruled out that other toothed whales may have been present at distances beyond a few 100 m from the boat. The other cetacean species commonly sighted in the recording area are long-finned pilot whales (*Globicephala melas*), killer whales (*Orcinus orca*), Atlantic white sided dolphins (*Lagonorhynchus acutus*), white beaked dolphins (*L. albirostris*) and sperm whales, all of which are known to use broadband echolocation clicks. The buzz clicks recorded here were only heard in sequences also containing upsweep pulses. Therefore, we regard both the upsweep pulses and the buzz clicks to be recorded from Northern bottlenose whales.

Echolocation signals from the northern bottlenose whales are very similar in their time-frequency pattern (upsweeps) to signals from the three other species of beaked whales recorded so far (Cuvier's and Blainville's beaked whale by

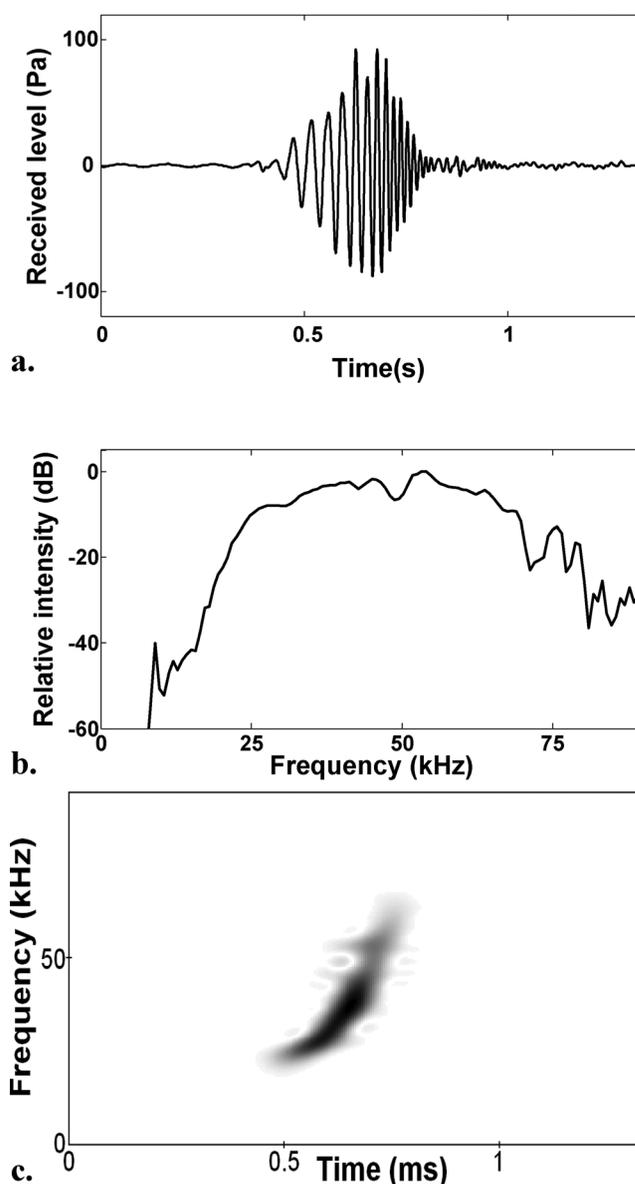


FIG. 2. (a) On-axis pulse from a northern bottlenose whale (*Hyperoodon ampullatus*). Sampling frequency 192 kHz, signal is linearly interpolated 10 times. (b) Spectrogram of the pulse. FFT size 256, Hann Window, sampling frequency 192 kHz. (c) Wigner-Ville plot of the pulse. The grey scale is a linear measure of relative intensity.

Johnson *et al.*, 2004 and 2006, and Gervais' beaked whale by Gillespie *et al.*, 2009). It is worth noting that the sound production organ of northern bottlenose whales is remarkably different from other beaked whale species such as Blainville's and Cuvier's beaked whales. The soft tissues of the sound production apparatus are much larger in bottlenose whales than in the other species. The melon, which is used to transfer the signals to the water from the phonic lips where they are generated, is very large in bottlenose whales (Møhl and Clarke, unpublished data) and relatively small and unpronounced in e.g., the Cuvier's beaked whale (Cranford *et al.* 2008). Thus, there is no clear link between the size of sound production tissue and melon and the production of upsweep pulses. In addition, all beaked whales as well as the Kogias and the sperm whale have a spermaceti organ (Clarke 1978, 2003; Huggenberger *et al.*, 2006; Cranford *et al.*, 2008).

