The echolocation transmission beam of free-ranging Indo-Pacific humpback dolphins (*Sousa chinensis*)

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While the transmission beam of odontocetes has been described in a number of studies, the majority of them that have measured the transmission beam in two dimensions were focused on captive animals. Within the current study, a dedicated cross hydrophone array with nine elements was used to investigate the echolocation transmission beam of free-ranging Indo-Pacific humpback dolphins. A total of 265 on-axis clicks were analyzed, from which the apparent peak to peak source levels ranged between 168 to 207 dB (mean 184.5 dB $\pm$ 6.6 dB). The 3-dB beam width along the horizontal and vertical plane was 9.6° and 7.4°, respectively. Measured separately, the directivity index of the horizontal and vertical plane was 12.6 and 13.5 dB, respectively, and the overall directivity index (both planes combined) was 29.5 dB. The beam shape was slightly asymmetrical along the horizontal and vertical axis. Compared to other species, the characteristics of the transmitting beam of Indo-Pacific humpback dolphins were relatively close to the bottlenose dolphin (*Tursiops truncatus*), likely due to the similarity in the peak frequency and waveform of echolocation clicks and comparable body sizes of the two species.

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I. INTRODUCTION

Odontocetes rely on sound for critical activities such as communication, foraging, navigating, avoiding predators, and spatial orientation (Au, 1993; Richardson *et al.*, 1995). Their ability to echolocate has enabled these animals to thrive in a range of environments (Au, 1993; Au and Hastings, 2008; Jefferson *et al.*, 2011). Localizing any given object using echolocation depends on the highly directional clicks being reflected back to the phonating animal and being detected and processed by its sensitive hearing system (Au, 1993; Au *et al.*, 2000). The transmission of these highly directional clicks as a beam means less energy is expended by the phonating animal as it scans the environment for targets (Madsen and Wahlberg, 2007) and there is always a negative correlation between the directivity index (DI) beam

and the beam width in some studied species (Au *et al.*, 1999; Finneran *et al.*, 2014). In order to better understand how these animals use, or even adapt, to different acoustic environments or search for targets, there is a need to investigate the characteristics of the transmission beam (including the beam shape, directionality, angular resolution, and energy) (Rasmussen *et al.*, 2004).

Transmission beam patterns in captive odontocetes have been described in false killer whales, *Pseudorca crassidens* (Au *et al.*, 1995; Ibsen *et al.*, 2012; Kloepper *et al.*, 2012a, 2015), bottlenose dolphins, *Tursiops truncatus* (Au, 1993; Au *et al.*, 2012; Branstetter *et al.*, 2012; Ibsen *et al.*, 2012; Finneran *et al.*, 2014, 2016), beluga whales, *Delphinapterus leucas* (Au *et al.*, 1987), Risso's dolphins, *Grampus griseus* (Smith *et al.*, 2016) and harbor porpoises, *Phocoena phocoena* (Au *et al.*, 1999; Madsen *et al.*, 2010; Koblitz *et al.*, 2012). However, while these studies comprehensively characterize the transmission beam for those particular species, there is some uncertainty when inferring conclusions for free-ranging populations based on data obtained from captive populations because of differences in acoustic

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environments and/or the task being performed. The acoustic environment inside tanks and pools may be completely different to anything in the wild, and may lead to effects on the biosonar behavior of a captive individual (Au, 1993; Siemers and Schnitzler, 2004; Ibsen *et al.*, 2007). Consequently, care needs to be taken when inferring the characteristics of the echolocation signal (including the transmission beam) to free-ranging individuals in very different acoustic environments where individuals are faced with different tasks. Typically, free-ranging individuals in the wild face a greater variety of tasks, whether the goal of echolocating is for communication, navigating, foraging, or avoiding dangerous situations. As a result, one can expect the echolocation beam to be highly dynamic, with the echolocating animal controlling the transmission beam to economize on searching for different targets (Moore *et al.*, 2008; Madsen *et al.*, 2010; Starkhammar *et al.*, 2011; Kloepper *et al.*, 2012a).

