

Asymmetry and dynamics of a narrow sonar beam in an echolocating harbor porpoise

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A key component in the operation of a biosonar system is the radiation of sound energy from the sound producing head structures of toothed whales and microbats. The current view involves a fixed transmission aperture by which the beam width can only change via changes in the frequency of radiated clicks. To test that for a porpoise, echolocation clicks were recorded with high angular resolution using a 16 hydrophone array. The beam is narrower than previously reported (DI = 24 dB) and slightly dorso-ventrally compressed (horizontal -3 dB beam width: 13° , vertical -3 dB beam width: 11°). The narrow beam indicates that all smaller toothed whales investigated so far have surprisingly similar beam widths across taxa and habitats. Obtaining high directionality may thus be at least in part an evolutionary factor that led to high centroid frequencies in a group of smaller toothed whales emitting narrow band high frequency clicks. Despite the production of stereotyped narrow band high frequency clicks, changes in the directionality by a few degrees were observed, showing that porpoises can obtain changes in sound radiation.

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I. INTRODUCTION

All microbats (Microchiroptera) and toothed whales (Odontoceti) investigated so far use echolocation as a primary sensory modality for spatial orientation and food acquisition (Griffin, 1958; Au, 1993). When toothed whales echolocate, ultrasonic clicks of very high intensity are produced within the nasal complex by forcing pressurized air past pairs of phonic lips (Cranford *et al.*, 1996; Cranford, 2000). The produced clicks propagate through a rostrally placed fatty melon into the water. Returning echoes from objects in the water column are subsequently transmitted to the inner ear through fat bodies in the lower jaw and other regions of the head (Au, 1993; Cranford *et al.*, 1996; Ketten, 2000). Successful echolocation of a prey item requires that the returning echo is received with a sufficient signal to noise ratio to allow for detection in the auditory system, calling for high source levels and acute hearing.

The acoustic signals of echolocating toothed whales are emitted in a highly directional beam. The higher the directionality the larger the source level for a given amount of radiated energy, leading to a longer detection range of prey on the acoustic axis for a noise limited situation. In addition, a directional sound beam reduces the clutter and reverberation from, e.g., the surface or bottom. The directionality of echolocation clicks is thus an important parameter for evaluating the performance and evolutionary driving forces of toothed whale biosonar systems (Au, 1993; Madsen and Wahlberg, 2007).

In toothed whales the beam patterns of echolocation clicks have been measured for a number of species, including the bottlenose dolphin, *Tursiops truncatus* and *T. aduncus* (Au *et al.*, 1978; Au *et al.*, 1986; Au, 1993; Wahlberg *et al.*, 2011), the beluga, *Delphinapterus leucas* (Au *et al.*, 1987), the false killer whale, *Pseudorca crassidens* (Au *et al.*, 1995), the white-beaked dolphin, *Lagenorhynchus albirostris* (Rasmussen *et al.*, 2004), the sperm whale, *Physeter macrocephalus* (Mohl *et al.*, 2003; Zimmer *et al.*, 2005b), Cuvier's beaked whale, *Ziphius cavirostris* (Zimmer *et al.*, 2005a), finless porpoise, *Neophocaena phocaenoides* (Akamatsu *et al.*, 2005), Peale's dolphin, *Lagenorhynchus*

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australis (Kyhn *et al.*, 2010), Commerson's dolphin *Cephalorhynchus commersonii* (Kyhn *et al.*, 2010) and the harbor porpoise, *Phocoena phocoena* (Au *et al.*, 1999) (Table I).

The beam width is either parameterized by the directivity index (DI), expressing the ratio between the source level of a directional and an omnidirectional transducer radiating the same acoustic power, or by the -3 dB (half power) beam width (BW) in degrees. The -3 dB BW is defined as the angle between the directions at which the sound pressure level is reduced by 3 dB to either side of acoustic axis in the horizontal or vertical plane. The measured beams of most species are narrow and similar in beam width, with the -3 dB BW ranging from 6.5° in the beluga to $9\text{--}10^\circ$ in the bottlenose dolphin (Au *et al.*, 1987; Au, 1993; Wahlberg *et al.*, 2011). The harbor porpoise is an exception in that it is reported to have a wider beam with a -3 dB BW of 16° (Au *et al.*, 1999). Most sonar beams described to date are rotational symmetric, but for many of the quoted estimates, the methodologies have not allowed for detection of rotationally asymmetric beams. Only for the false killer whale a lateral compressed beam has been found with a vertical -3 dB BW of 9.7° and a horizontal -3 dB BW width of 6.2° (Au *et al.*, 1995).

The width of the sound beam depends on a range of factors, including the frequency content of the radiated signals, the size and morphology of the skull, the melon and the air

sacs connecting to the phonic lips and nasal passages (Aroyan *et al.*, 1992; Au *et al.*, 1995; Cranford, 2000). The beam pattern may be modeled by the one generated by a flat circular piston oscillating in an infinite baffle. This model was introduced by Strother and Mogus (1970) for bats and by Au *et al.* (1978) for toothed whales. Such a model is attractive due to its relative simplicity, and it matches measured beam characteristics fairly well (Au, 1993; Madsen and Wahlberg, 2007; Beedholm and Møhl, 2006). Based on this model, directionality depends solely on the spectrum of the emitted signal and the aperture of the emitter. This allows for computation of what has been coined an equivalent aperture providing the size of a flat piston with the same radiation pattern as that of the animal in question for a given sound. Thus, the directionality of an emitted signal increases when the transducer aperture increases and/or higher frequencies are emitted (Madsen *et al.*, 2004; Urick, 1983).

