

Echolocation signals of wild harbour porpoises, *Phocoena phocoena*

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Accepted 25 October 2006

Summary

Field recordings of harbour porpoises (*Phocoena phocoena*) were made in the inner Danish waters with a vertical array of three or four hydrophones. The back-calculated source level ranged from 178 to 205 dB re 1 μ Pa pp @ 1 m with a mean source level of 191 dB re 1 μ Pa pp @ 1 m. The maximum source level was more than 30 dB above what has been measured from captive animals, while the spectral and temporal properties were comparable. Calculations based on the sonar equation indicate that harbour porpoises, using these high click intensities, should be capable of detecting fish and nets and

should be detectable by porpoise detectors over significantly larger distances than had previously been assumed. Harbour porpoises in this study preferred a relatively constant inter-click interval of about 60 ms, but intervals up to 200 ms and down to 30 ms were also recorded.

Key words: *Odontoceti*, *Phocoena phocoena*, biosonar, target detection, click, source level, inter-click interval, bycatch, acoustic monitoring.

Introduction

The harbour porpoise (*Phocoena phocoena* L.) is the smallest and most abundant of the toothed whales in the coastal waters of the North Atlantic and the North Pacific. Like other toothed whales (*Odontoceti*), harbour porpoises use biosonar for foraging and orientation. The echoes returned from biosonar signals emitted by the animal are used to determine the direction and distance to potential prey items or obstacles in the water.

The performance of a biosonar system can be evaluated by means of the sonar equation in its transient form (Au, 1993). This equation relates the emitted sound energy flux density to the energy flux density of the returning echo. The simplest form of the sonar equation, in which noise is ignored, states that the energy flux density of the returning echo is equal to the energy flux density of the outgoing signal minus the propagation loss due to geometric spreading and sound absorption, plus the reflective properties of the ensonified target:

$$EE = SE - 2TL + TS_E, \quad (1)$$

where *EE* is the returning echo energy flux density (in dB re 1 μ Pa²s), *SE* is the source energy flux density (the acoustic energy flux density 1 m in front of the sound source measured on its acoustic axis, in dB re 1 μ Pa²s), *TL* is the transmission loss (the reduction in sound energy between a point 1 m from the source and the target, in dB) and *TS_E* is the target strength

(the ratio of the reflected energy flux density measured 1 m from the target relative to the energy flux density impinging on the target, also in dB). Instead of using the notation energy flux density, the acoustic output of a sound source can be presented as the sound pressure level, which is the intensity of the signal, or the sound energy per unit time. Most studies on harbour porpoise biosonar report the sound pressure level rather than the energy flux density, even though the latter is more relevant when discussing biosonar performance (Au, 1993; Kastelein et al., 1999). In this paper, we favour the energy flux density notation, but for comparison with earlier work we also report the sound pressure level 1 m in front of the animal, also known as the source level.

Harbour porpoises produce high-frequency, narrowband signals. These so-called clicks, measured from animals in captivity, have a duration of ~100 μ s, a peak frequency of ~130 kHz, an inter-click interval of ~60 ms and a maximum source level of 172 dB re 1 μ Pa pp @ 1 m (Dubrovskij et al., 1971; Møhl and Andersen, 1973; Akamatsu et al., 1994; Teilmann et al., 2002). This is more than 40 dB less intense than has been measured from other toothed whales [e.g. bottlenose dolphin (Au et al., 1974); sperm whale (Møhl et al., 2003); narwhal (Møhl et al., 1990); white-beaked dolphin (Rasmussen et al., 2002)]. Consequently, the biosonar of harbour porpoises is expected to have considerably shorter detection ranges than that of larger odontocetes, such as the

bottlenose dolphin. This is consistent with target detection experiments involving captive animals, where the detection ranges of similar sized steel spheres were about five times shorter for porpoises than for bottlenose dolphins (Kastelein et al., 1999).

In spite of the intense research interest in this species, practically nothing is known about the acoustic behaviour of harbour porpoises in the field. Actually, only one field study (Goodson and Sturtivant, 1996) is known to us, but it contains no quantitative data. Observations of other species of toothed whales have shown that animals echolocating in open water produce signals that are orders of magnitude more intense than those from animals recorded in tanks. This can have large implications on how we interpret the animals' biosonar performance, not only during prey detection and capture but also during interactions with fishing gear that may lead to incidental entanglement (Perrin et al., 1994; Cox et al., 1998; Vinther, 1999). For designing sustainable methods that reduce bycatch and also for passive acoustic monitoring of harbour porpoise distribution, it is crucial to know the animals' biosonar performance, especially in terms of the sound pressure levels being emitted by the animals in their natural habitat.

The aim of the present study was to provide information on the source properties and use of the echolocation clicks of wild harbour porpoises and compare the results with data obtained from captive specimens. The results show that the clicks can be considerably more intense in the field than has previously been reported from captivity. The implications of this are discussed in relation to biosonar performance, bycatch and passive acoustic monitoring.

