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A Comparative Study of Echolocation Parameters of Wild and Captive Indo-Pacific Humpback Dolphins (*Sousa chinensis*)

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Abstract

Our understanding of the vocalizations of captive Indo-Pacific humpback dolphins (*Sousa chinensis*) is limited compared to our knowledge of these sounds in wild animals. Echolocation signals of wild Indo-Pacific humpback dolphins were recorded in the central-western Gulf of Thailand, and captive animals' sounds were recorded in an ocean park in Trat Province, Thailand, using a cross array with five hydrophones. Both wild and captive animals produced broadband transient clicks of short duration (21 ± 4 μs in the wild and 36 ± 2 μs in captivity). The inter-click intervals (37 ± 13.5 ms) for wild animals were longer than for captive animals (25 ± 1.2 ms). Statistical analysis showed that mean peak-to-peak (p-p) source levels of on-axis echolocation clicks varied significantly between wild (185 ± 5.8 dB re 1 μPa) and captive (169 ± 2.8 dB re 1 μPa; $p < 0.001$) environments. The frequency domain parameters of echolocation clicks of wild humpback dolphins were similar to those of captive humpback dolphins, characterized by a mean centroid frequency of 106 ± 7.1 kHz and 105 ± 3.7 kHz, respectively. These results provide the first comparison of sound properties from both wild and captive humpback dolphins and could be valuable for the development of passive acoustic monitoring species classification tools to inform management and conservation efforts.

Key Words: echolocation clicks, source parameters, wild and captive, Gulf of Thailand, Indo-Pacific humpback dolphins, *Sousa chinensis*

Introduction

Toothed whales produce short duration, ultrasonic clicks at high source levels while echolocating to acquire information about the surrounding environment (Au, 1993). Characterizing the source parameters of echolocation clicks is important for understanding how toothed whales use echolocation in the wild and to optimize detection and classification algorithms for use in passive acoustic monitoring (PAM; Madsen & Wahlberg, 2007; Nowacek et al., 2016). Click parameters of different species with different body sizes clearly differ in both waveform and spectrum characteristics. An increasing number of odontocete biosonar studies indicate an overall inverse scaling of frequency with body size (Kyhn et al., 2009; Wahlberg et al., 2011b; de Freitas et al., 2015; Jensen et al., 2018). In addition to body size, biosonar source parameters may be affected by differences in habitat (Jensen et al., 2015; Ladegaard & Madsen, 2019). The behavior and sounds of a species play an important role in its adjustment to the captive environment. However, no comparative studies of the sounds of wild and captive Indo-Pacific humpback dolphins have been conducted.

Bioacoustic studies can facilitate identifying relationships between populations where genetic or morphological information are insufficient. Although vocalizations of Indo-Pacific humpback dolphins (*Sousa chinensis*) in some habitats (such as Chinese Mainland, Hong Kong, Australia, and Malaysia) have been described in recent decades (Schultz & Corkeron, 1994; Van Parijs & Corkeron, 2001a, 2001b; Goold & Jefferson, 2004; Sims et al., 2012; Wang et al., 2013; Fang et al., 2015; Hoffman et al., 2015; Kimura et al., 2016), knowledge about the biosonar source parameters of Indo-Pacific humpback dolphins compared to bottlenose dolphins (*Tursiops truncatus*) is limited. Like other delphinids, Indo-Pacific humpback dolphins produce echolocation clicks and frequency-modulated whistles (Van Parijs et al., 2000; Van Parijs & Corkeron, 2001b). The on-axis clicks from the echolocation beam of a dolphin recorded with a hydrophone array are useful for analyzing the acoustic characteristics of echolocation clicks (Au & Herzing, 2003). For instance, Fang et al. (2015) obtained source parameters of high-frequency echolocation clicks of Indo-Pacific humpback dolphins in Sanniang Bay, China, using a cross-type hydrophone array with five elements. Geographic variation in the whistles of Indo-Pacific humpback dolphins has been investigated at two coastal locations along western Peninsular Malaysia via recording with a towed hydrophone (Hoffman et al., 2015). Echolocation characteristics of Indo-Pacific humpback dolphins in the wild have been reported in many previous studies (Goold & Jefferson, 2004; Sims et al., 2012; Fang et al., 2015; Kimura et al., 2016). However, no research has been conducted on vocalization of Indo-Pacific humpback dolphins in captivity.

Indo-Pacific humpback dolphins generally inhabit areas with water depths shallower than 20 m and show high site fidelity to specific habitats (Chen et al., 2011). The Gulf of Thailand is the main habitat for humpback dolphins (Jutapruet et al., 2015); however, information on the acoustic behavior of the species in the Gulf of Thailand is lacking. This study provides the first quantitative acoustic investigation of the echolocation clicks of Indo-Pacific humpback dolphins in the Gulf of Thailand using a five-hydrophone cross array and a high-speed digital sampling recording system. To address this question, echolocation signals of captive Indo-Pacific humpback dolphins in an ocean park in Thailand were recorded using the same five-hydrophone cross array. Additionally, we conducted a comparative study of the biosonar source parameters of wild and captive humpback dolphins in Thailand. A comparative study of acoustic parameters in both free-ranging and captive humpback dolphins will provide a better understanding of delphinid activity as related to both environments (Dudzinski, 2010). Our findings provide a preliminary description of the characteristics of echolocation clicks of wild and captive Indo-Pacific humpback dolphins, and they help to establish baseline acoustic parameters needed to implement PAM methods to monitor the species in Thailand. This study may also benefit future acoustic research, management, and conservation strategies for Indo-Pacific humpback dolphins in the region.