In light of these limitations, there are some studies which characterize the transmission beam of free-ranging individuals of various species, such as white beaked dolphins, *Lagenorhynchus albirostris* (Rasmussen *et al.*, 2004), Ganges river dolphins, *Platanista gangetica* (Bahl *et al.*, 2007; Ura *et al.*, 2007; Jensen *et al.*, 2013), Cuvier's beaked whales, *Ziphius cavirostris* (Zimmer *et al.*, 2005a), and sperm whales, *Physeter macrocephalus* (Møhl *et al.*, 2003), Narwhals, *Monodon monoceros* (Koblitz *et al.*, 2016), Amazon river dolphin, *Inia geoffrensis* (Ladegaard *et al.*, 2015), harbor porpoise, *Phocoena phocoena* (Kyhn *et al.*, 2013), Dall's Porpoise *Phocoenoides dalli* (Kyhn *et al.*, 2013), Peale's dolphins, *Lagenorhynchus australis* (Kyhn *et al.*, 2010), Commerson's dolphins, *Cephalorhynchus commersonii* (Kyhn *et al.*, 2010), and Atlantic spotted dolphins, *Stenella frontalis* (Jensen *et al.*, 2015). However, most studies only characterized the vertical plane of the transmission beam as opposed to both the vertical and horizontal planes. Consequently, while the echolocation signals emitted by odontocetes have been measured from a range of species, the knowledge about the transmission beam of odontocetes is still incomplete, especially for species which are not held in captivity (Wahlberg and Surlykke *et al.*, 2014).

Locally referred to as the Chinese white dolphin, the Indo-Pacific humpback dolphin (*Sousa chinensis*) is a small cetacean, the body size can be up to 2.8 m in length and 280 kg in weight (Ross *et al.*, 1994; Wang, 1999; Jefferson, 2000). They inhabit shallow coastal waters, including estuarine environments (Jefferson and Hung, 2004). The distribution of this species is extensive, from south-eastern Africa to southern China and northern Australia (Reeves *et al.*, 2010). Humpback dolphins produce sounds that can be broken down into whistles, burst pulses, and echolocation clicks (Van Parijs and Corkeron, 2001; Sims *et al.*, 2012; Alvaro *et al.*, 2014; Hoffman *et al.*, 2015; Wang *et al.*, 2016). The apparent source levels of echolocation clicks from free-ranging Indo-Pacific humpback dolphins range between 177 and 207 dB re 1 μ Pa @ 1 m (average of 186 dB $\pm$ 6.76 dB re 1 μ Pa @ 1 m and 95% energy duration of 22 μ s), with a peak and center frequency of 109 and 95 kHz, respectively, and a 3-dB bandwidth of 50 kHz (Fang *et al.*, 2015). While

the source parameters of echolocation clicks emitted from free-ranging Indo-Pacific humpback dolphins have been investigated, no information on the echolocation transmission beam was found, for either captive or free-ranging individuals. We therefore aimed to investigate the transmission beam for free-ranging Indo-Pacific humpback dolphins to fill this knowledge gap and to better understand how these animals may alter their echolocation beam patterns in shallow water environments. To do so, we used a newly designed cross hydrophone array consisting of nine elements to record the echolocation beam *in situ*, along both the vertical and horizontal axes.

II. MATERIALS AND METHODS

A. Study area

The current study was conducted in Sanniang Bay (21°32'–21°37'N; 108°42'–108°56'E), Guangxi Province, China (Fig. 1). A population of approximately 100 individuals is found year-round within the bay where their distribution is relatively restricted (Pan *et al.*, 2006). This area was selected for the current study due to the lower anthropogenic pressure within the bay, and thus lower risk for anthropogenic noise contamination. Water depths within the study area were between 3.5 and 6 m.