Materials and methods

Study area and setup

The recordings were made in the inner waters of Denmark in August 2005 at three separate locations: the Bay of Aarhus (56°08' N, 10°22' E), Bogense, north of Funen (55°35' N, 10°02' E) and 'Tragten', northern Little Belt (55°33' N, 09°46' E). The water depth varied between 12 and 25 m.

Recordings were made with a linear, vertical array consisting of either three or four Reson TC 4034 hydrophones with a sensitivity of -220 dB re 1 V/1 μ Pa in the frequency range up to 250 kHz (Reson A/S, Slangerup, Denmark). The array configurations are depicted in Fig. 1. A relative calibration of the hydrophones was performed in an anechoic tank to make sure that the sensitivity of the hydrophones corresponded within 3 dB to that given by the manufacturer within the frequency range 120–150 kHz.

The hydrophones were mounted in holes made in a 5 cm-diameter and 6 m-long, rigid PVC pipe, aligned within a few mm on the vertical axis (Fig. 1).

Two different recording systems were used. The 3-hydrophone array was connected through a custom-built band pass and amplifier unit to a Wavebook 512 (IOtech, Cleveland, OH, USA) for digitisation. Sampling frequency for each of the

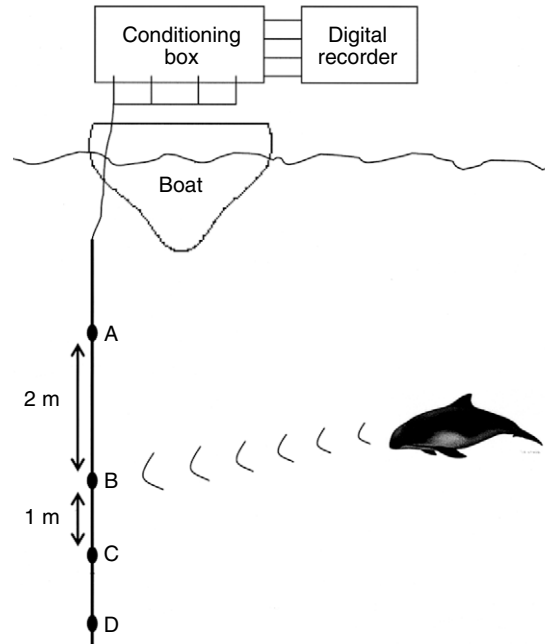


Fig. 1. The experimental set up consists of a linear, vertical array of three (A,B,D) or four (A–D) hydrophones connected *via* a conditioning box to a digital recorder.

three channels was 330 kHz, 12 bit resolution. The 4-hydrophone array was connected through a custom-built band pass and amplifier unit to a lunchbox computer containing a 4-channel sound card (AD-Link, NuDAQ 20 MHz 4-channels, 12 bit; Danbit, Copenhagen, Denmark). The sampling frequency for each of the four channels was 400 kHz. A first-order (-6 dB octave $^{-1}$) high-pass filter at 10 Hz and a eighth-order (-48 dB octave $^{-1}$) low-pass filter at 150 kHz were used for the Bay of Aarhus recordings, and a first-order (-6 dB octave $^{-1}$) high-pass filter at 100 Hz and a second-order (-12 dB octave $^{-1}$) low-pass filter at 200 kHz were used for the recordings made in Bogense and Little Belt. An overall gain of 60 dB was used at all three locations.

Source level measurements

The sound pressure level that we recorded on our systems is termed the received level. From the received level, we wish to estimate the source level, which is defined as the sound pressure level back-calculated to 1 m in front of the harbour porpoise on its acoustic axis. To do this we need to know the distance between the array and the porpoise in order to estimate the transmission loss. The distance was back-calculated, using a custom-built Matlab (Mathworks, Natick, MA, USA) routine, from the time-of-arrival distances (TOADs) of the same signal between the different hydrophones [similar to the equations given in Wahlberg et al. (Wahlberg et al., 2001)]. The speed of sound in water that we used was 1495 m s $^{-1}$, as calculated from the Medwin equation (Medwin, 1975) from salinity and temperature measurements made on location. Assuming spherical spreading, the

transmission loss is given by $TL=20\log(R)+R\alpha$, where R is the distance between the porpoise and the array and α is the frequency-dependent absorption at the centroid frequency of the received signal [0.04 dB/m at 135 kHz (Fisher and Simmons, 1977)].

The source level (SL) can be calculated from the sonar equation as the sum of the received level (RL) and the estimated transmission loss (TL): $SL=RL+TL$. We assume the click to be recorded on the acoustic axis. It is however very difficult, or almost impossible, to determine accurately whether the porpoise is pointing its acoustic axis at one of the hydrophones in the array. For broadband clicks from delphinids, an increased number of notches and thereby an increased distortion in the spectrum of the clicks indicate that they are recorded off the acoustic axis (Madsen et al., 2004; Beedholm and Møhl, 2006). This does not apply to narrowband porpoise clicks (Au et al., 1999). In this paper we therefore refer to the measurements as ‘apparent source levels’ (ASL), which equals the back-calculated sound intensity at a distance of 1 m from a directional source in an unknown direction (*sensu* Møhl et al., 2000). At worst, we underestimate the on-axis source levels, as the clicks may very well have been recorded off the acoustic axis, and the apparent source level should thus be regarded as conservative estimates of the true source level.