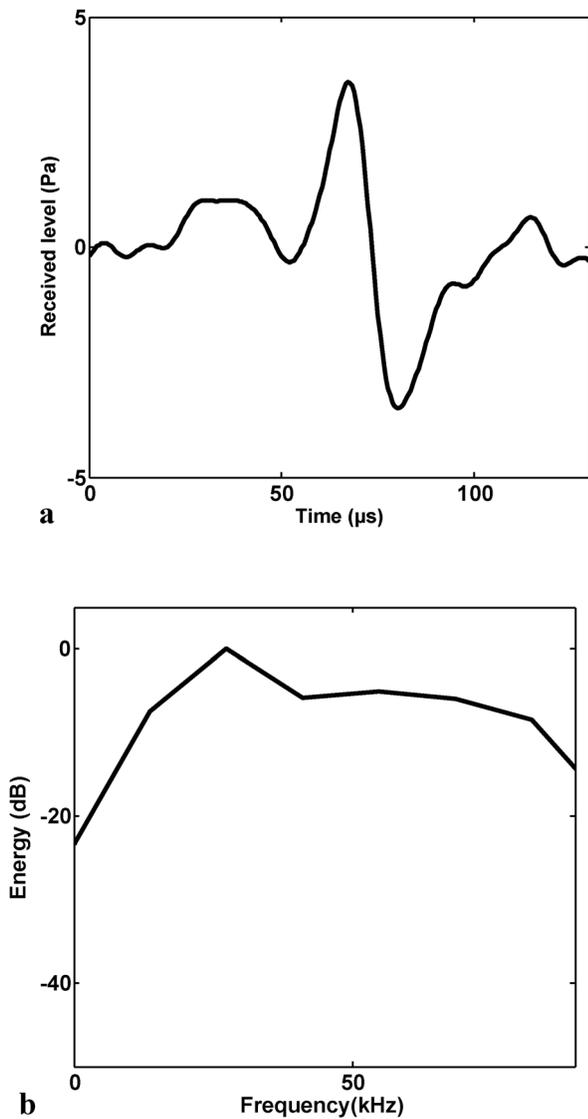


FIG. 3. (a) Oscillogram and (b) spectrum of a buzz click from a northern bottlenose whale (*Hyperoodon ampullatus*). Sampling rate 192 kHz, interpolated 10 times. Spectrogram: FFT size 256, Hanning window.

These three groups of toothed whales produce three very different types of echolocation signals. Thus the function of the spermaceti organ in shaping the signals remains unclear. However, the extreme size of the sperm whale spermaceti organ as compared to the one found in the other species may indicate that it plays a role in producing the extreme source levels reported from this species (Møhl *et al.*, 2003).

The reason why beaked whales emit the very unusual upsweep signal is not known. In most species of echolocating bats, the echolocation signals are sweeping downwards. It is generally believed that this is to increase the energy of the call without reducing the bandwidth, which serves to improve ranging and classification of targets (e.g., Simmons, 1971). In terms of the lively discussion which has been ongoing for many years as to whether bats can perform a cross-correlation operation of the incoming echo with a model of the transmitted pulse, it mostly pertains to the degree to which phase is preserved in, and used by, the auditory system. In terms of detection, Møhl (1986) did not find