B. Data collection

A dedicated cross type hydrophone array with nine elements was used to record the echolocation clicks of free-ranging Indo-Pacific humpback dolphins [Fig. 2(A)]. The frame of the array was aluminum alloy, 155 cm in length and 2 cm in diameter. To control for the potential reverberation of the signal within the aluminum structure, each individual hydrophone (TC 4013, Reson, Denmark, frequency range 1 Hz–170 kHz $\pm$ 3 dB, -211 dB $\pm$ 3 dB re 1 V/ μ Pa sensitivity) was secured to a 15 cm long solid steel rod (0.2 cm diameter) spaced 76 cm apart. Each hydrophone was connected to a one-channel variable gain amplifier (VP2000; Reson, Slangerup, Denmark), set at 50 dB gain. Recordings were bandpass filtered between 1 and 150 kHz to remove any extraneous noise associated with recording from the boat (5.7 m long Mosquito with 60 horse-power outboard engine) and digitized (as .TDMS files) using three National Instruments 9223 data acquisition boards (16-Bit, 1 MS/s/ch), a cDAQ 9178 chassis, and stored onto a laptop computer, at a rate of 1000 kHz per second. To further reduce any noise contamination, recordings were undertaken in good weather conditions (sea state ≤ 3 on the Beaufort scale). The recording system was controlled using a custom-designed program in LabVIEW 10.1 software.

Upon sighting a pod of dolphins, the research vessel slowly approached until within 100 m of the nearest animal. The hydrophone array was deployed after the vessel's engine was turned off and positioned vertically in the water column, with the top hydrophone being 0.5 m below the surface. Recordings commenced as soon as the array was successfully positioned and continued until the nearest animal moved beyond a distance of 100 m. Recordings were only

FIG. 1. Map of study area Sanniang Bay, China and the GPS tracking of recording platform (black solid line).

FIG. 2. The schematic diagram of the nine element symmetric cross array (A) with correspondent waveforms of an on-axis clicks received by different elements along the array's horizontal and vertical axis (B).

undertaken during socializing or foraging events because only then could the boat remain close enough for long enough to obtain sufficient data.

C. System calibration

The localization system was calculated in open water using by an echosounder (EY60, Simrad, Norway) deployed at different distances. A 120 kHz signal was used for the calibration because of the overlap to humpback dolphin echolocation clicks. The measured distances associated standard errors were plotted in Fig. 3.

D. Data processing

Recordings were examined using DIAdem 2012 acoustic software (National Instruments, Austin, TX) and analyzed in MATLAB using code specifically written for these data. Analysis was only carried out on candidate clicks. The most important selection criterion for candidate clicks was the transmission axis of the recorded signal, i.e., analyses were only done on signals that were recorded along the transmission axis (on-axis) of the phonating animal. This is further compounded by the highly variable and unpredictable orientation of the phonating animal. To ensure only on-axis clicks were analyzed, a series of published criteria were used for the selection of candidate clicks: (1) the source must be oriented toward the hydrophone array; (2) click trains were successfully received by all hydrophones within the array; (3) candidate clicks received by the center hydrophone must have the highest peak-peak sound pressure level (SPL) compared to the other hydrophones; and (4) candidate clicks must have a signal-to-noise ratio over 20 dB (Fang *et al.*, 2015).

Apparent peak-peak source levels (dB re 1 $\mu\text{Pa}_{\text{p-p}}$) of each candidate click was calculated using

$$\text{ASL}_{\text{p-p}} = \text{RL} + 20 \log R + \alpha R, \quad (1)$$

where RL is the received SPL at the center hydrophone, R is the distance between the click source and receiving hydrophone, and αR is frequency-dependent absorption (Au, 1993;

FIG. 3. Calibration measurement for the symmetrical cross array used in this study. The mean and SD of the calculated range are plotted against the actual range.