A group of smaller toothed whales, the Phocoenidae, *Cephalorhynchus spp.* dolphins, the pygmy and probably dwarf sperm whales (Kogiidae) all emit narrowband high frequency (NBHF) clicks (Madsen *et al.*, 2005). Since directionality depends on the relation between emitter size and frequency, smaller toothed whales using a high frequency emphasis in their signals may at least in part be able to compensate for their size and be able to generate the same

TABLE I. Summary of toothed whale transmission beam pattern measurements.

Species	Horizontal -3 dB BW	Vertical -3 dB BW	Directivity index [dB]	Source
Sperm whale	n.a	n.a	27	Mohl <i>et al.</i> (2003)
<i>Physeter macrocephalus</i>				
Sperm whale	n.a	n.a	26.7	Zimmer <i>et al.</i> (2005b)
<i>Physeter macrocephalus</i>				
Cuvier's beaked whale	n.a.	n.a.	>25 .	Zimmer <i>et al.</i> (2005a)
<i>Ziphius cavirostris</i>				
Beluga	6.5	6.5	32.1	Au <i>et al.</i> (1987)
<i>Delphinapterus leucas</i>				
Bottlenose dolphin	9.7	10.2	25.8	Au (1993)
<i>Tursiops truncatus</i>				
Bottlenose dolphin	n.a.	n.a.	26.5	Au <i>et al.</i> (1986)
<i>Tursiops truncatus</i>				
Bottlenose dolphin	9.8	10	n.a	Au <i>et al.</i> (1978)
<i>Tursiops truncatus</i>				
Bottlenose dolphin	9	9	26	Wahlberg <i>et al.</i> (2011)
<i>Tursiops truncatus</i>				
Bottlenose dolphin	8	8	29	Wahlberg <i>et al.</i> (2011)
<i>Tursiops aduncus</i>				
False killer whale	6.2	9.7	28.5	Au <i>et al.</i> (1995); Au <i>et al.</i> (1999)
<i>Pseudorca crassidens</i>				
(Type IV signals)				
White-beaked dolphin	8	8	29	Rasmussen <i>et al.</i> (2004)
<i>Lagenorhynchus albirostris</i>				
Peale's dolphin	n.a	n.a	25	Kyhn <i>et al.</i> (2010)
<i>Lagenorhynchus australis</i>				
Commerson's dolphin	n.a	n.a	25	Kyhn <i>et al.</i> (2010)
<i>Cephalorhynchus commersonii</i>				
Harbor porpoise	16.5	16.5	22.1	Au <i>et al.</i> (1999)
<i>Phocoena phocoena</i>				
Harbor porpoise	13.1	10.7	24	this study
<i>Phocoena phocoena</i>				

directionality as larger species using a lower frequency emphasis. Recent field measurements of two other NBHF species showed that their beam widths are indeed similar to the ones of other smaller toothed whales (Kyhne *et al.*, 2010). A previous study on the harbor porpoise, however, suggests that this NBHF species has the widest beam of all toothed whales investigated (Au *et al.*, 1999).

Moore *et al.* (2008) showed that the bottlenose dolphin can change its beam width and steer its beam (i.e., move the acoustic axis of the beam relative to its body axis) when faced with a task that requires the detection of objects placed off the acoustic axis. A variable beam width would seemingly be advantageous during prey pursuit and could at least partially be caused by shifts in the frequency of the emitted click (Madsen *et al.*, 2004). Recently Jakobsen and Surlykke (2010) have shown that bats widen their beam during the last phase of prey pursuit by lowering the frequency emphasis of their calls. A wider beam allows the bat to track insects at close distances despite escape manoeuvres of the prey. It is not clear how, to what degree and with what purpose toothed whales may be doing the same, and up until the study of Moore *et al.* (2008) beam dynamics of toothed whales have only been considered to relate to changes in frequency (Au *et al.*, 1995; Madsen *et al.*, 2004).

Such lack of insight relates to the fact that most previous studies on the beam characteristics of odontocetes average over many measurements, making it impossible to investigate beam dynamics. In this study we wished to address if a NBHF species, such as a porpoise emitting relatively stereotyped signals, can also change its beam pattern when echolocating.

Using a 16-channel hydrophone array we here report the vertical and horizontal beam pattern of an echolocating harbor porpoise with high angular resolution. We show that the porpoises beam is narrower than previously measured, dorso-ventrally compressed and dynamic.

II. MATERIALS AND METHODS

A. Hydrophone array and recording system

Recordings were made with 16 individually calibrated Reson TC-4013 hydrophones arranged in a plus-shaped array (four arms separated by 90°) with one central hydrophone and three hydrophones on each arm (upwards, downwards, left and right). The hydrophones were located at distances of 10.6, 17.5, and 35.2 cm in each direction from the central hydrophone, corresponding to 3°, 5°, and 10° off center when the clicking porpoise is 2 m away. The three arms extending upwards, left and right, had an additional hydrophone 53.5 cm from the central hydrophone, 15° off center (Fig. 1). The array was made of solid PVC pipes with a diameter of 3 cm. The hydrophones were mounted with their symmetry axes oriented vertically at the end of 7 cm long (1.5 cm diameter) PVC pipes extending from the array frame. In this way any possible weak reflections from the array would arrive more than 94 μs after the direct path, and thus after the main part of the porpoise click. Signals were amplified by 38 dB and filtered using a custom-made 16 channel amplifier and filter, and then simultaneously A/D