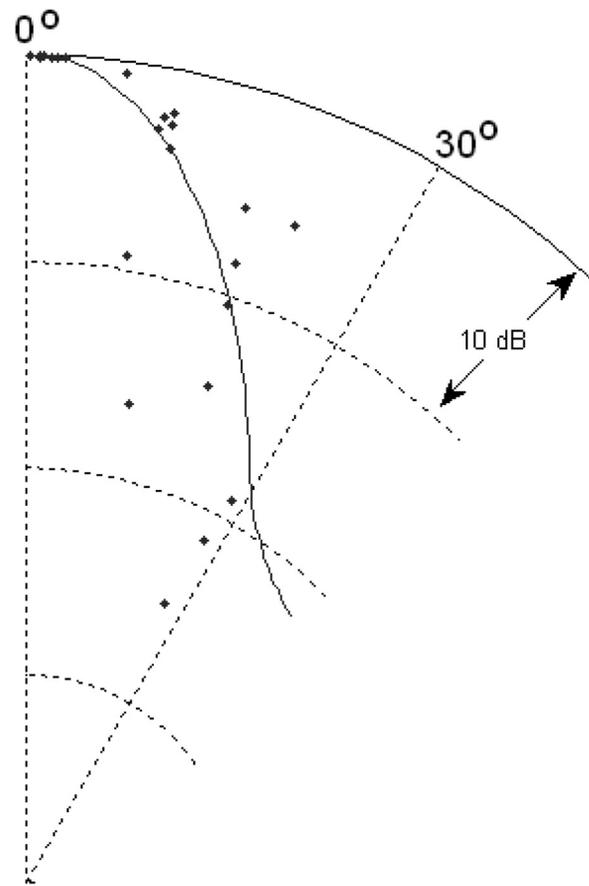


FIG. 4. Directionality pattern of pulses from the northern bottlenose whale (*Hyperoodon ampullatus*). The beam pattern of each pulse has been Lagrange-interpolated and shifted so they all are aligned at 0° where the interpolation function is maximum. The solid line is the beam pattern of a circular piston having an aperture of 12.2 cm diameter and emitting an on axis bottlenose whale pulse.

experimental support for the hypothesis of coherent cross-correlation in bat sonar. One explanation for the direction of sweeping in bats is that by sweeping downwards, the wave traversing the basilar membrane will continuously activate new areas, thus avoiding a form of forward or upward masking. Another possibility is that the harmonics associated with voiced sound production result in a messier signal onset if one starts at the low-frequency end, where the harmonics are more closely spaced. By sweeping downwards a more systematic path from higher to lower frequencies through the auditory filters is achieved. Beaked whale clicks do not have prominent harmonics so that factor would not suggest a disadvantage in using an upward sweep. However, the cochlea itself will delay a signal in a frequency dependent way. Low frequencies are delayed more than high frequencies, mainly because they have sharper tuning. Therefore, the overall impulse response of the ear is a downsweep, which may provide for at least some time-compression of an upsweep.

The duration of beaked whale frequency-swept pulses are long compared to clicks from all other *Odontocetes* [Table I and Fig. 2(a)]. Comparing pulses of same peak amplitude, a longer pulse can contain more energy and give a better echo detection. For signals of a duration shorter than the integration time of the hearing system (which for the bottlenose dolphin, *Tursiops truncatus*, was measured by