Methods

Recording Sites

Acoustic recordings in the wild were conducted in the coastal waters of Donsak and Khanom regions in the central-western Gulf of Thailand during daylight hours between 12 and 20 August 2018 (Figure 1). The coastal waters of Donsak and Khanom regions are key habitats for Indo-Pacific humpback dolphins (Reeves et al., 2008), with most areas being less than 7 m deep. A total of 49 individual Indo-Pacific humpback dolphins have been identified and catalogued using a Mark-Recapture Model from boat-based photo-identification surveys in the study area (Jaroensutasinee et al., 2011).

An 8-m-long high-speed vessel manufactured in Thailand was used for the field surveys. During surveys, once a group of Indo-Pacific humpback dolphins was encountered, they were followed for further observation and acoustic recording. To minimize potential disturbance to dolphin behavior introduced by the survey vessel, we typically approached the humpback dolphins from the side at a speed of < 5 kts and at a distance of at least 20 m, after which the engine was turned off and the vessel was allowed to drift. When recording conditions were ideal, the vessel was maneuvered into a position to maximize

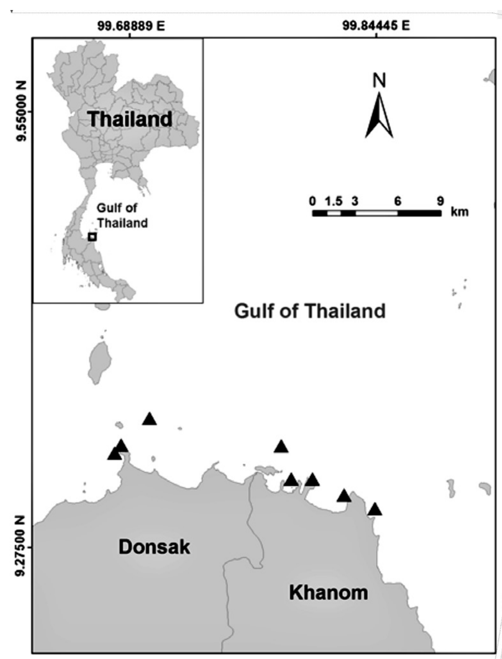

Figure 1. Map of the coastal waters of Donsak and Khanom regions in the central-western Gulf of Thailand, showing the study area and locations of acoustic recordings (triangle)

acoustic recording time. Immediately after a recording was initiated, the geographical position was registered using a handheld GPS device (Garmin eTrex 10; Kansas City, KS, USA). The start and end times were also noted for each event. Water depth at each recording location was measured using a handheld depth sounder (Hondex PS-7 LCD Digital Sounder; Honshu, Japan). Two trained observers used 7 × 50 binoculars (Navigator; Steiner-Optik, Bayreuth, Germany) to determine group size and to document the behavior of dolphins at the surface. Photographs were taken by a third observer using a Canon digital SLR camera (EOS 1D Mark IV; Tokyo, Japan) fitted with a 100 to 400 mm lens.

Acoustic recordings were also conducted at an ocean park in Trat Province in Thailand during daylight hours between 22 and 24 December 2018. Five captive young Indo-Pacific humpback dolphins were housed in a round pool with a diameter of 30 m and a depth of 7 m. The humpback dolphins were around 20 y old and in healthy condition during the recordings.

Data Collection

A five-hydrophone cross array, designed to collect on-axis clicks, was used to measure the echolocation clicks of the Indo-Pacific humpback dolphins in the wild and in captivity (Figure 2). The spacing between the central hydrophone and the other hydrophones was 54 cm and was aligned with an interconnected set of PVC pipes. The top hydrophone was held at a depth of 2 m. The hydrophones manufactured by the Institute of Applied Acoustics (RHSA 10; Hangzhou, China) were connected to an eight channel USB-6356 A/D converter (National Instruments, Austin, TX, USA) sampling at a frequency of 1 MHz at a 16-bit resolution. The converter had a maximum voltage range of 10 V. The five hydrophones were calibrated by the China National Defense Underwater Acoustics Calibration Laboratory prior to the study. The sensitivity of the hydrophones was -181 dB re 1 V/μPa, with an omnidirectional receiving characteristic and a flat frequency response (±3 dB) between 25 Hz and 250 kHz. Recordings were initiated and terminated manually, and data were automatically stored on a laptop hard disk. During recording periods at sea, no cetacean species other than Indo-Pacific humpback dolphins were visually sighted in the study area. Therefore, all collected clicks were considered to be produced by the target species.