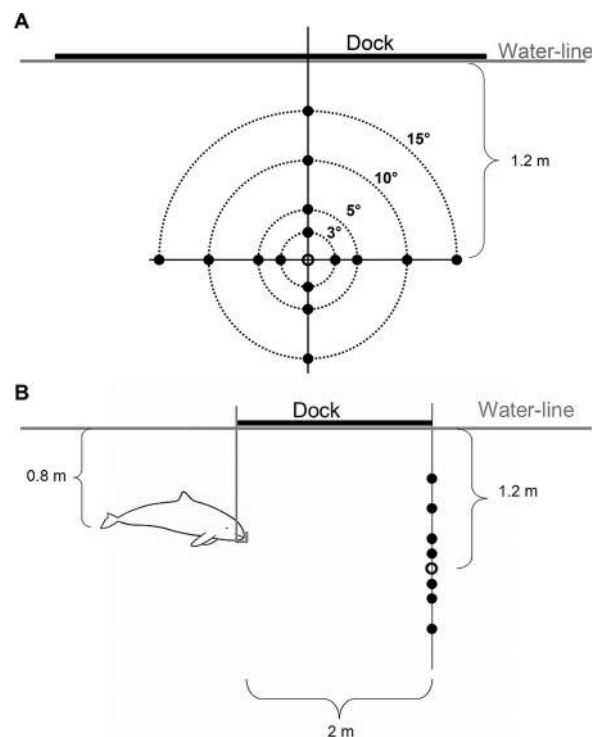


FIG. 1. Recording set-up. (a) Animal's perspective. Degrees are relative to the central hydrophone and when the animal is stationed 2 m in front of the array. Central hydrophone is indicated with an unfilled circle and peripheral hydrophones with filled circles. (b) Side view. Animal was positioned at a depth of 0.8 m and pointing downwards, the central hydrophone was at a depth of 1.2 m.

converted with 16 bit resolution at a sampling rate of 500 kHz per channel (National Instruments PXI-6123). An underwater video camera (Profiline CTV7040) was used to monitor the harbor porpoise movements on station. The signal from the video camera was digitized with a Sony GV-D1000E DV Video Walkman. All 16 channels from the hydrophone and the video recordings were saved in a ring buffer, and after triggering the system the past 4 s of recordings were stored on a laptop computer using a customized version of SIMI Motion (version 7.3 build 269).

B. Calibration of the hydrophones

The 16 hydrophones were calibrated in an anechoic tank using a B&K 8105 hydrophone as a transducer and a B&K 8103 hydrophone as the standard. Calibration was made in the frequency range between 110 and 150 kHz, which is the relevant range for harbor porpoise signals. The hydrophones had an average sensitivity of -212 dB re $1V/1\mu Pa$ at 130 kHz and each one had a flat (within 2 dB) frequency response within the tested frequency range. The difference between the hydrophone of highest and lowest sensitivity was 1.3 dB. To correct for sensitivity differences due to hydrophone attachment or array arrangement, we placed an omnidirectional transducer (HS 150, Sonar Research & Development Ltd, Beverley, UK) 2 or 4 meters in front of the array on each recording day and emitted porpoise-like clicks (15 cycle pulses at 130 kHz). These signals were then used

to normalize all hydrophone sensitivities with respect to the center hydrophone during post processing.

C. Animal and training

The trials were made at Fjord&Bælt in Kerteminde, Denmark, where four harbor porpoises are housed in an outdoor facility. The facility is connected to the harbor of Kerteminde through nets. Wind and current conditions during recordings were very calm, resulting in good underwater visibility. One 12 year old male harbor porpoise (FBC-01) was trained to station voluntarily in a u-shaped chin rest 2 m in front of the hydrophone array with the tip of the rostrum touching a small square PVC target. The depth of the central hydrophone of the array was 1.2 m, and the depth of the target was 0.8 m, when the animal was on station it was pointing downwards. The correct position of the animal is referred to as “on station” hereafter. The animal was sent to station by the trainers and observed visually from above by the trainers, and with an underwater video camera, attached to the array and facing the animal, by the experimenter. The visual observations ensured that the animal was on station during the recordings. No behavioral tasks were required from the animal during the recordings, but it nevertheless echolocated towards the hydrophone wall.

D. Analysis

Data analysis was made using routines written in MATLAB 7.0 (MathWorks, Inc.). Clicks were detected using a threshold based peak detector. Only clicks with a source level of 132 dB re 1 μ Pa (peak to peak) or higher were analyzed. The source level is defined as the sound intensity back-calculated to 1 m range on the acoustic axis (Urick, 1983). The intensity in any other direction of the sound source we denote the apparent source level (ASL) sensu Møhl *et al.* (2003). The apparent source level in units of peak to peak was measured for each detected click of the 16 channels. The clicks with a maximum apparent source level on the central hydrophone (after being compensated for the difference in sensitivity between the receivers) were regarded as being recorded on the acoustic axis and saved for further analysis. The beam patterns were plotted as the apparent source level as a function of the angle relative to on axis. A piston modeled beam pattern was fitted to the measured beam patterns using the equations in Au (1993), and the directionality index was estimated using the equation of Møhl *et al.* (2003).

III. RESULTS

When stationed in the U-shaped chin rest two meters in front of the array, the porpoise mostly emitted clicks with a high repetition rate and low source level (SL) interspersed with a few clicks emitted at lower repetition rates and higher SL. At high repetition rates, the inter-click intervals varied between 2.5 and 15 ms. Out of a total number of 74 trials, two trials resulted in recordings of on-axis click trains which are characterized by consecutive signals with maximum sound level on the central hydrophone. In these clicks a maximum variation in source level of 8 dB (132–140 dB re

1 μ Pa_{pp}) was measured. The average click (N= 464) signal waveforms did not differ when recorded off-axis at the angles covered here [Figs. 2(a) and 3] and the averaged spectra [Fig. 2(b)] show that the spectral composition is very similar in the forward direction out to 15° off axis.