Harbour porpoises emit trains of clicks in a narrow, forward-oriented beam (Au et al., 1999). When the sound beam of an echolocating porpoise intersects a hydrophone, a series of clicks are recorded, usually first increasing and then decreasing in amplitude. We call such a click sequence a ‘scan’ (*sensu* Møhl et al., 2003).

The criteria for selecting clicks for source level measurements were: (1) the click was detectable on all channels, (2) the direct path of the click was stronger than any trailing surface or bottom reflections, (3) the click was of maximum amplitude in a scan and (4) the porpoise was localized within 75 m of the array.

Analysis

Analysis of data was performed with Adobe Audition 1.5 (Syntrillium, Adobe, Mountain View, CA, USA) and custom-written routines in Matlab 6.5.1 (Mathworks) to estimate click parameters.

A number of parameters were extracted or calculated from each click. These parameters were chosen to obtain data for accurate comparison with previous work on signals from harbour porpoises and other species.

The centroid frequency (f_c) is the frequency dividing the spectrum in equal halves of energy, and the peak frequency (f_p) is the highest frequency in the spectrum. The click duration (τ) was determined using two techniques: the -10 dB duration ($\tau_{-10\text{dB}}$) and the 95% energy duration (τ_E). The $\tau_{-10\text{dB}}$ is the click duration 10 dB below the peak of the click envelope (Fig. 2A). To calculate the τ_E of the signal, a window is defined around the signal, and the duration is determined as the interval containing 95% of the energy within that window (Fig. 2B) (see also Madsen, 2005). The bandwidth (BW) was

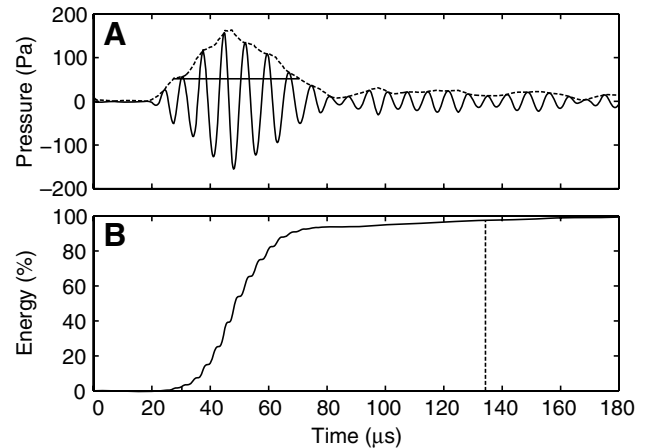


Fig. 2. (A) Harbour porpoise click with signal envelope (dotted line) and the -10 dB duration of the click (horizontal line). (B) Accumulated energy content (%) in the click over time. The interval between the dotted lines is covering 95% of the energy content of the signal.

determined as the -3 dB BW (3 dB below the spectral peak), the -10 dB BW (10 dB below the spectral peak) and the RMS BW [the root-mean-square BW of the signal spectrum (Madsen, 2005)]. The Q-value, or quality factor (Au, 1993), was calculated as the centroid frequency divided by the RMS BW. The inter-click interval (ICI) was determined as the interval between successive clicks in a click train, measured with a semi-automated routine (click detector) written with Matlab. The click sequences were selected manually from the data as being of a favourable signal-to-noise ratio. The click detector detected all signals exceeding a certain peak threshold, set by the operator. By running a few tests, it was shown that the click detector detected $>99\%$ of the clicks in sequences of decent signal-to-noise ratio and produced very few erroneous results.

Click intensity (ASL_{pp} , $ASL_{-10\text{dB}}$, $ASL_{95\%E}$) and energy flux density ($E_{-10\text{dB}}$, E_{95}) measurements were done according to Madsen (Madsen, 2005).

Array calibration and measurement accuracy

In order to test if our chosen transmission loss model [$TL=20\log(R)+R\alpha$] was realistic, the array was used in the field to localize an omni-directional sound source [Brüel & Kjær 8105 (Nærum, Denmark) connected to an Agilent Waveform Generator (Agilent Technologies Denmark A/S, Nærum, Denmark)] emitting artificial porpoise clicks at different distances at a depth of 3 m. The depth of the hydrophone array was 3 m (to the top hydrophone) and the water depth was ~ 12 m.

The transmission loss measurements are displayed in Fig. 3A. The received level as a function of the measured range (5, 10, 25 and 50 m) follows the theoretical line for spherical spreading plus absorption. The variation in the received level within each of the four ranges was 3–4 dB. Fig. 3B displays the RMS error for the acoustic range