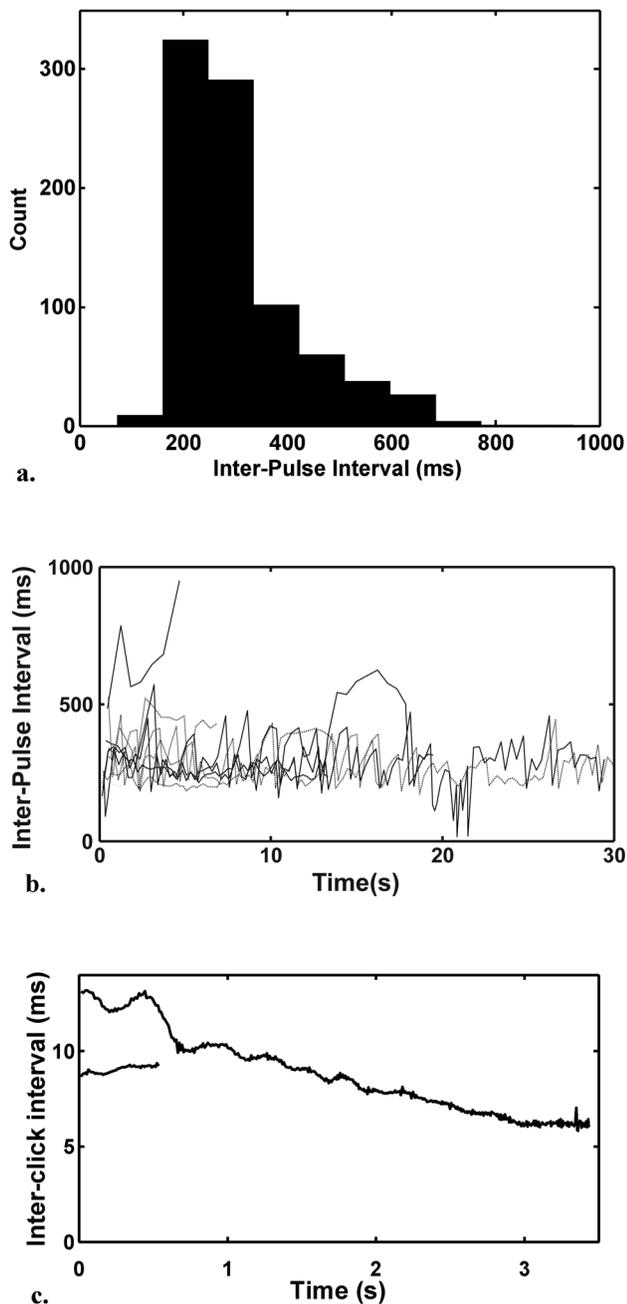


FIG. 5. (a) Histogram of 896 interpulse intervals from pulses of northern bottlenose whales (*Hyperoodon ampullatus*). (b) Interpulse intervals from 10 pulse sequences. (c) Inter-click intervals from two sequences of buzz clicks.

Au, 1993, and Dubrovskiy, 1990, to 200–300 μ s, and which can be expected to be at least as long in bottlenose whales), the threshold for detecting the signal decreases as $10 \log \tau$, where τ is the signal duration. A beaked whale pulse has a duration which is about 10 times longer than the duration of a bottlenose dolphin click, which could improve the echo detection threshold by 10 dB.

Besides the upsweep pulses (Fig. 2), the northern bottlenose whales also emitted shorter broadband clicks at higher repetition rates (Fig. 3). This has also been observed in Blainville's beaked whale (Johnson *et al.*, 2006). When the range to the target is short, the shorter clicks could provide a more accurate range resolution and reduce the risk of confusing one echo with the next.

The directionality pattern of the bottlenose whale (Fig. 4) does not seem to be more pronounced than for other beaked whales. The Cuvier's beaked whale has an estimated directivity index of 25 dB (Zimmer *et al.*, 2005). It is, however, difficult to discuss these results in detail, as both the previous measurements of Cuvier's beaked whale and the measurements presented here are imprecise. We are not able to guarantee that the analyzed signals were recorded exactly on the acoustic axis. Any deviation from the on axis condition may result in an underestimation of the directionality. Still, even though we may assume that the huge sound production organ of the northern bottlenose whale would be capable of generating signals of more acute directionality compared to the other species of beaked whales, existing data does not prove this to be the case.

The interpulse and interclick intervals reported here (Fig. 5) are similar to the ones from previous measurements of bottlenose whales (Hooker and Whitehead, 2002) and also from those of other beaked whales. The species of beaked whales recorded so far have been clicking at rates somewhere in between the rates of Delphinids and sperm whales. In general, animals using echolocation try to avoid masking their own echoes, so that a new click is not emitted until the previous echo from the focal object has returned to the whale (Au, 1993; Madsen *et al.* 2005b; Jensen *et al.*, 2009; Verfuss *et al.*, 2009). The interpulse and interclick intervals can therefore be used as a coarse assessment of the range to the target of interest. If this holds true also for bottlenose whales one may conclude that the animals of this study are investigating prey up to relatively large ranges (from about 50 to 700 m). However, studies of *Mesoplodon* have shown that from this species the signals are emitted at a low repetition rate even when the target is quite close to the animal (Madsen *et al.*, 2005b). Perhaps this is explained by beaked whales employing a very different echolocation strategy and they may have a very different perception of the echoes than Delphinids. For most Delphinids, the interclick intervals are very stable both during the search and buzz phase. In the recordings made here, there are great variations in the interpulse intervals in each sequence, especially during the nonbuzz phase [Fig. 5(b)]. Whether these excursions in the interpulse intervals also reflect a different form of perception of echolocation signals from what is generally assumed for Delphinids and harbor porpoises is however an open question.