Møhl *et al.*, 2000). The distance R between the source and receiving hydrophone was determined by comparing the signal's time-of-arrival between the center hydrophone and two neighboring hydrophones along the horizontal (Urlick, 1983; Au and Hastings, 2008). A sound speed of 1530 ms^{-1} was calculated using the Medwin equation (Medwin 1975), where salinity was 27 ppt and sea surface temperature was 29°C .

The absorption losses in seawater (α) was approximated by (Au, 1993)

$$\alpha = \frac{A_2 f_2 f^2}{f_2^2 + f^2} \text{ dB/m}, \quad (2)$$

where f is frequency (in Hz), the other parameters A_2 and f_2 are separately given by $A_2 = 48.83 \times 10^{-8} + 65.34 \times 10^{-10} \text{ Ts/m}$, $f_2 = 1.55 \times 10^7 (T + 273.1) \exp[-3052/(T + 273.1)] \text{ Hz}$ and T is the temperature in degrees Celsius.

The DI for both the horizontal and vertical plane was calculated to assess the sharpness of the echolocation transmission beam (Au, 1993), and was given by

$$\text{DI} = 10 \log \left(\frac{2\pi}{\int_0^{2\pi} p^2(\theta) d\theta} \right), \quad (3)$$

where $p(\theta)$ is the beam pattern in vertical or horizontal dimensional, and θ is angle in the vertical or horizontal dimension.

To assess the overall sharpness of the echolocation transmission beam, the two-dimensional DI was calculated (Au, 1993) and given by

$$\text{DI} = 10 \log \frac{4\pi}{\int_0^{2\pi} \int_{-\pi/2}^{\pi/2} \left(\frac{p(\theta, \varphi)}{p_0} \right) \sin \theta d\theta d\varphi}, \quad (4)$$

where $p(\theta, \varphi)/p_0$ is the beam pattern in two-dimensional, θ is the angle in the vertical plane, and φ is the angle in horizontal plane.

III. RESULTS

Over 684 recordings files, covering almost 19h, with clicks were successfully obtained from a number of free-ranging Indo-Pacific humpback dolphins within the study area. A range of behaviors, such as milling, traveling, resting, socializing, and foraging were observed during the field-surveys.

In total, 265 candidate clicks (distance $< 50 \text{ m}$) were selected for further analysis, having met the required criteria for on-axis clicks. Representative examples of waveform and spectrum of a typical on-axis click received by the center and peripheral hydrophones are provided in Fig. 2(B), respectively. The waveform and spectrum of all on-axis clicks are shown in Figs. 4(A) and 4(B). The on-axis $\text{ASL}_{\text{p-p}}$ at the center hydrophone ranged between 168 and 207 dB re 1 $\mu\text{Pa}_{\text{p-p}}$, with a mean value of approximately $184.5 \pm 6.6 \text{ dB re } 1 \mu\text{Pa}_{\text{p-p}}$. The peak frequency was $111.0 \pm 5.1 \text{ kHz}$ and 95% energy duration (durations were based on the time interval from 2.5% to 97.5%

FIG. 4. Example of the waveforms (A) and spectrums (B) of all on-axis clicks recorded by the center hydrophone of the array.

of the cumulative energy flux density) $25.0 \pm 5.3 \mu\text{s}$. The properties of on-axis clicks (Table I) were quite close to the prior study (Fang *et al.*, 2015).

To investigate the echolocation transmission beam of the phonating animal, the off-axis $\text{ASL}_{\text{p-p}}$ of each candidate click received by the peripheral hydrophones were normalized against the on-axis $\text{ASL}_{\text{p-p}}$ received by the center hydrophone. The corresponding angles between each peripheral hydrophone and the center hydrophone (which represented the transmission axis) were calculated using the distances between the source and center hydrophones (a) as well as the distance between the center and peripheral hydrophone (b). The results of the on- and off-axis $\text{ASL}_{\text{p-p}}$ with its corresponding angles in both the horizontal and vertical plane were plotted in Figs. 5(A) and Fig. 5(B), respectively.