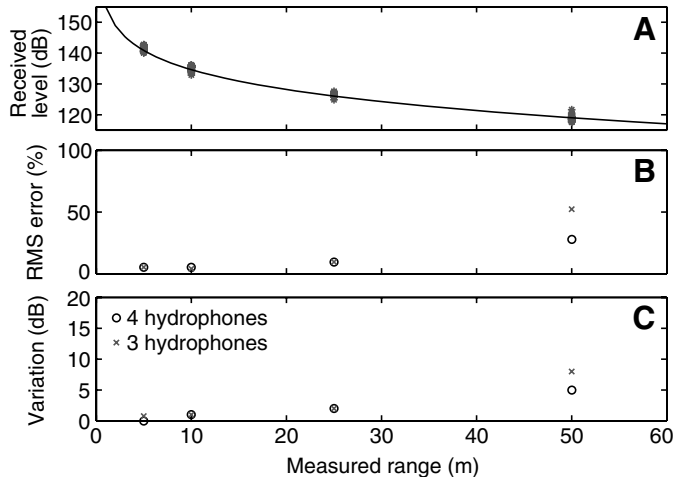


Fig. 3. Results from the transmission loss measurements and acoustic ranging calibration, using an omni-directional calibrated sound source emitting harbour porpoise clicks at a known range from 3 m depth. (A) Received level (dB re 1 μ Pa pp) as a function of measured range for the 4-hydrophone array. The line is a transmission loss model consisting of spherical spreading and absorption. (B) RMS error (see text) in acoustic localization as a function of the measured range for the 4-hydrophone array and the 3-hydrophone array. (C) The maximum variation in the transmission loss due to ranging variation as a function of measured range for the 4-hydrophone array and the 3-hydrophone array.

estimation for the 4-hydrophone array and the 3-hydrophone array, calculated as:

$$\text{RMS error} = \sqrt{\frac{\sum_i (a_i - m)^2}{N}}, \quad (2)$$

where a is the acoustically derived range, m is the range measured with a rope, and N is the number of acoustic measurements made ($N=17-30$).

The maximum variation in ranging errors is expressed in decibels calculated from the corresponding transmission loss (Fig. 3C). Both the localization RMS error and the transmission loss error ('variation') increase with the increasing distance between the porpoise and the array (Fig. 3B,C). The measurements show that the chosen transmission loss model is acceptable within 4 dB at distances up to at least 50 m at this source and array depth (Fig. 3A).

Results

Several hours of recordings were made at the three locations. The recordings from Little Belt contain thousands of harbour porpoise clicks from at least 10 different animals, swimming fast, but closely, past the boat. The recordings from the Bay of Aarhus and Bogense each contain hundreds of clicks from 5–10 different animals, presumably involved in travelling or individual feeding behaviour. The animals were in general

Table 1. Click parameters from wild and captive harbour porpoises

Parameters	Wild porpoises	Captive porpoises*
ASL_{pp} (dB re 1 μ Pa pp @ 1 m)	178–205	157–172
ASL_{-10dB} (dB re 1 μ Pa RMS @ 1 m)	166–194	
$ASL_{95\%E}$ (dB re 1 μ Pa RMS @ 1 m)	161–191	
E_{-10dB} (dB re 1 μ Pa ² s @ 1 m)	123–150	
E_{95} (dB re 1 μ Pa ² s @ 1 m)	123–151	
τ_{-10dB} (μ s)	44–113	(77–125)
τ_E (μ s)	57–175	
f_c (kHz)	130–142	
f_p (kHz)	129–145	128–135
BW_{-3dB} (kHz)	6–26	
BW_{-10dB} (kHz)	14–46	
BW_{RMS} (kHz)	5–12	
$Q_{RMS(BW)}$	12–30	
ICI (ms)	30**–200	20–110

ASL, apparent source level; pp, peak-to-peak; RMS, root mean square; E , energy flux density; τ , click duration; f_c , centroid frequency; f_p , peak frequency; BW, bandwidth; Q , f_c/BW_{RMS} ; ICI, inter-click interval. It is unknown how the duration was measured in the studies with captive porpoises.

*Data from Au et al. (Au et al., 1999), Kastelein et al. (Kastelein et al., 1999) and Teilmann et al. (Teilmann et al., 2002).

**A single sequence of very rapid ICIs (6 ms) was recorded, but not included in the data.

more vocal, more active, less shy and easier to approach in the Little Belt area compared with the Bay of Aarhus and Bogense. At the same time, there was much more intensive boat traffic and therefore much higher underwater noise conditions in Little Belt than in the two other locations.

Based on the criteria described above, 37 clicks from 33 different scans were selected as candidates for being recorded on or close to the acoustic axis and used in the analysis. Clicks within the same scan are from the same individual, whereas clicks from different scans are most likely from different animals. An example of a harbour porpoise click is shown in Fig. 2A. The accumulated energy content in the click over time is displayed in Fig. 2B.

All click parameters are summarized in Table 1. Apparent source levels from 178 to 205 dB re μ Pa pp @ 1 m were derived. When measured as the -10 dB energy flux density, the maximum ASL corresponds to 150 re 1 μ Pa²s @ 1 m and the minimum ASL corresponds to 123 dB re 1 μ Pa²s @ 1 m. The clicks were considerably weaker in Bogense and Bay of Aarhus as compared with the clicks recorded in Little Belt (Fig. 4). There is a clear relationship between the porpoise-to-array range and the apparent source level for the clicks recorded in Little Belt up to ~ 30 m, but outside this range the ASL seems to be independent of range (Fig. 4). For the clicks recorded in Bogense and the Bay of Aarhus, the ASL got more intense when moving away from the array up to 75 m (Fig. 4).