Data Analysis

Field recordings were converted to .wav files and were visually examined using *Adobe Audition*, Version 3.1 (Adobe Systems Inc., San Jose, CA, USA). Files with echolocation clicks were separated and labeled accordingly, while the files with a low signal-to-noise ratio (SNR: < 6 dB) or lack of signals were excluded. The calculation formula of SNR was calculated using Eq. (1):

$$SNR = 20 * \log 10(S / N) \quad (1)$$

where ***S*** is root mean square (rms) amplitude of echolocation clicks and ***N*** is rms amplitude of noise.

Acoustic analysis of the recorded sounds was carried out using customized *MATLAB*, Version 7.1 (MathWorks, Inc., Natick, MA, USA), algorithms. The spectral characteristics of clicks were calculated on the selected part of the signal using a Fast Fourier Transformation (FFT: 512 points, Hann window) with zero padding to fill the gaps around

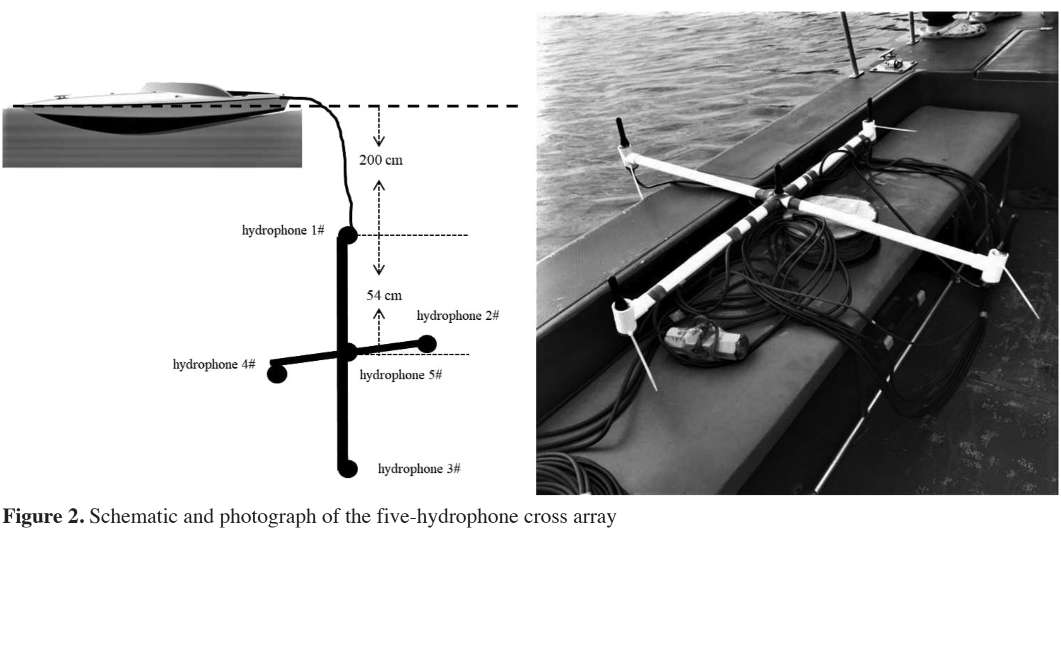

Figure 2. Schematic and photograph of the five-hydrophone cross array

the actual signal. Toothed whale echolocation signals are highly directional, with a 3-dB beam width in some species smaller than ±5° (Koblitz et al., 2012; Jensen et al., 2018). Recording of clicks at varying degrees off-axis can lead to erroneous classification of echolocation click types. The criteria used to determine whether a click was on-axis or off-axis were based on methods described in previous studies (Madsen et al., 2004; Jensen et al., 2009; Kyhn et al., 2009; Fang et al., 2015). Specifically, the criteria were (1) click trains were single and did not overlap with other click trains; (2) clicks were detected by all five hydrophones, with the highest received level recorded on the central hydrophone; (3) the amplitude of clicks were higher than that of reflected clicks; and (4) the distance between the dolphins and the array had to be > 1 m and < 20 m. All extracted clicks were visually verified to ensure they did not contain surface and bottom reflections.

Localization of animal vocalizations plays an important role in understanding the spectral characteristics of dolphin sounds. Due to different propagation paths, a signal emitted by the source arrives at the various receivers with different time delays. Therefore, it is possible to use these time delays to calculate the location of the source. For source-level estimates, it is necessary to obtain the distance between the animals and the array. A schematic of a five-hydrophone array and a source sound located at coordinates (S_x, S_y, and S_z) are shown in Figure 3. The distance between the animals and the recording array can be determined by measuring differences in the time of arrival between the signal at the center and the four other hydrophones. The difference in the arrival time between the central and the other hydrophones was denoted as τ_{0l}, where $\tau = 1, 2$, and 3, and the distance in meters between the dolphins and the central hydrophone, R, was expressed as

$$R = \frac{2a^2 - c^2{\tau_{01}}^2 - c^2{\tau_{03}}^2}{2c(\tau_{01} + \tau_{03})} \qquad (2)$$

where a represents the distance between the central and the four other hydrophones and c represents the speed of sound.