Angles between the source and receiving hydrophones were divided into eight degree-bins ($\pm[0^\circ-10^\circ]$, $\pm[5^\circ-15^\circ]$, $\pm[15^\circ-25^\circ]$, $\pm[25^\circ-35^\circ]$), with the center hydrophone being 0° , and the averages of normalized source level with standard deviation (SD) in the 8° bins were plotted to illustrate the echolocation transmission beam in Figs. 5(C) and Fig. 5(D). These degree-bins were selected based on their use in previous studies on captive dolphins and thereby allowing for a more appropriate comparison with other species. The beam patterns were then fitted using the cubic spline interpolation process [Figs. 5(E) and 5(F)]. Following the cubic spline interpolation process, the beam pattern model showed the overall beam shape to be slightly asymmetrical in both

horizontal and vertical, and the 3-dB beam width along the horizontal and vertical plane were approximately 9.6° and 7.4° , respectively. Directivity indices for the horizontal and vertical plane were 12.6 and 13.5 dB, respectively, and the overall directionality of the echolocation transmission beam was 29.5 dB.

The source levels of the analyzed on-axis clicks as functions of the recording range are present in Fig. 6

IV. DISCUSSION AND CONCLUSIONS

This is the first study to use a nine element cross-type hydrophone array to investigate the echolocation transmission beam of free-ranging Indo-Pacific humpback dolphins along both the horizontal and vertical planes. The horizontal and vertical 3-dB beam width was 9.6° (DI of 12.6 dB) and 7.4° (DI of 13.5 dB), respectively, and the overall DI was 29.5 dB. One should note there was a high variability in the source level measurements, which could influence the results as signal directionality is greater with higher source levels (Finneran *et al.*, 2014). Given the current study was measuring free-ranging individuals, the hydrophone array was unable to be kept at a constant distance from the animal and consequently, the beam shapes presented in this paper were averaged across all measured clicks of varying ranges. As such, it is not possible to comment on how the varied source levels affected the DI.

The echolocation transmission beam from a range of species has been characterized in previous studies (Table II). The 3-dB beam width angle is commonly used to evaluate the beam directionality and is defined as the signal's sound pressure being within 3 dB of the maximum decibel level (Au, 1993). Our results show the horizontal plane of the transmission beam in Indo-Pacific humpback dolphins to be relatively similar to captive bottlenose dolphins (Au, 1993) and free-ranging Ganges river dolphins (Bahl *et al.*, 2007). When compared to other free-ranging examples, such as bottlenose dolphins (Wahlberg *et al.*, 2011) and white-beaked dolphins (Rasmussen *et al.*, 2004), the transmission beam of Indo-Pacific humpback dolphins along the horizontal plane is slightly larger. Along the vertical plane, the 3-dB beam width of Indo-Pacific humpback dolphins within the current study (approximately 7.4°) was also similar to bottlenose dolphins (Wahlberg *et al.*, 2011) and white-beaked dolphins (Rasmussen *et al.*, 2004), however, broader than beluga whales, whose 3-dB beam width angle along the vertical

TABLE I. Summary the parameters of the on-axis clicks ($n = 265$) received by the center hydrophone of the array from the free-ranging Indo-Pacific humpback dolphins.

	Mean $\pm$ SD ($n = 265$)	Range
SL_PP (dB re: 1 μPa)	184.5 ± 6.6	167.6–207.3
SL_RMS (dB re: 1 μPa)	173.8 ± 6.9	155.5–196.6
$\tau_{95\%E}$ (μs)	25.0 ± 5.3	15.0–38.0
$\tau_{3\text{ dB}}$ (μs)	9.3 ± 1.4	6.0–13.0
$\tau_{10\text{ dB}}$ (μs)	20.8 ± 3.9	15.0–33.0
fp (kHz)	111.0 ± 5.1	56.6–119.1
fc (kHz)	97.4 ± 7.1	73.2–113.3
BW-3 dB (kHz)	51.3 ± 14.7	26.4–95.7
BW-10 dB (kHz)	104.2 ± 9.3	75.2–125.0
BW-RMS (kHz)	103.7 ± 7.3	82.0–121.1
ICI (ms)	25.8 ± 18.1	12.4–193.2
R (m)	8.3 ± 9.1	2.5–83.3