For each of the on-axis clicks the apparent source level (ASL) measurements with the nine hydrophones in the horizontal plane and the eight hydrophones in the vertical plane were used to determine a horizontal and a vertical beam. Overlaying the beam patterns of all 464 on-axis clicks show variations of the ASL relative to the on-axis SL at each hydrophone. This variation increases with increasing off-axis angle [Figs. 4(a), 4(c), 5(a) and 5(c)]. Part of the observed variations can be explained by the spatial sampling. The hydrophone arrangement with the first ring of hydrophones three degrees from the central hydrophone led to clicks directed up to 1.5° away from the central hydrophone to be classified as on-axis. Since the animal was not fixed but free to move, movements in the range of $\pm 1.5^\circ$ increased the variability of the beam. To account for these variations we made cubic spline interpolations over the nine beam measurement points in the horizontal plane and eight in the vertical plane. The interpolated beam maximum was, as expected, not exactly on the central hydrophone but often off by $\pm 1.5^\circ$ [Figs. 6(a) and 6(c)]. We assumed that this

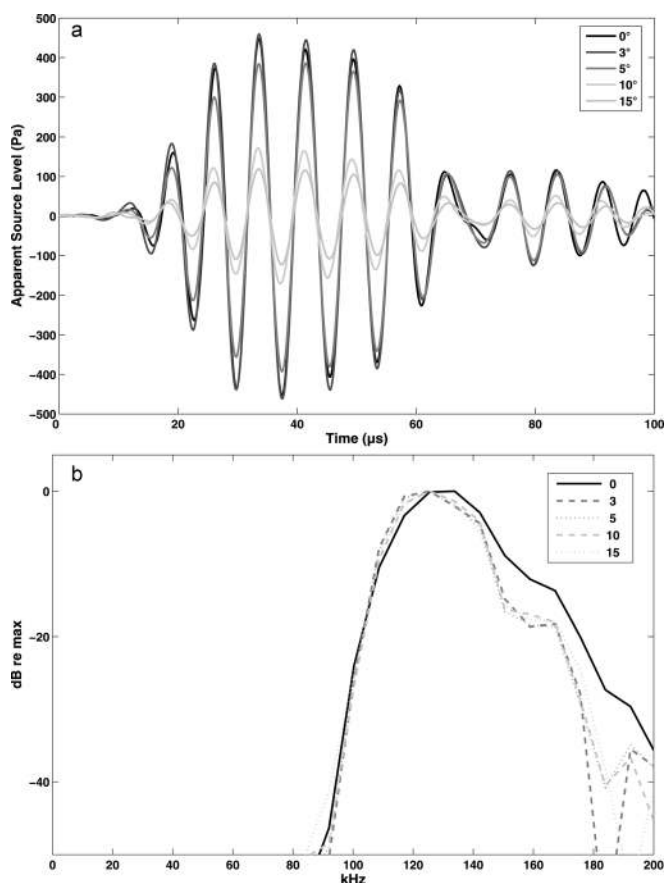


FIG. 2. (a) Averages of 464 harbor porpoise clicks recorded at five different angles (0°, 3°, 5°, 10°, and 15°) relative on axis. Sampling frequency was 500 kHz and signals were interpolated with a factor of 10. (b) Mean normalized spectra of 464 signals from Fig. 2(a). FFT size 600, Hanning window, sampling frequency 500 kHz.

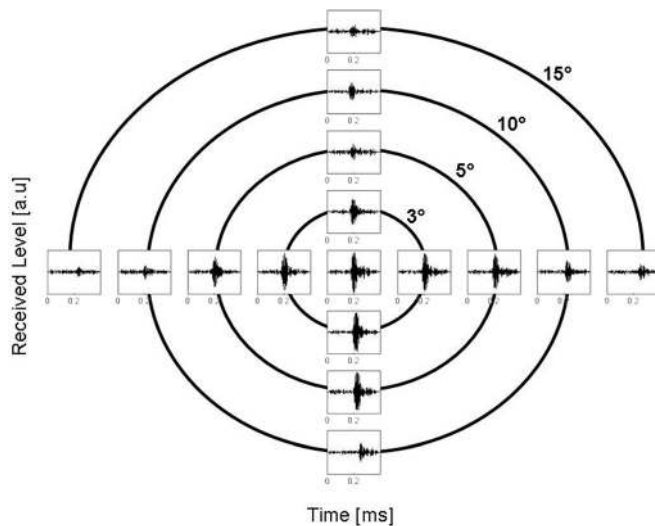


FIG. 3. Received harbor porpoise echolocation signals on each hydrophone of the array, as seen from the animal's perspective at 2 m range.

jitter was caused by small variations of the direction of the animal's acoustic axis and we accounted for these minor movements of the animal in the following way: For each click, the vertical and horizontal beam patterns were interpolated with cubic spline interpolation and then aligned to the interpolated maximum [Figs. 4(b), 5(b) and 6(b), 6(d)]. A composite beam pattern was made by averaging over these interpolated and aligned 464 beam patterns [Figs. 4(d) and 5(d)].

After accounting for the beam jitter within ± 1.5 the click amplitudes still showed some variation which increased with increasing off-axis angle. Additionally, the horizontal and the vertical beam patterns were not symmetrical around the acoustical axis [Figs. 4(d) and 5(d)].

The average horizontal one-sided -3 dB beam width was 6.2° (std: 0.84°) to the left and 6.9° (std: 1.1°) to the right of the acoustic axis. The average one-sided vertical -3

dB beam width was 4.8° (std: 1.3°) above and 5.8° (std: 1.1°) below the acoustic axis. The average -3 dB horizontal beam width was thus 13.1° (std: 1.2°) in the horizontal plane and 10.7° (std: 0.99°) in the vertical plane, resulting in a slight, but significant dorso-ventrally compressed beam (paired t test, $p < 0.001$, d.f. = 463).