The speed of sound was calculated from the Leroy equation as 1,520 m/s using the water temperature (23.5°C) and salinity (35 ppm) at the recording sites at sea (Leroy et al., 2008). The source level of echolocation clicks was calculated using Eq. (3):

$$SL = RL + TL = RL + \beta \log R + \alpha R \qquad (3)$$

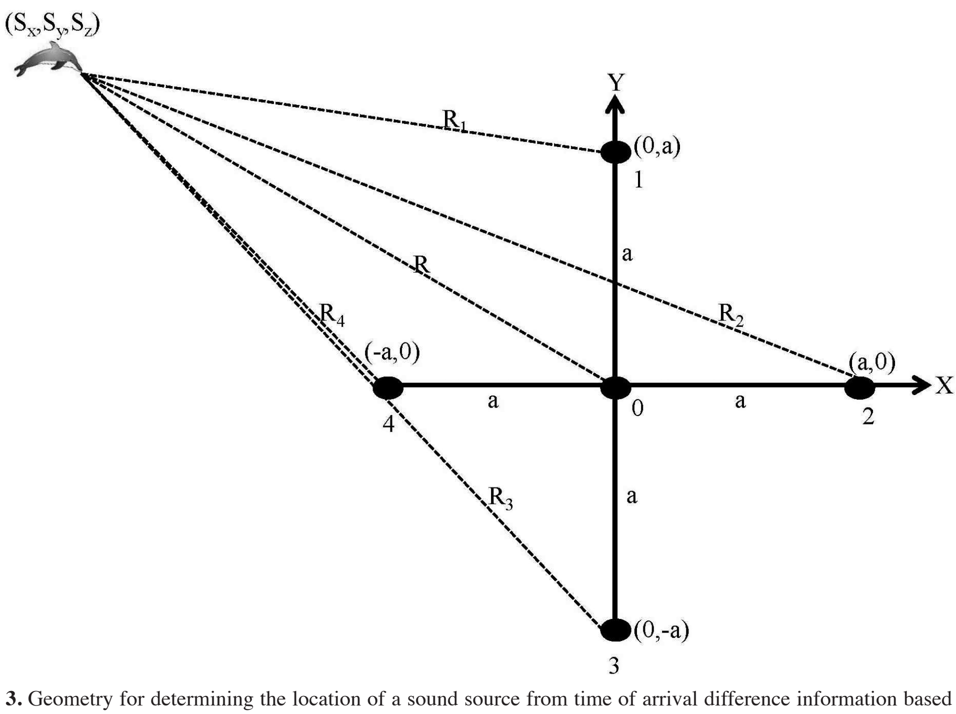

Figure 3. Geometry for determining the location of a sound source from time of arrival difference information based on a cross hydrophone array with five hydrophones

where RL is the received level, TL is the transmission loss, β is the spreading coefficient, and a is the frequency-dependent absorption coefficient.

Sound near the source propagates uniformly in all directions; thus, transmission loss was estimated from the sum of spherical spreading (Madsen & Wahlberg, 2007; DeRuiter et al., 2010). A spreading coefficient of 20 was used. The absorption coefficient was 0.03 dB^{m-1} at 105 kHz (close to the mean of the centroid frequency of the clicks in the current study). Other click parameters analyzed were the inter-click interval (ICI), 95% energy duration, peak frequency, centroid frequency, bandwidth (-3 dB, -10 dB, and rms), received level (peak-to-peak [p-p] and rms), energy flux density (EFD) calculated by 10*log to the time integral of the squared pressure over the duration of the click, and directivity index (Madsen & Wahlberg, 2007; de Freitas et al., 2018; Niu et al., 2019). Descriptive statistics (mean and standard deviation) and statistical analysis of echolocation click parameters were conducted using customized *MATLAB*, Version 7.1, with a significance level of 0.05.

Results

Over the 8 d of field surveys, a total of 3 h of acoustic recordings was collected at eight recording sites across the two regions (Figure 1). Free-ranging Indo-Pacific humpback dolphins encountered during the recordings were in groups ranging from two to seven individuals, with a mean (± SD) of 4.3 ± 1.6 individuals per group. A total of 140 on-axis clicks were detected from 65 click trains. The same number of on-axis clicks of captive humpback dolphins were selected from 1 h and 20 min of recordings. Differences in individual vocalizations were not considered in the current study.

Figure 4 presents an example of the normalized time domain waveform, cumulative energy curve, and power spectra of echolocation clicks produced by wild and captive Indo-Pacific humpback dolphins. All measured source parameters of on-axis clicks are summarized in Table 1. Both the free-ranging and captive Indo-Pacific humpback dolphins produced broadband transient clicks of short durations. The click 95% energy duration was shorter for free-ranging animals (21 ± 4 μs) than