A power spectrum of a click is depicted in Fig. 5. The peak

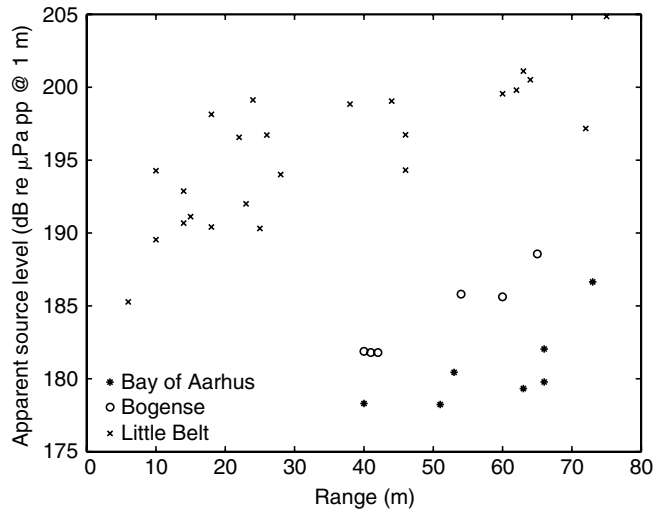


Fig. 4. The estimated apparent source level of harbour porpoise clicks as a function of the back-calculated range between the porpoise and the array.

and centroid frequencies ranged from 129 kHz to 145 kHz (Table 1).

The distribution of 822 inter-click intervals is displayed in Fig. 6. There is a prominent peak around 50–60 ms (median=58 ms). The maximum ICI used was 200 ms and the minimum ICI used was 30 ms. One single click sequence with very short ICIs (6 ms) was detected but not included in Fig. 6.

Discussion

Source levels of clicks

The recorded apparent source levels are at least an order of magnitude higher than reported for captive animals (Table 1). This is in accordance with data from other odontocete species. Bottlenose dolphins contained in net cages in an open bay (Au et al., 1974) were able to produce signals 40 dB more intense

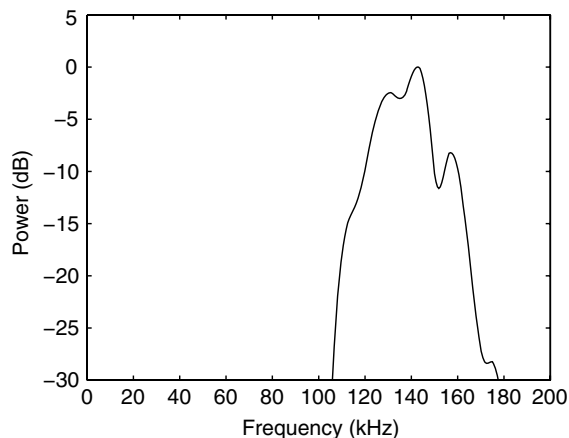


Fig. 5. Power spectrum of a harbour porpoise click (FFT size 64, spectrum interpolated with a factor 10, sampling rate 400 kHz, rectangular window).

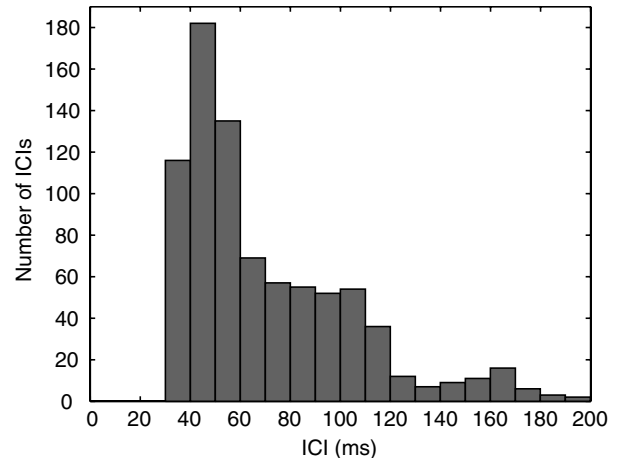


Fig. 6. Histogram of inter-click intervals (ICIs) from wild harbour porpoises ($N=822$; median 58 ms; s.d. 34 ms; bin width 10 ms).

than signals from animals in concrete tanks (Evans, 1973). The reason for this may be that the animal is reluctant to emit high-powered signals in highly reverberant environments, such as concrete tanks, due to the possible annoyance of being exposed to very high levels of returning echoes (Au, 1993). Field recordings of other species of dolphin have confirmed that this is not unique for the bottlenose dolphin (Madsen et al., 2004; Au and Benoit-Bird, 2003).

The biosonar performance of a toothed whale under low noise and reverberation conditions is described by the transient form of the sonar equation (Eqn 1). The returning echo energy flux density is a function of the emitted source energy flux density and the target strength. As the target strength is dependent on the frequency content of the impinging signal (Urlick, 1983), the energy flux density of the returning echo will depend on both the frequency and energy content of the emitted signal. Most toothed whales emit broadband clicks during echolocation. In theory, these animals could regulate their biosonar performance by changing both the frequency content and the intensity of the click independently. In practice, however, these parameters are closely interrelated so that high intensity clicks will also contain higher frequencies (Au, 1993).