The porpoise beam width was not fixed but showed some variation: While the -3 dB beam width to the left of the acoustic axis was constant for clicks 48–77, an increase of 2° and more could be seen on the right side of the beam (Fig. 6(b)). This increase exceeds 2 standard deviations.

The click amplitudes measured in the vertical plane with the upper 15° hydrophone indicate the presence of a sidelobe (Fig. 5). We have had no hydrophone at the lower 15° position so that we can make no statement on the vertical beam shape below 10° . Within the $\pm 15^\circ$ measuring range, no side lobe in the horizontal beam pattern was indicated (Fig. 4).

The best fit of the data to a modeled flat, circular piston emitting a porpoise click in an infinite baffle was obtained with a horizontal equivalent aperture of 6.5 cm and a vertical equivalent aperture of 8.3 cm (Fig. 7). The variability seen in the data could be explained by aperture changes from 5.5 to 7.4 cm in the horizontal plane and from 7.1 to 9.6 cm in the vertical plane.

IV. DISCUSSION

A. Toothed whales have similar beam widths across taxa

We show here that the harbor porpoise echolocation beam is narrower than previously reported and thus not as different from other toothed whales as previously published data would indicate. *Au et al. (1999)* reported that the harbor porpoise beam is the broadest of all toothed whales investigated so far with a -3 dB beam width of 16° in both the vertical and horizontal plane, corresponding to a DI of 22.1 dB.

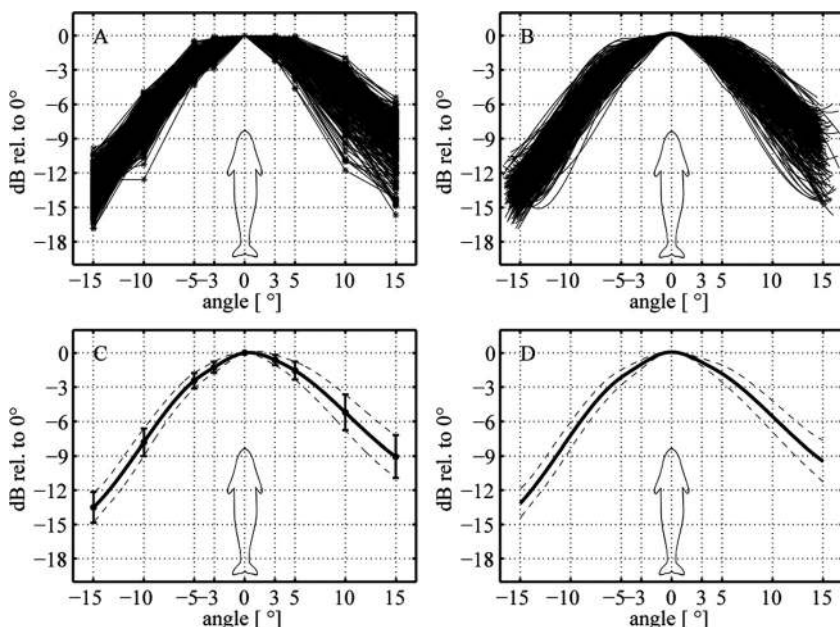


FIG. 4. (a) Horizontal beam pattern for 464 on-axis clicks of a harbor porpoise. (b) Interpolated and shifted horizontal beam pattern for all on-axis clicks. (c) Averaged horizontal beam pattern. Error bars show mean and 1 standard deviation of the measurements for each receiver. Black solid line is the averaged interpolated beam pattern. One standard deviation of all interpolated beams is depicted by the black dashed line. (d) Averaged horizontal beam pattern corrected for scanning movements. Dashed lines show 1 standard deviation. By correcting for the scanning, the standard deviation is reduced.

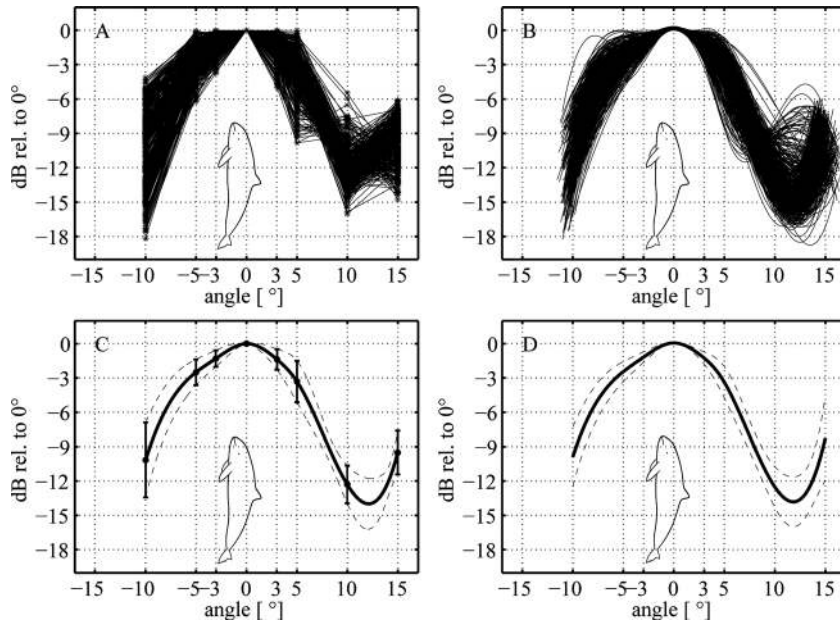


FIG. 5. (a) Vertical beam pattern for 464 on-axis clicks of a harbor porpoise. (b) Interpolated and shifted vertical beam pattern for all on-axis clicks. (c) Averaged vertical beam pattern. Error bars show mean and one standard deviation of the measurements for each receiver. Black solid line is the averaged interpolated beam pattern. The 1 standard deviation of all interpolated beams is depicted by the black dashed line. (d) Averaged vertical beam pattern corrected for scanning movements. Dashed lines show standard deviation. By correcting for the scanning, the standard deviation is reduced.