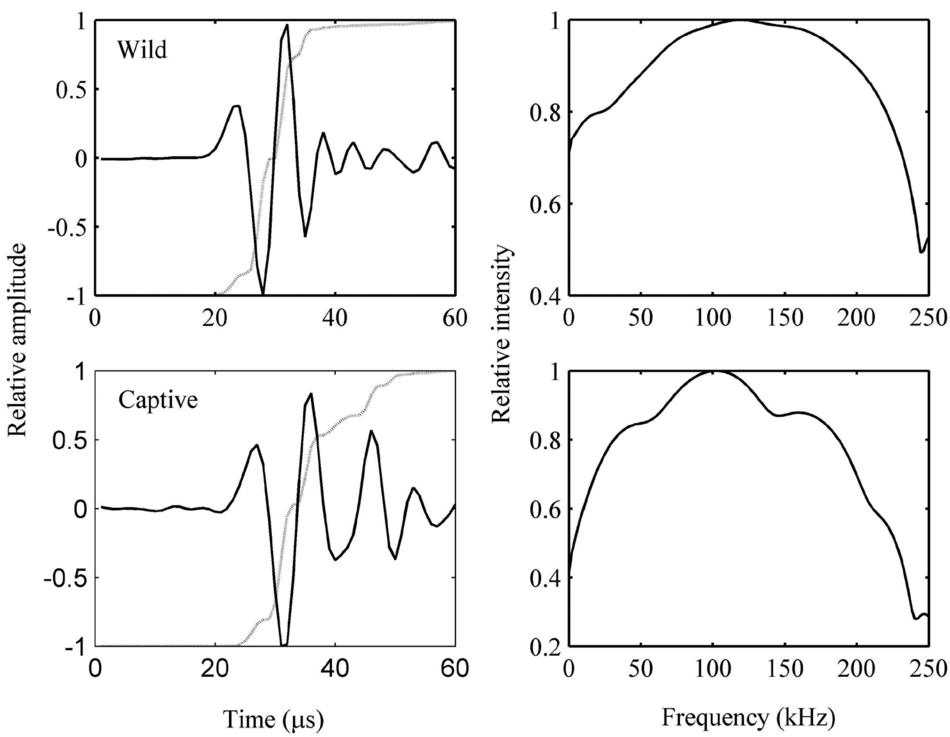

Figure 4. Representative on-axis echolocation clicks recorded from wild and captive Indo-Pacific humpback dolphins (*Sousa chinensis*). Time domain (black line) and cumulative energy curve (grey line) of wild and captive humpback dolphins are plotted on the left. Adjacent to the right are the corresponding individual power spectra, respectively (sampling frequency: 1 MHz, FFT size: 512 points, Hann window, normalized around the mean of the spectrum).

Table 1. Source parameters of the echolocation signals from wild Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Khanom and Donsak regions, Gulf of Thailand, compared with captive Indo-Pacific humpback dolphins in ocean park in Trat Province, Thailand. The bold values of parameters indicate the parameters are statistically different.

	Free-ranging Indo-Pacific humpback dolphins in Khanom and Donsak, Gulf of Thailand		Captive Indo-Pacific humpback dolphins in ocean park in Trat Province, Thailand	
Parameters	Mean ± SD	Range	Mean ± SD	Range
Number of on-axis clicks	140		140	
Duration (µs)	21 ± 4	14-32	36 ± 2	24-41
SL_{p-p} (dB re 1 µPa p-p)	**185 ± 5.8**	172-197	**169 ± 2.8**	159-175
SL_{rms} (dB re 1 µPa rms)	172 ± 5.7	158-184	155 ± 2.5	147-160
Energy flux density (dB re 1 $\mu Pa^2 s$)	**126 ± 5.6**	114-138	**111 ± 2.5**	103-116
Peak frequency (kHz)	107 ± 9.5	78-125	103 ± 2.9	97-113
Centroid frequency (kHz)	106 ± 7.1	82-117	105 ± 3.7	93-109
-3 dB bandwidth (kHz)	66 ± 13	32-93	58 ± 6.0	43-70
-10 dB bandwidth (kHz)	139 ± 15	109-171	128 ± 8.3	109-140
rms bandwidth (kHz)	31 ± 3.1	22-39	29 ± 0.8	26-30
Inter-click interval (ms)	37 ± 13.5	17-67	25 ± 1.2	22-32
Range (m)	11.3 ± 2.9	4.8-17.9	4.0 ± 0.7	2.2-6.3

captive animals (36 ± 2 µs). However, the ICIs (37 ± 13.5 ms) for free-ranging animals were longer than for captive animals (25 ± 1.2 ms). The mean p-p, rms, and EFD source levels for free-ranging animals were 185 ± 5.8 dB re 1 µPa at 1 m, 172 ± 5.7 dB re 1 µPa at 1 m, and 126 ± 5.6 dB re 1 $\mu Pa^2 s$, respectively. The source levels were lower for captive animals than for free-ranging animals (169 ± 2.8 dB re 1 µPa at 1 m, 155 ± 2.5 dB re 1 µPa at 1 m, and 111 ± 2.5 dB re 1 $\mu Pa^2 s$, respectively). The power spectra of on-axis clicks appeared to be unimodal (Figure 4), with equal peak frequencies of 107 ± 9.5 kHz for free-ranging animals and 103 ± 2.9 kHz for captive animals. The other frequency domain parameters, such as centroid frequencies (106 ± 7.1 kHz and 105 ± 3.7 kHz for free-ranging and captive animals, respectively) and rms bandwidths (31 ± 3.1 dB and 29 ± 0.8 dB for-free-ranging and captive animals, respectively), were also similar.