The harbour porpoise and the rest of the Phocoenidae family, plus dolphins of the genus *Cephalorhynchus* and the pygmy sperm whale of the genus *Kogia*, produce narrowband clicks of high frequency (Dubrovskij et al., 1971; Møhl and Andersen, 1973; Dawson and Thorpe, 1990; Au et al., 1999; Marten, 2000). The variation in the frequency content of harbour porpoise signals is small (Au et al., 1999) compared with odontocetes using broadband signals. Therefore, the only way in which the porpoise can affect the returning echo energy flux density is to alter the emitted source energy flux density, as seen by the sonar equation. An increased source energy flux density will lead to a higher received echo energy flux density, everything else being equal, and hence a better chance for the animal to detect and classify the target. However, there may be good reasons for odontocetes not to use the highest possible sound

pressure levels. Some fish species are known to be able to detect biosonar signals (Astrup and Møhl, 1993; Mann et al., 2001). There are also physical limitations to the intensity of the signals an odontocete can produce, depending on the size of the animal and the frequency of the signals used. In addition, in reverberant environments containing extraneous echoes (clutter), the received clutter level will depend on the emitted source energy flux density, so that the animal may not necessarily improve its signal-to-clutter ratio by increasing the energy flux density of its signals.

In Table 1, the apparent source level, click duration, peak frequency and ICI from field data are compared with existing data from animals in captivity. In spite of the considerably higher source levels in the field recordings, the other source parameters are very similar. This seems to indicate that harbour porpoises can maintain many signal features such as signal duration and frequency content over a large dynamic range of source levels.

The source levels recorded in one of the study areas, Little Belt, were significantly higher than those recorded in the other two areas. We have no clear explanation for this. It could be a result of the extensive boat traffic in the Little Belt area, leading to increased background noise levels. However, there is no reason to believe that the background noise will change in the porpoises' frequency range (~120–140 kHz) and hence influence the porpoises' echo-to-noise ratio. Another reason could be that the clicks were, by chance, recorded more off-axis in the other two areas. In general, the porpoises seemed to be more vocal, less shy and easier to approach in the Little Belt area, thereby improving the chance of getting on-axis recordings. Finally, the animals in Little Belt were probably involved in more intense foraging compared with the porpoises in the other areas, and this activity may have triggered a much more intense biosonar activity.

In previous studies, where arrays have been used to record dolphin biosonar signal, a positive relationship between the source level and the range between the dolphin and the array has been reported (e.g. Au and Benoit-Bird, 2003). Such data have been interpreted as evidence for automatic gain control (AGC; a mechanism that regulates the amplitude of the perceived echo level, either by improving the hearing abilities or increasing the source level of the emitted signals, for varying ranges to the target) in the sound production or hearing system of odontocetes (Au and Benoit-Bird, 2003). Also, in our study, the highest apparent source levels are found at the greatest ranges from the array (Fig. 4). This could putatively be used as evidence of AGC. However, for such a conclusion to be valid, we must be certain that the porpoise is actually echolocating on the array and not just making an accidental scan across it. Also, it is crucial that the dynamic range of the recording system can handle both close and distant on-axis clicks without clipping them. In addition, a bias in the localization system towards longer distances may occur if the hydrophones were not perfectly aligned. Thus, a valid explanation for the observed increased ASL with range may be found without concluding that porpoises are using AGC. For example, it

turned out that the positive relationship between ASL and range in Fig. 4 within 30 m from the array in the Little Belt recordings was completely explained by clipping of received levels above ~172 dB re 1 μ Pa pp. More studies are needed on the target detection abilities of harbour porpoises to resolve this issue. The only study of this kind performed to date seems to indicate that there is no AGC in this species (Beedholm et al., 2006).

It is important to note that in previous field studies where AGC has been inferred (see Au and Benoit-Bird, 2003), it was not possible to confirm that the animals were echolocating towards the hydrophones, and therefore the variation in click source levels could not be discerned from the effect of recording the clicks at various degrees off the acoustic axis. In addition, it should be noted that the study of Au and Benoit-Bird also has the potential bias of larger localization errors at greater distances due to minor errors in the positions of the hydrophones, especially when recording off the array symmetry axis. The only study known to us where both the relative changes in output levels and the returning echo levels could be simultaneously estimated on a free-ranging odontocete (a ziphiid, *Mesoplodon densirostris*) did not show any clear indication of AGC (Madsen et al., 2005).

Improvement of net and fish detectability and passive acoustic monitoring due to an increased source level

The high source levels obtained in this study are important for understanding the foraging behaviour of wild harbour porpoises in terms of at which distance they may detect their prey. The results are also crucial for understanding mechanisms underlying the bycatch problem in terms of at which distances porpoises are able to detect gillnets. In addition, if wild harbour porpoises use considerably higher source levels than has been previously assumed, the distance at which acoustic data loggers can detect harbour porpoises will be significantly increased, thereby affecting the interpretation of data obtained from passive acoustic monitoring of this species.