We found the beam to be narrower, especially in the vertical plane with a -3 dB beam width of 10.7° but also in the horizontal plane with a -3 dB BW of 13.1° , corresponding to a DI of 24 [derived using the approximate relationship, $V_{3dB} \approx 185^\circ \times 10^{(-DI/20)}$ (Lurton, 2002; Zimmer *et al.*, 2005a)]. This indicates that the beam is in fact only slightly broader than the beam of most other smaller toothed whales (Au, 1993; Wahlberg *et al.*, 2011; Kyhn *et al.*, 2010). This is lending weight to the contention that toothed whale sonars have been faced with an evolutionary driving force to achieve high directionality in order to increase the source level in the forward direction and to reduce reflections from the periphery. Reported beam width in all species ranges from 6.5° for the beluga (Au *et al.*, 1987) to 13.1° in the horizontal plane of the harbor porpoises, corresponding to a DI difference of approximately 9 dB. Similar echolocation beam directionalities across species of various sizes have been recently discovered in bats. Five species ranging in size from 8 to 26 g and in the main frequency emitted from

20–55 kHz, all have strikingly similar directionalities, since small bats echolocate at higher frequencies (Jakobsen, 2010). It is intriguing that species living in extremely different acoustic environments all seem to have ended up with similar beam patterns. This seems to hold true both for across bat species as well as across smaller toothed whales.

The use of high frequencies around 130 kHz generates a narrow transmission beam for the many small NBHF species. Simultaneously, echolocation clicks at these high frequencies make NBHF species inaudible to a major predator, the killer whale (*Orcinus orca*). Whether predation or obtaining high directionality (or both) is the major reason for the use of high frequencies is currently not known. The present data strongly indicate that all smaller toothed whales investigated have surprisingly similar beam widths across taxa and habitats, and that the achievement of a narrow beam therefore is at least in part responsible for the high centroid frequencies of the small NBHF species (Kyhn *et al.*, 2010). The differences in beam width between this study and the one by Au *et al.* (1999) can

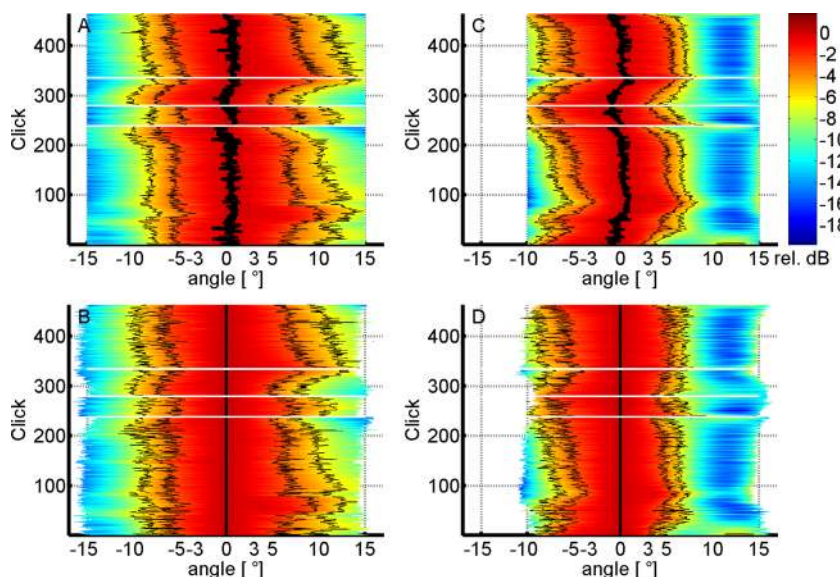


FIG. 6. (Color online) (a) Interpolated horizontal beam pattern for 464 harbor porpoise clicks (click # on y axis). Fat black line shows direction of interpolated maximum, thin black lines -3 dB and -6 dB BW. White horizontal lines represent beginning of new on-axis click train. The animal's beam is on average 0.5° directed to the right. (b) Beam patterns shifted so that direction of maximal intensity is at 0° , i.e., accounting for the scanning movements of the animal. (c) Interpolated vertical beam pattern for each click (click # on y axis). Fat black line shows direction of interpolated maximum, thin black lines -3 dB and -6 dB BW. White horizontal lines represent beginning of new on-axis click train. Again the beam is often more off-axis before and after it is considered to be on-axis. (d) Beam patterns shifted so that direction of maximal intensity is at 0° , i.e., accounting for the scanning movements of the animal.