There was no significant difference between click centroid frequencies (p = 0.235) and rms bandwidths (p = 0.072) for Indo-Pacific humpback dolphins in the wild or in captivity (Figure 5). Statistical analysis found that the source levels ($p < 0.001$ for both p-p and EFD) of Indo-Pacific humpback dolphins' on-axis echolocation signals varied significantly between wild and captive environments (Figure 6). Figure 7 indicates that centroid frequencies for humpback dolphins in the wild and in captivity increased slowly with the increase of p-p source levels. Centroid frequencies increased 275 Hz per 1 dB increase in p-p source levels for free-ranging humpback dolphins and ~100 Hz per 1 dB for captive humpback dolphins. Regression lines indicate that the value of coefficient of determination, R^2, for free-ranging animals was low ($R^2 = 0.05$), but the value of R^2 for captive animals was higher than for wild animals ($R^2 = 0.31$).

Discussion

In this study, we present the first comparisons of the acoustic parameters of echolocation clicks produced by wild and captive Indo-Pacific humpback dolphins in Thailand. Our results show that free-ranging and captive Indo-Pacific humpback dolphins produce broadband, short-duration echolocation clicks that are similar to other odontocetes of similar body size such as the bottlenose dolphins (Wahlberg et al., 2011b; de Freitas et al., 2015), Australian snubfin dolphins (*Orcaella heinsohni*; de Freitas et al., 2018), and Irrawaddy dolphins (*Orcaella brevirostris*; Niu et al., 2019). Previous studies examined the acoustic behavior of Indo-Pacific humpback dolphins, Irrawaddy dolphins, and Indo-Pacific finless porpoises (*Neophocaena*

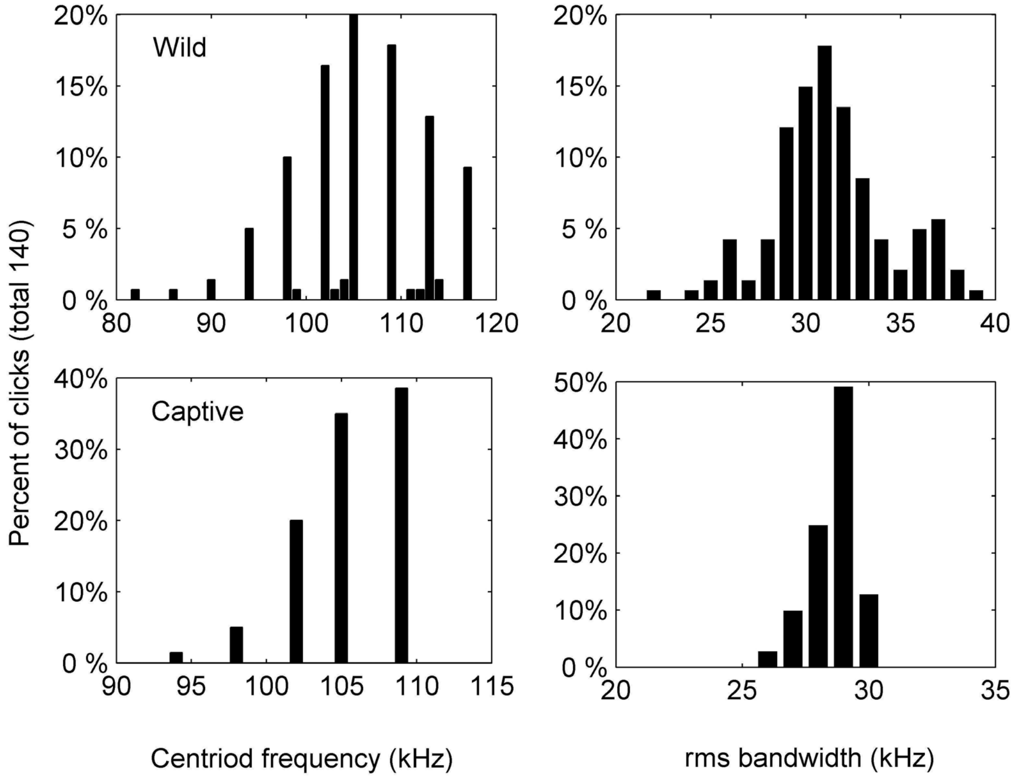

Figure 5. Histograms of centroid frequency and rms bandwidth for on-axis clicks of Indo-Pacific humpback dolphins recorded in the wild and in captivity. Bin width for peak frequency is 2 kHz, and bin width for rms bandwidth is 1 kHz.

phocaenoides) in the Gulf of Thailand (Beasley & Davidson, 2007; Jutapruet et al., 2017). However, the extent of the habitat use, population structure, and relative abundance of these three species are poorly understood (Jutapruet et al., 2017). Identification of these data can provide baseline information needed for developing precautionary and practical zoning in the design of marine mammal protected areas in the region. Only a few habitat protections and management measures designed for these three cetacean species are currently implemented in the central-western Gulf of Thailand (Jutapruet et al., 2015). Consequently, there has been an increased interest in acoustic repertoires of these three species for use in PAM for conservation efforts.