It should be noted that the following calculated detection distances for harbour porpoises are only theoretically derived and that other parameters besides the source level may influence the detection ability of the porpoise.

In the only existing target detection experiment made with harbour porpoises, Kastelein et al. found that harbour porpoises could detect a 5.08 cm water-filled stainless-steel sphere at a maximum distance of 15.9 m (Kastelein et al., 1999). The harbour porpoise in these target detection trials was emitting clicks with source levels of 165–170 dB re 1 μ Pa pp.

In order to calculate the distance at which a harbour porpoise can detect a fish, we need to know the relationship between the echo energy received by the porpoise and the distance to the target. For this, the following equation is used (see Kastelein et al., 1999):

$$EE = SE - 40 \log(R) - 0.04(2R) + TS_E = SL_{pp} - 56.7 - 40 \log(R) - 0.08R + TS_E \quad (3)$$

Here, we use the relationship between source energy (SE) and

peak-to-peak source level ($SE=SL_{pp}-56.7$ dB) for harbour porpoises (Kastelein et al., 1999).

In the following, we assume that the ambient noise level is the same in our field recordings as in the target detection trials conducted by Kastelein et al. (Kastelein et al., 1999) so that the detection threshold is identical. In the study by Kastelein et al., the echo energy flux density at threshold was 27 dB re $1 \mu\text{Pa}^2\text{s}$. We may use this information to estimate the distance at which a porpoise can detect a fish. With a source level of 165 dB re $1 \mu\text{Pa pp}$ (Kastelein et al., 1999), Eqn 3 gives a detection distance of 10 m for captive porpoises to detect a fish of target strength -40 dB (similar to that of an adult herring). For a wild porpoise producing signals of a mean source level of 191 dB re $1 \mu\text{Pa pp}$, the detection distance increases to 40 m for detecting the fish, using Eqn 3. Thus, the distance over which a porpoise can detect a fish will increase by up to four times when increasing the source level from 165 to 191 dB re $1 \mu\text{Pa pp}$.

One may use a similar argument to estimate how the new source level estimates may change the detection distance to gillnets. Kastelein et al. addressed the detection distance of porpoises to bottom-set gillnets (Kastelein et al., 2000). They calculated the maximum detection distance to be 3–6 m using source level data from captive porpoises combined with the results of the above-mentioned detection experiments (Kastelein et al., 1999). The detection distance of wild porpoises can be calculated as follows with the help of data from Kastelein et al. (Kastelein et al., 2000) and the data presented here. Eqn 3 is used twice, both for the data obtained in captivity ('old') and the data obtained in the field ('new'). Assuming that the echo level at threshold is the same in the field as in the study by Kastelein et al. (Kastelein et al., 1999), we can reduce the two equations to one, and the TS can be eliminated. This gives the following equation:

$$TL_{\text{new}} = (SE_{\text{new}} - SE_{\text{old}} + 2TL_{\text{old}})/2 = [SE_{\text{new}} - SE_{\text{old}} + 40 \log(R_{\text{old}}) + 0.04(2R_{\text{old}})]/2. \quad (4)$$

The new detection range can now be deduced from TL_{new} . Using source levels of 165 dB re $1 \mu\text{Pa pp}$ ('old') and 191 dB re $1 \mu\text{Pa pp}$ ('new'), the detection distance will theoretically increase to 13–26 m, or at least four times compared with the detection distances estimated by Kastelein et al. (Kastelein et al., 2000).

The results presented here on source levels of wild harbour porpoises also affect the interpretation of data obtained with acoustic data loggers. The distance (R) over which an acoustic data logger can detect a porpoise will depend on the detection threshold (DT) of the detector and can be estimated from the passive sonar equation:

$$DT = SL - TL = SL - 20 \log(R) - 0.04R. \quad (5)$$

In the following calculations, we use data from an acoustic data logger called a T-POD (Chelonia Ltd, Long Rock, Cornwall, UK). For this equipment, a minimal detection threshold of 123 dB re 1 Pa pp and a maximal threshold of 132 dB re 1 Pa pp were measured by Kyhn (Kyhn, 2006). Source levels of 165 dB re $1 \mu\text{Pa pp}$ [captive source level

Table 2. Comparison of estimated detection distances from wild and captive harbour porpoises to a fish, a gillnet and for an acoustic data logger

	Wild porpoises	Captive porpoises*
Fish	40 m	10 m
Gillnet	13–26 m	3–6 m
T-POD	260–400 m	38–85 m

The calculations are based on assumptions described in the text and should only be regarded as very coarse estimates.
*Data from Kastelein et al. (Kastelein et al., 1999; Kastelein et al., 2000) was used in the calculations.

measured by Kastelein et al. (Kastelein et al., 1999)] and 191 dB re $1 \mu\text{Pa pp}$ (mean source level from wild porpoises found in the present study) were used. By inserting this data into Eqn 5 we can numerically estimate the maximal distance (R) over which a T-POD can detect a porpoise. For the minimum T-POD threshold, this gives an increased detection distance from 85 to 400 m when increasing the source level from the captive to the wild situation. For the maximal threshold, the corresponding increase in detection distance is from 38 to 260 m.