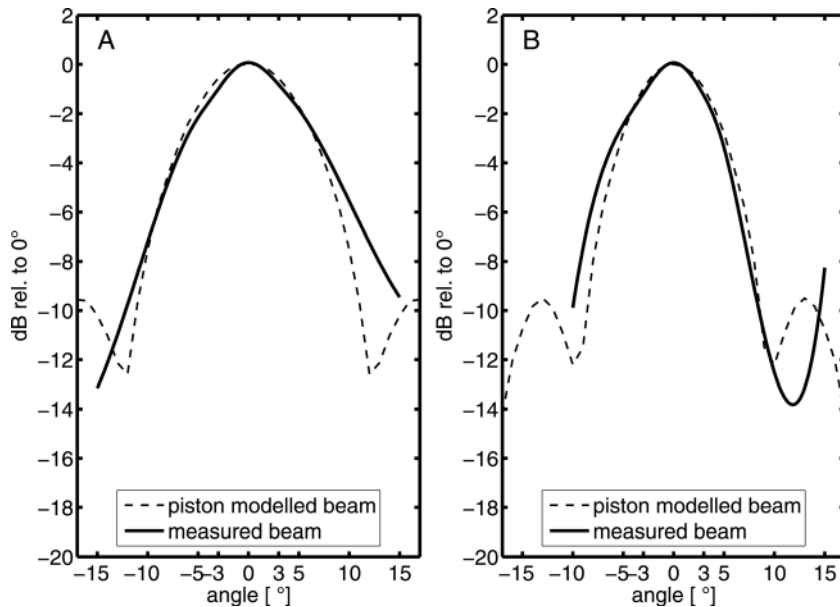


FIG. 7. The measured harbor porpoise transmission beam pattern compared to a modeled beam pattern using a porpoise click emitted by an oval piston with an aperture of 6.5 cm in the (a) horizontal and 8.3 cm in the (b) vertical plane.

possibly be explained by a number of methodological differences. By using more receivers in each plane we achieve a higher angular resolution. The use of a linear array (vertical or horizontal) did not make it possible for *Au et al. (1999)* to determine whether the acoustic axis of the beam is centered in both dimensions simultaneously without using a series of other criteria (*Madsen and Wahlberg, 2007*). Moreover, by using a hoop, the position of the animal might have varied between trials resulting in a larger beam width when averaging. It is extremely unlikely, however, that a varying range between animal and array could have been large enough to significantly affect the beam width measurements. By measuring the beam in both dimensions simultaneously we ensured that we recorded the beam on-axis and only analyzed clicks where the ASL was highest on the central hydrophone (i.e., ASL = SL). The angular distance between the central hydrophone and the first ring of hydrophones surrounding was 3° [Fig. 1(a)]. Thus clicks directed up to 1.5° off-axis in any direction could be classified as on-axis, clicks that were directed further away from the center were not considered for further analysis. This very strict criterion allows us to reduce the apparent variability in the beam width and pattern measurements compared to previous studies. In the subsequent analysis we measured the vertical and horizontal -3 dB beam width for each click simultaneously and then averaged the beam width for each dimension, in comparison to averaging over measurements at one receiver and then computing a beam width from the composite beam pattern (*Au et al., 1987; Au et al., 1999*). In addition, we cannot exclude that the different results between us and those of *Au et al. (1999)* could be due to individual differences between the animals investigated or the context in which they were recorded. For example, a larger transmitting aperture will lead to a narrower beam for the same radiated frequency. The animal under investigation here was 12 years old whereas the animal studied by *Au and colleagues* was younger and smaller (*Au et al., 1999*). In fact, differences in beam width have been found when looking at different individuals of bottlenose dol-

phins. However, these differences were on the order of less than 1° (*Au, 1993; Au et al., 1978*), and it is therefore unlikely that individual differences alone resulted in a 6° narrower beam width.

B. The beam is slightly dorso-ventrally compressed

The harbor porpoise echolocation beam is not rotational symmetric as previously suggested (*Au et al., 1999*), but rather dorso-ventrally compressed. Most studies on toothed whales beam patterns, including the harbor porpoise, report or assume that the beam had the same width in the vertical and in the horizontal plane (*Au et al., 1978; Au, 1980; Au et al., 1987; Au et al., 1999; Zimmer et al., 2005b*). Our results show a slightly broader beam in the horizontal plane than in the vertical plane. That raises the question if such a difference is the result of a functional driving force or simply a passive consequence of the functional anatomy of the porpoise head. It may be speculated that it is an evolutionary advantage for a shallow water forager such as the harbor porpoise to have a dorso-ventrally compressed beam. Since porpoises mainly swim with their dorsal side oriented upwards (*Akamatsu et al., 2010*), this beam shape would lead to a reduction of especially bottom reflections while still allowing a wider beam in the horizontal plane. By this adaptation, the amount of reverberation from the sea bed could be reduced while still ensonifying a reasonably large volume of water in search for prey. The only other species for which a non-rotational symmetric beam was reported was the false killer whale with a beam narrower in the horizontal (-3 dB BW of 6.2°) than in the vertical plane (-3 dB BW of 9.7°) (*Au et al., 1995*). This species, an open water forager, will not have an obvious advantage from reducing bottom reflections. The differences in beam shape between the harbor porpoise and false killer whale, if not due to differences in methodology, might be the result of different evolutionary factors acting upon the sonar systems of the two species. Alternatively, the differences may be too small to have

functional significance and just be the passive result of other driving forces acting on the functional head morphology of these echolocators. While the bilateral symmetry is high in porpoises, the configuration of reflective bones and air sacs are quite different in the vertical plane (Huggenberger *et al.*, 2009) and can possibly explain the observed differences.