Although the clicks of Indo-Pacific humpback dolphins have been investigated in many studies (Goold & Jefferson, 2004; Sims et al., 2012), few have reported on the characteristics of the on-axis clicks of Indo-Pacific humpback dolphins using a hydrophone array and recording system capable of recording the on-axis clicks of species (Fang et al., 2015). The acoustic parameters of echolocation clicks in free-ranging Indo-Pacific humpback dolphins in Gulf of Thailand were similar to those of clicks reported by Fang et al. (2015) using the same five-hydrophone array recording system in Sanniang Bay in China. Sanniang Bay is characterized by shallow waters with a depth of < 6 m and speed of sound of 1,518 m/s, similar to the depths (< 7 m) and speed of sound (1,520 m/s) in this study. The mean distance between dolphins and hydrophones in the two studies were also similar (9.7 and 11.3 m for dolphins in Sanniang Bay, China, and Gulf of Thailand, respectively).

Although dynamic biosonar adjustments likely contribute to the variation in source parameters reported in many studies (Au & Benoit-Bird, 2003; Kloepper et al., 2014), there is a paucity of knowledge on the relationship between environment and variation in toothed whale biosonar parameters (de Freitas et al., 2015; Ladegaard & Madsen, 2019). It has been certified that source level increases with increasing target range (Au & Benoit-Bird, 2003; Li et al., 2006). The mean distance between Indo-Pacific humpback dolphins and the hydrophone array was 11.3 m in the wild and 4 m in captivity. The calculated source levels with an average of

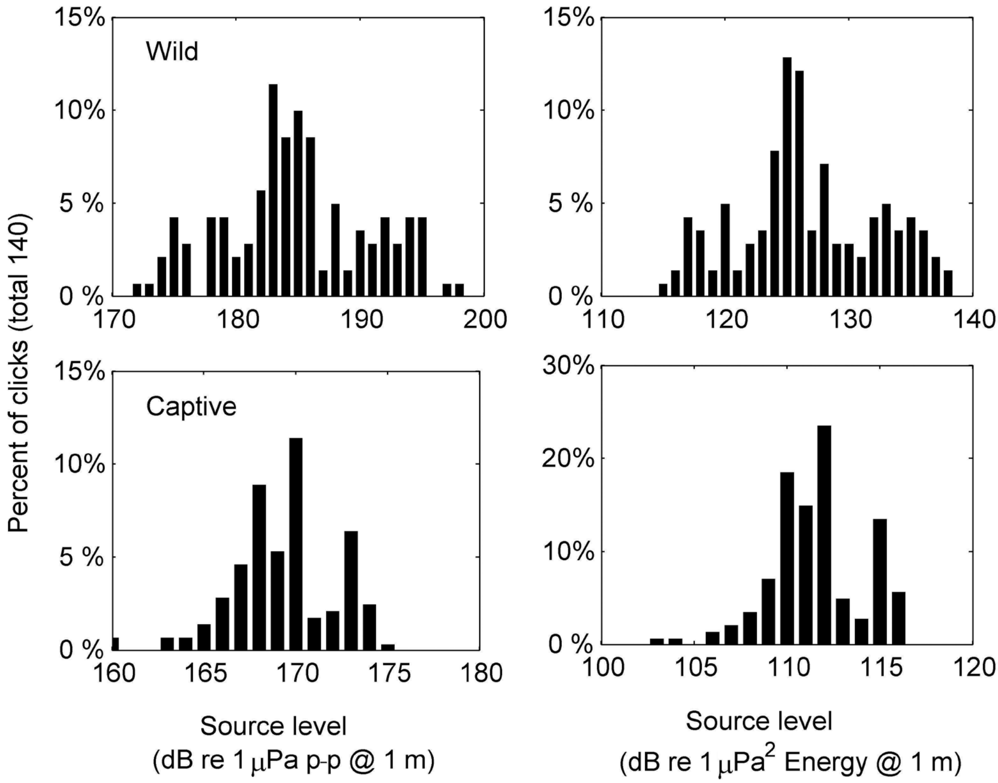

Figure 6. Histograms of p-p source level (left) and EFD source level (right) for on-axis clicks of Indo-Pacific humpback dolphins in the wild and in captivity; bin width is 1 kHz.

185 dB re 1 μPa for wild humpback dolphins were higher than clicks of captive humpback dolphins (average = 169 dB re 1 μPa). The captive humpback dolphins in this study lived in a round pool with substantial surface reverberation caused by the hard walls of the pool. The intensity of reverberation is directly proportional to the intensity of the projected signal. Therefore, animals probably produced lower source levels to reduce the reverberation interference in a reverberation limited situation, and the lower source levels may have been a result of that reverberant environment rather than the distance to the hydrophone (Au, 1993; Wahlberg et al., 2011a).