Thus, overall the harbour porpoises should be able to detect or be detected over significantly larger distances than has been previously assumed (summarized in Table 2). It should be noted that there is likely to be a large dynamic range in the emitted source levels and thereby also in the ranges at which fish and nets can be detected by the porpoises and the ranges at which automatic detectors can detect the animals.

Transmission loss of harbour porpoise signals and measurement accuracy

The transmission loss is a central factor when calculating the energy flux density of a sound source. Several formulas are known for estimating the transmission loss in different propagation conditions. Most often the transmission loss model for spherical spreading and absorption [$TL=20\log(R)+R\alpha$] is used when calculating the source level of echolocating odontocetes (Au, 1993). This simple propagation model states that the energy generated by the source is radiated, as if it was distributed over the surface of a sphere surrounding the source (Urlick, 1983). It is usually assumed that the spherical transmission loss model is accurate up to a source-received distance of at least a few tens of metres when recording biosonar signals in shallow waters. Beyond this the signal will start to interact with the water surface or the bottom.

The accuracy in the source levels derived in this study depends on the ranging accuracy of the localization system and on the accuracy in the assumed transmission loss model (spherical spreading and absorption). We therefore tested if the spherical spreading and absorption model for transmission loss was applicable to our data.

The transmission loss measurements were within 4 dB of those predicted by the spherical spreading and absorption

[$20\log(R)+R\alpha$] model within a sound source-array distance of 50 m (Fig. 3A). Even though the transmission loss may vary significantly when the source or the hydrophones are shallower or deeper than is assumed in Fig. 3A, it seems safe to apply the spherical spreading and absorption transmission loss model to all data analysed in this study.

The transmission loss used in the calculation of the source level is back-calculated from the estimated range between the porpoise and the array. Thus the accuracy of the transmission loss depends on the accuracy of the range estimate. The accuracy of the range estimation will diminish with increasing distance between the porpoise and the array. The accuracy of the localization of the porpoise and hence the range was evaluated by comparing the RMS error between the measured range (determined with a rope) and the acoustic range (estimated from the TOADs) during the transmission loss experiment. The RMS error (RMS taken of the relative error) was very similar for the 4-hydrophone array and the 3-hydrophone array within 25 m from the array (Fig. 3B). Beyond this range the extra hydrophone gave a more accurate estimation of range and therefore a smaller error in the derived source levels than by using only three hydrophones. At a 50 m range, there was an RMS error of 28% for the 4-hydrophone array and 52% for the 3-hydrophone array. The impact on the transmission loss estimates due to the error in the measured ranges increases with increasing distance between the porpoise and the array (Fig. 3C). There is hardly any variation in the transmission loss (≤ 2 dB) at a distance up to 25 m. At a distance of 50 m there is a variation of 5 dB for the 4-hydrophone array and a variation of 8 dB for the 3-hydrophone array. These values are regarded as the result of a worst-case scenario, as they are calculated from the maximum measured ranging deviation between the acoustic range and the range measured with a rope. In addition, an omnidirectional sound source was used for the calibrations whereas harbour porpoise clicks are very directional. An omnidirectional sound source will cause more interactions between sound paths reflected at the surface and the bottom and the direct sound path. Therefore, probably both the localization errors and the deviations from a spherical spreading transmission loss given here are significantly exaggerated. Adding the anomaly in transmission loss to the ranging error, this implies that all apparent source levels reported here are measured with a total error of less than 10 dB {calculated as $[(TL \text{ error})^2 + (\text{ranging error})^2]^{1/2}$ } at a distance of 50 m and for shorter distances this is considerably less.

Inter-click intervals

The preferred ICI by harbour porpoises in the presented recordings was ~60 ms (Fig. 6), which is similar to that found in experiments with captive animals. Teilmann et al. found in a detection study that the porpoise preferred a mean ICI of 59 ms (Teilmann et al., 2002). Preference for a certain ICI is also found in other odontocete species, e.g. Madsen and co-workers have shown that foraging beaked whales prefer a certain ICI (~400 ms) in their search and approach phase (Madsen et al., 2005).

In a study conducted on actively swimming harbour porpoises, Verfuß et al. measured ICIs between 10 and 120 ms from a swimming porpoise in a pool (Verfuß et al., 2005). They showed that there was a clear relationship between the assumed target distance and the ICI. There is, however, a great variation in the ICIs both in the presented field recordings and in the study by Verfuß et al. on captive animals. Therefore more studies are needed to elucidate the relationship between target distance and the ICI.

We thank M. F. Christoffersen, M. Hansen, M. Wilson, H. Schack, P. T. Madsen, P. Finamore, G. Friis, V. Damm and L. Flensburg for assistance in the field and P. T. Madsen, L. Miller, B. Møhl and V. Hepworth for lending us equipment. J. Jensen constructed the array rig, and the amplifier unit was designed by N. U. Kristiansen. We thank P. T. Madsen and two anonymous reviewers for comments on an earlier draft of this paper. This work was funded by Aage V. Jensen's Foundation and the Danish Forest and Nature Agency. M. Wahlberg was supported by the Carlsberg Foundation and the Oticon Foundation.

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