C. Beam is not mirror-symmetric in either plane

The beam is not symmetric, neither in the vertical nor the horizontal plane. In the vertical plane, a prominent dorsal side lobe is present. The vertical main lobe of the beam is narrower in the dorsal (-3 dB BW: 4.8°) than in the ventral (-3 dB BW: 5.9°) direction. The asymmetry of the beam increases further off-axis (-6 dB BW dorsal: 6.5° vs ventral: 8.2°). Recently, a frequency dependent two lobed echolocation beam was described for the bottlenose dolphin (Starkhammar *et al.*, 2011). A downwards projected lobe contained energy between 20 and 70 kHz and a slightly upwards projected lobe contained energy at frequencies between 30 and 80 kHz. The observed asymmetry in the harbor porpoise, however, is most likely due to dorso-ventral head asymmetry since the different lobes had the same frequency content. The right half of the -3 dB horizontal beam width is slightly (0.7° or 11%) wider than the left half, again with increasing asymmetry further away from the acoustic axis (-6 dB BW left: 9.1° vs right: 10.6°). The small horizontal asymmetry, although statistically significant, does presumably not have any biological relevance but could be caused by the fact that porpoises are clicking primarily with the right pair of phonic lips (Madsen *et al.*, 2010). Simultaneous measurements of the clicking intensity on the right and left side of the melon generally show more intense radiation towards the right than towards the left side (Au *et al.*, 2010; Madsen *et al.*, 2010). Horizontally asymmetric sonar beams of toothed whales have not been discussed to date but it is seen in the composite beam patterns of the false killer whale (Au *et al.*, 1995). In this species, the right side of the beam seems to be wider than the left side, similar to what is observed in the harbor porpoise. This could hint to single source right-handed click production in the false killer whale as well.

D. Beam pattern variation

Measuring the beam pattern of single clicks in both the vertical and horizontal simultaneously and only including on-axis clicks based on a rigorous criteria allows us to study the beam pattern and the variation in great detail. Most previous studies averaged over many clicks (Au *et al.*, 1978; Au *et al.*, 1986; Au *et al.*, 1999; Rasmussen *et al.*, 2004), leading to an average beam pattern with often large standard deviations, which were at least in part caused by animal movements; hence, beam dynamic could not be addressed in most studies due to averaging. Here we can in fact demonstrate variation in the beam pattern of 464 on-axis harbor porpoise clicks. This indicates that the porpoise is able to produce a dynamic beam, since this variation is not seen when analyzing recordings from a directional transducer. The observed variation in the range of 2° is small compared to the beam dynamics of a

bottlenose dolphin that was able to vary its vertical beam width from 10 to 29° and its horizontal beam width from 15 to 40° (Moore *et al.*, 2008). In the study by Moore *et al.* (2008), the bottlenose dolphin was faced with an angular target detection task, where a wider and dynamic beam would be advantageous. In our experiment, the harbor porpoise was not faced with any task, so future studies will have to test if this species is also able to produce a beam as dynamic as the bottlenose dolphin's beam. Bats widen their beam when they close in on their prey by lowering the emission frequency, thus reducing the chance of the prey to escape by evasive manoeuvres (Jakobsen and Surlykke, 2010). Also the dynamics of the bottlenose dolphin's beam were in part caused by frequency shifts, the lower the peak frequency the wider the beam in the horizontal (Moore *et al.*, 2008). Since the harbor porpoise did not change the frequency content of its clicks, the dynamic beam in harbor porpoises are based in conformation changes in the transmitting structures such as melon movements, or changes of the reflective structures in the forms of air sac shapes and volumes. The air sacs might have the function of an inner noseleaf similar to the noseleaf of bats (Zhuang and Muller, 2006) that influences the directionality of the sonar beam, since sound is reflected at the borders between tissue and air due impedance differences. Further, three muscles are attached to the tissue surrounding the fatty melon, which is acting as an acoustic wave guide (Au *et al.*, 2006; Huggenberger *et al.*, 2009; Madsen *et al.*, 2010). These muscles can change the shape of the melon and thus perhaps change sound transmission properties and eventually beam shape. Changes in melon size have been reported for this species (Miller, 2010) and were observed during experimental sessions, making it a likely cause for the observed beam dynamics.

E. Relation to the piston model

Most studies used a flat circular piston to model toothed whale echolocation beam patterns, except Au *et al.* (1995) for the false killer whale. The directional properties for this species was best modeled using a planar rectangular transducer of the size 10.1×16.1 cm (Au *et al.*, 1995). The best fit to the average beam pattern of the harbor porpoise in this study was obtained assuming a flat oval piston in an infinite baffle emitting a porpoise click with a horizontal aperture of 6.5 cm and a vertical aperture of 8.3 cm.

The model fits the measured horizontal and vertical beam over a 15° range on either side of the acoustic axis very well. However, the measured dorsal side lobe does not match the piston model, which could be due to the dynamics of single clicks or simply because the porpoise sound emission system cannot be modeled perfectly with a piston. The variability seen in the data could be explained by effective size changes of the emitter (i.e., the melon) through muscle contraction in the range 5.5 to 7.4 cm in the horizontal plane and from 7.1 to 9.6 cm in the vertical plane. Thus while the flat piston model is a good first approximation for beam pattern modeling in echolocating toothed whales, it cannot accommodate the beam dynamics demonstrated here for constant centroid frequencies.

F. Conclusion

All smaller species of toothed whales produce echolocation beams with surprisingly similar high directionality indices around 24 dB (Au, 1993; Kyhn *et al.*, 2010), suggesting that sonar needs at least in part seem to have determined the high centroid frequencies of the small NBHF species (Kyhn *et al.*, 2010). The harbor porpoise has a slightly dorso-ventrally compressed beam which might be an adaptation for this shallow water species where bottom reflections are reduced while the search volume in the horizontal is kept large. Horizontal beam asymmetry supports recent findings, showing that harbor porpoises click with the right pair of phonic lips, whereas vertical echolocation beam asymmetry is probably due to dorso-ventral head asymmetry. The dynamics in the porpoise's sonar beam are possibly due to changes of the melon shape, emphasizing that sound radiation from toothed whale nasal complexes cannot be modeled using a flat piston with a fixed aperture. Thus, even with very stereotyped NBHF clicks, porpoises can change their sound transmission to aid biosonar based tracking of prey targets.

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