FIG. 5. Received beam pattern of clicks from Indo-Pacific humpback dolphins from the array's horizontal plane (A), and the array's vertical plane (B). Beam pattern plot by mean and SD of normalized source levels of each degree bin and average angles in the horizontal (C) and vertical (D) plane. The beam pattern obtained by fitting the data with the cubic spline function in horizontal plane (E) and vertical plane (F).

plane is approximately 6.5° (Au *et al.*, 1987). The 3-dB bandwidth along the horizontal is broader than the 3-dB bandwidth in vertical, which was observed from Indo-Pacific humpback dolphins in the current study, has also been reported in the harbor porpoise, *Phocoena phocoena* (Koblitz *et al.*, 2012).

While previous studies have investigated the echolocation transmission beam shape using the vertical and horizontal axes, fewer studies have described the beam shape using

the DI for two planes, especially in the wild. Generally, the overall DI is a ratio of the received power by an omnidirectional receiver to a directional receiver (Au, 1993). The overall DI of the Indo-Pacific humpback dolphins was very similar to that of *Tursiops aduncus* and *Lagenorhynchus albirostris* (Wahlberg *et al.*, 2011; Rasmussen *et al.*, 2004). Circular piston models are often used to fit the echolocation transmission beam of dolphins (Au, 1993; Wang *et al.*, 2015). Wang *et al.* (2015) calculated the DI of an Indo-

FIG. 6. The source levels as a function of the recording range between animals and the center hydrophone ($y = 18.7 \log_{10}(x) + 169.9$, $R^2 = 0.59$).

Pacific humpback dolphin using a 6 cm radius circular piston model and the result was commensurate with the current study. The DI value is a function of the maximum power at a certain sound frequency and the head structure of the phonating animal (Au *et al.*, 1999). Within the current study, transmission beam properties are relatively similar to that emitted by bottlenose dolphins. This similarity could be attributed, at least in part, to their comparable body sizes and weights, as well as the similarities in echolocation clicks between bottlenose and Indo-Pacific humpback dolphins. For example, both species produce echolocation clicks at a peak frequency around 110 kHz (Rasmussen *et al.*, 2004; Fang *et al.*, 2015). Furthermore, the transmission beam of harbor porpoises (the smallest odontocete to have been studied to-date) shows the lowest DI (Au *et al.*, 1999; Koblitz *et al.*, 2012). Notwithstanding, the reason for harbor porpoises emitting broadband sonar to scan its environment is unclear. One hypothesis for the varying beam widths between species could be due to the trade-off between body size and energy requirements for survival. For example, since body sizes are related to the sound source levels and food intake

requirements, it may be economical to concentrate the sound energy using a narrower beam to locate distant targets, while smaller species can afford a more broadbeam that provides a wider acoustic view but is not as far reaching.

The symmetry of the beam shape can potentially provide information on how sounds propagate within the head of the phonating animal, as well as the position of the vocal organs. Previous studies have suggested that a more common shape of the sonar beam is rotationally symmetric (Au *et al.*, 1987; Au, 1993; Wahlberg *et al.*, 2011; Smith *et al.*, 2016), although some studies have shown that the sonar beam of some species are asymmetric (Au *et al.*, 1995; Koblitz *et al.*, 2012). The results within the current study show the echolocation transmission beam from Indo-Pacific humpback dolphins to be asymmetric. Asymmetry along the horizontal plane is believed to be related to the position of the air sacs, while asymmetry along the vertical plane may relate to the size of the skull or adaptations to the environment, but the skull also may affect the beam shape in the vertical plane (Arroyan *et al.*, 1992; Koblitz *et al.*, 2012). However, many factors may influence the shape and directionality of the echolocation transmission beam, such as the target variables, signal variability (e.g., SPL, center frequency), the orientation of the phonating animal in space and time, the skull cavity, and the geometry of the melon (Finneran *et al.*, 2014; Smith *et al.*, 2016; Kloepper *et al.*, 2012b).