Previous studies with bottlenose dolphins indicate that when in pools and pens, dolphins typically produce clicks with low centroid frequencies and narrower frequency bandwidths compared to the clicks of conspecifics recorded in open water experiments (Au, 1993). However, there was no significant difference of centroid frequencies (p = 0.235) and rms bandwidths (p = 0.072) between free-ranging and captive Indo-Pacific humpback dolphins (Table 1). This result is consistent with centroid frequencies (106.9 ± 10.9 kHz) of young humpback dolphins in captivity as described by Li et al. (2013). Higher frequencies and wider bandwidths of echolocation clicks provide higher target detection and discrimination capability (Au, 1993). The centroid frequency of humpback dolphins in this study showed a weak positive correlation to p-p source level ($R^2 = 0.05$ for wild Indo-Pacific humpback dolphins and $R^2 = 0.31$ for captive Indo-Pacific humpback dolphins; Figure 7). The positive relationship of centroid frequencies with the p-p source levels detected here were also reported in this species in Sanniang Bay, China (Fang et al., 2015).

Click durations and ICIs were significantly different between free-ranging and captive Indo-Pacific humpback dolphins ($p < 0.001$). Click durations of wild humpback dolphins were shorter than those of captive humpback dolphins. However, free-ranging humpback dolphins produced longer ICIs than captive humpback dolphins. ICIs of Indo-Pacific humpback dolphins were similar to a previous study of dolphins in Sanniang Bay, China (Fang et al., 2015). Toothed whales normally wait until the echo from a potential target has been received before emitting a subsequent click (Au, 1993). Therefore, ICIs exceed

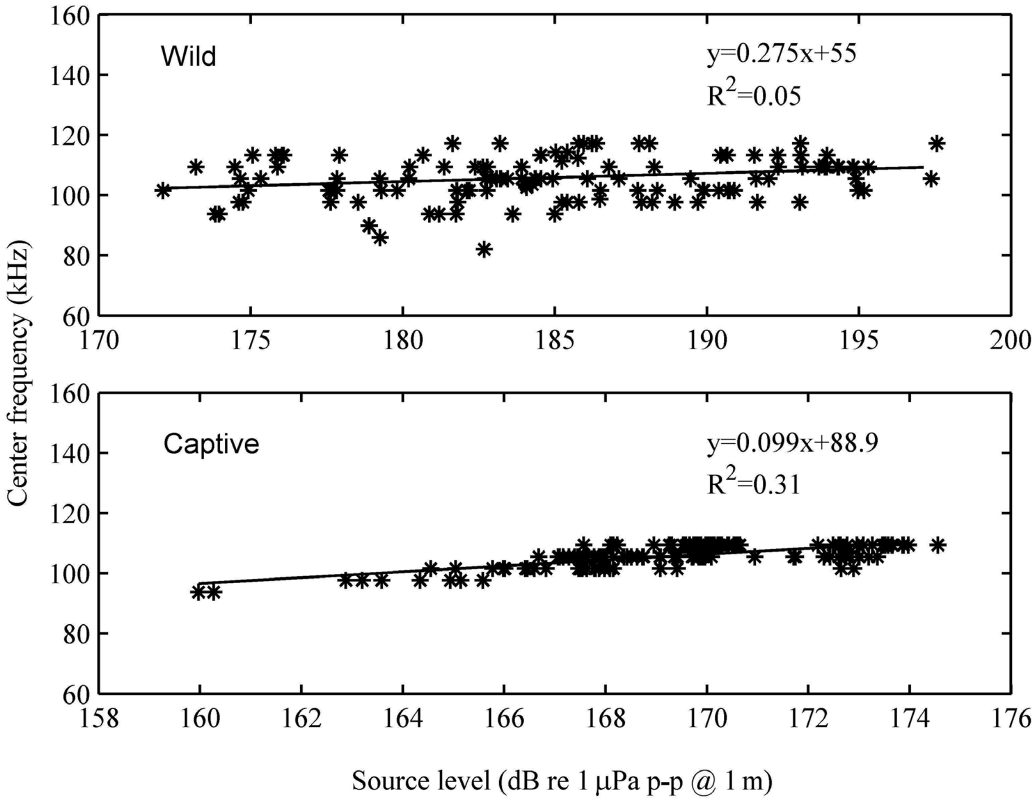

Figure 7. Centroid frequencies of on-axis clicks as a function of p-p source levels. Clicks of animals in the wild and in captivity increase in centroid frequency with increasing p-p source level. Linear regression (black line) of animals in the wild and in captivity have an R^2 value of $R^2 = 0.05$ and $R^2 = 0.31$, respectively.

the two-way travel time plus a processing lag time. Captive humpback dolphins with shorter ICIs in this study indicate that animals limited to shorter echolocation distances will produce clicks at faster repetition rates. Shorter ICIs led to a higher temporal resolution of their auditory scene, and the simultaneous reduction in source levels decrease the ensonified range (Wisniewska et al., 2012).

Although click parameters were different between wild and captive Indo-Pacific humpback dolphins, it is unclear whether these parameters were affected by the environment. More research should be carried out in the future to address the issue.

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