Eighteen years ago, Au (1993) made an initial classification of toothed whale echolocation signals. Many recordings of different species have been made since then, and two new categories have been discovered (Fig. 6). Even though broadband recordings of toothed whale echolocation signals are still lacking for many species, the recordings at hand indicate that all existing species can be grouped into these four categories. Such a grouping is quite different from the situation for bats, where a large variation in echolocation signals is found, depending on e.g., habitats, geographic location, size and prey type (Schnitzler and Henson, 1980; Schnitzler and Kalko, 2001). For toothed whales there is also a huge diversity in habitats. The more than 70 species of toothed whales can be grouped into many feeding niches, such as shallow and deep waters, pelagic and coastal and

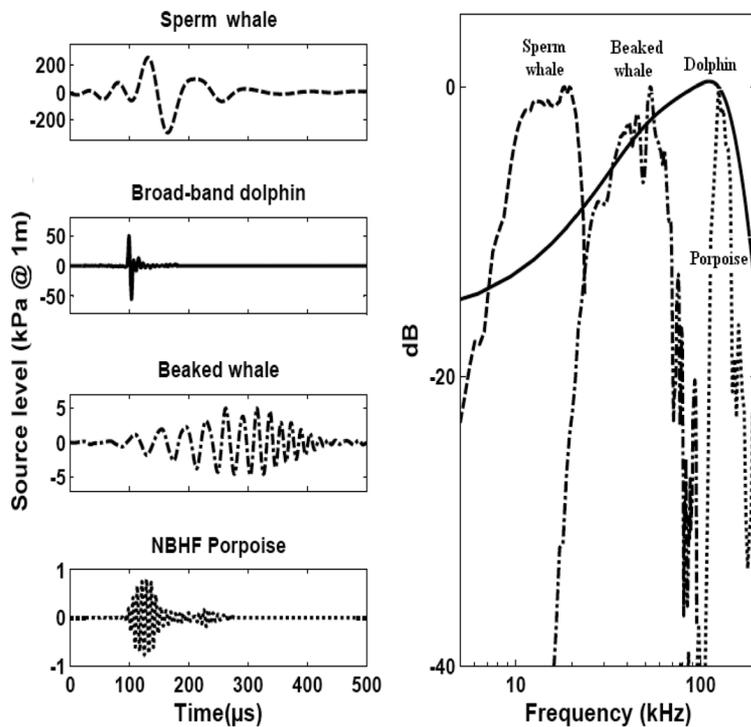


FIG. 6. The four different classes of toothed whale biosonar signals. All time series are linearly interpolated 10 times and filtered with a 1 kHz high-pass filter and an antialiasing filter with an appropriate cutoff frequency. All spectra are made with a Hann window weighting of the time series. (a) Sperm whale (*Physeter catodon*, data from Møhl *et al.*, 2003, sampling rate 48 kHz, FFT size 128 points). (b) Bottlenose dolphin (*Tursiops truncatus*, data from Jensen *et al.*, 2009, sampling rate 800 kHz, FFT size 256 points), (c) Northern bottlenose whale (*Hyperoodon ampullatus*, data from this study, sampling rate 192 kHz, FFT size 256), (d) Harbor porpoise (*Phocoena phocoena*) narrow-band high frequency (NBHF) signal; Wahlberg, unpublished data, sampling rate 500 kHz, FFT size 128.

even riverine waters. Prey ranges from small, schooling fish to larger fish and squid, and up to, in the case of killer whales, birds, seals and even other cetaceans. There seems, however, to be no clear correlation between the sonar pulse type used by the animals and the prey in question. Beaked whales, pilot whales, *Kogias* and sperm whales all forage on deep-sea squid but use quite different kinds of signals. Delphinids, who almost all use very similar short echolocation clicks, may prey on animals as diverse as small squid (pilot whales and Risso's dolphins, *Grampus griseus*) to fish and even to sea birds and other marine mammals. These prey items will reflect sound with very different efficiency, so there could in theory be many possibilities for the whale to adapt the echolocation signals to improve the ability to detect the different kinds of prey. However, there is no clear difference in the type of signal these species are using when pursuing such vastly different types of prey. Likewise, species with almost identical echolocation signals may search for vastly different prey types in very different habitats (e.g., Risso's dolphin and the false killer whale, *Pseudorca crassidens*; Madsen *et al.*, 2004; and *Kogias* and harbor porpoises, Madsen *et al.*, 2005a).

The only clear correlations between biosonar and foraging behavior in toothed whales seems to be in how often the animals are using their signals, rather than the signal shape. The most obvious example can be found in killer whales. Some killer whale pods hunting for salmon and herring are almost continuously emitting sounds whereas other groups hunting for marine mammals are usually very quiet. Instead of making use of echolocation, the marine mammal hunting killer whales seem to mainly rely on vision and passive hearing for detecting and localizing prey, which has acute hearing in the frequency range where killer whales emit their signals (Barrett-Lennard *et al.*, 1996).

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¹This species is also known as *Physeter macrocephalus*.

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