The current study has shown that the cross hydrophone array can be used to investigate the echolocation transmission beam of free-ranging odontocetes, which is especially useful for species not held in captivity. However, there are several factors that need to be considered, particularly the unknown position of the fast swimming animal in shallow, turbid waters. Other factors include inherent range error of the acoustic localization system, the differing orientation of the propagation beam, and the animal's movement, the selected candidate clicks being slightly off-axis and the variation in beam properties controlled by the vocal organs (Rasmussen *et al.*, 2004). A key limitation within the current

TABLE II. Summary the echolocation transmission beam patterns in odontocetes, H_{-3dB} (3-dB beam width in horizontal), V_{-3dB} (3-dB beam width in vertical), DI_H (DI of horizontal plane), DI_V (DI of vertical plane), and DI (DI in two dimensions).

	H_{-3dB} [degree]	V_{-3dB} [degree]	DI_H [dB]	DI_V [dB]	DI [dB]	Source
<i>Tursiops truncatus</i>	9.7	10.2	n.a	n.a	25.8	Au (1993)
<i>Tursiops truncatus</i>	9	9	n.a	n.a	26	Wahlberg <i>et al.</i> (2011)
<i>Tursiops aduncus</i>	8	8	n.a	n.a	29	Wahlberg <i>et al.</i> (2011)
<i>Tursiops truncatus</i>	n.a	n.a	11	n.a	n.a	Branstetter <i>et al.</i> (2012)
<i>Tursiops aduncus</i>	7.5	n.a	n.a	n.a	25.8	Finneran <i>et al.</i> (2014)
<i>Delphinapterus leucas</i>	6.5	6.5	n.a	n.a	32.1	Au <i>et al.</i> (1987)
<i>Pseudorca crassidens</i>	6.2	9.7	n.a	n.a	28.5	Au <i>et al.</i> (1995, 1999)
<i>Lagenorhynchus albirostris</i>	8	8	n.a	n.a	29	Rasmussen <i>et al.</i> (2004)
<i>Physeter macrocephalus</i>	n.a	n.a	n.a	n.a	27	Möhl <i>et al.</i> (2003)
<i>Physeter macrocephalus</i>	n.a	n.a	n.a	n.a	26.7	Zimmer <i>et al.</i> (2005b)
<i>Ziphius cavirostris</i>	n.a	n.a	n.a	n.a	>25	Zimmer <i>et al.</i> (2005a)
<i>Phocoena phocoena</i>	16.5	16.5	n.a	n.a	22.1	Au <i>et al.</i> (1999)
<i>Phocoena phocoena</i>	13.1	10.7	n.a	n.a	24	Koblitz <i>et al.</i> (2012)
<i>Platanista gangetica</i>	10	14	n.a	n.a	n.a	Bahl <i>et al.</i> (2007)
<i>Grampus griseus</i>	8.7	8.7	n.a	n.a	28.0	Smith <i>et al.</i> (2016)
<i>Sousa chinensis</i>	9.6	7.4	12.6	13.5	29.5	Present study

study was the unknown position/orientation of the dolphins in relation to the array. While a selection protocol for candidate clicks was used to eliminate off-axis clicks, it was still very difficult to ensure all candidate clicks were on-axis due to the narrow echolocation transmission beam and limited size of the array. It is also important to note that recordings were undertaken in shallow waters (<20 m depth), thereby increasing the degree of boundary effects during the propagation of sound between the source and receiver and leading to the original signal being overlapped by echoes. Further research and development of hydrophone arrays is therefore required to address these limitations in the future. Notwithstanding, characterizing the echolocation transmission beam of free-ranging individuals is needed to better understand how these animals use sonar in varying environments.

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