

Sound Characteristics and Primary Descriptions of Vocalizations Associated with Behaviours of Captive Irrawaddy Dolphins (*Orcaella brevirostris*)

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Abstract

Even though there have been several studies on vocal repertoires and behaviours of Irrawaddy dolphins (*Orcaella brevirostris*) in recent decades, important pieces of information are still missing, especially the sounds produced in captivity where environmental differences can affect their physical and acoustic behaviour. Over 40 h of observations in March and November 2014, with almost 7,000 vocalizations sampled, it was determined that the captive Irrawaddy dolphins produced various types of sound, including two types of clicks ($n = 3,898$), five types of pulsed sounds ($n = 2,807$), and nine types of whistles ($n = 44$). This work also describes three newly discovered pulsed sounds and all nine whistle types in this species. Clicks were observed most frequently during feeding and swimming in navigational contexts. Pulsed sounds were mainly used in social or emotional contexts associated with various behaviours, including aggression, sexual arousal, and tourist encounters. Whistles, on the other hand, were scarcely heard, which might imply that the communication was not necessary. Whistling behaviours were contradictory to those reported for other wild delphinids; this difference was potentially caused by habituation in captivity. Vocalizations, which increased concurrently with activity levels, were recorded at a significantly higher rate ($p < 0.05$) when tourists were present during swim-with-dolphin programs. This is the first study to correlate Irrawaddy dolphin sounds and behaviours in captivity and represents the first time that all three sound categories have been recorded for this species in captivity.

Key Words: cetacean, behaviour, acoustic, sound, Irrawaddy dolphin, *Orcaella brevirostris*, captivity, swim-with-dolphin program, vocalization

Introduction

It has been debated whether dolphins have their own language since ancient times. To begin decoding the language, we must understand the basic characteristics of the *call*, which is an important component. Delphinid sounds are generally divided into three main categories: (1) clicks, (2) pulsed sounds, and (3) whistles (Frankel, 2009). Clicks are mainly used in navigation through echolocation (Au, 2009). Pulsed sounds play important roles in communication, social context, and emotional expression (Herman & Tavolga, 1980; Overstrom, 1983; Herzing, 1988, 1996; Dawson, 1991; Connor & Smolker, 1996; Janik, 2000a; Van Parijs & Corkeron, 2001; Lammers et al., 2006; Rankin et al., 2007). Whistles primarily serve in communication, self-identification, group cohesion, and social context (Sayigh et al., 1990; Smolker et al., 1993; Janik & Slater, 1998; Janik, 2000b; Rasmussen & Miller, 2002; Acevedo-Gutiérrez & Stienessen, 2004; Watwood et al., 2004; Díaz López & Shirai, 2009). Even though delphinid acoustic behaviours have been well studied all around the world for many decades, most of the previous research concentrated on bottlenose dolphins (*Tursiops* spp.) (Au, 1993; Reiss et al., 1997; Janik & Slater, 1998; Sayigh et al., 1999; Datta & Sturtivant, 2002; Harley, 2008; López-Rivas & Bazúa-Durán, 2010; Díaz López, 2011). Thus, we are interested in vocalizations of a delphinid species distributed in Thailand, the Irrawaddy dolphins (*Orcaella brevirostris*).

Some studies have been conducted on the acoustic behaviour of Irrawaddy dolphins in both the wild and in captivity. The very first study in captivity discovered only basic vocalizations, captured in short pulses called *pulse trains*, with the dominant frequency of about 60 kHz (Kamminga et al., 1983). It is believed that pulsed trains are used for echolocation. No audible whistles were detected. Later, studies on riverine populations in the Mahakam and Mekong Rivers (Borsani, 1999) and a coastal population in Balikpapan Bay in East Kalimantan, Indonesia (Kreb & Borsani, 2004) found various types of broadband single and multiple clicks, narrow- and broadband pulsed sounds, and narrowband frequency-modulated whistles. The most recent study by Jensen et al. (2013) reported that Irrawaddy dolphins living in coastal and riverine habitats produced echolocation clicks with a centroid frequency around 95 kHz, a high repetition rate (mean of 45 ms for inter-click interval), and a low peak-to-peak source level (about 195 dB re 1 μ Pa at 1 m) compared to other wild delphinids. These differences may reflect an adaptation to the shallow freshwater habitats that are acoustically complex in structure, resulting in high reverberation and acoustic clutter. Although Van Parijs et al. (2000) described all the sound types belonging to an Irrawaddy dolphin population inhabiting the coastal waters of northern Australia, this population was later classified as Australian snubfin dolphin (*Orcella heinsohni*) based on concordant character differences in morphology, osteology, and genetics (Beasley et al., 2002, 2005). Hence, the primary objectives in this study were to characterize all sound types below 22 kHz produced by captive Irrawaddy dolphins. This study also represents an initial effort to understand delphinid behaviours corresponding to their vocalizations in captivity. We suggest that with enhancements, this research field could begin to lay the groundwork that would benefit animal welfare.

Methods

Study Site and Animals

Three male Irrawaddy dolphins were studied in captivity at Pattaya Dolphin World & Resort, Chonburi Province, Thailand. All were adults with an average age of 30 y; all were in good health; and each had been habituated to the pool for 4 y. Each dolphin was identified by the shape of its dorsal fin, scars, and natural marks on the dorsal fin and surrounding area. The resort pool was made of concrete; was irregular in shape (pear-like); and was about 25 m in width, 50 m in length, and varied from 5 to 6 m in depth. The 6,000 m³ of recirculated sea water had poor visibility out to about 2 m. The

pool was divided into three stations, each with a swim platform for tourists to sit on during swim-with-dolphin (SWD) programs.

Recording Equipment

Acoustic recordings of underwater sounds were made using The Cetacean Research™ CR3 hydrophone (frequency range: 0.0001 to 240 kHz, sensitivity: -210 dB, re 1 V/ μ Pa) connected to a PreSonus AudioBox™ USB recording system (frequency response: 14 Hz to 70 kHz \pm 3.0 dB) at a sample rate of 44.1 kHz, and were recorded in wav file on SONY VAIO T Series laptop on a Microsoft Windows® 8.1 operating system. Video recording was done using SONY Cyber-Shot DSC-WX1 and an iPad Air.

Acoustic Data Collection

Observations were conducted for 5 d in March and 10 d in November 2014 during authorized periods, generally 0830 to 1730 h as approved by the owner of the dolphinarium. Acoustic recordings were collected during two types of sessions: (1) tourist session when tourists were present in the pool area and were participating in SWD—during these sessions, each dolphin stayed at one station, and its sounds were obtained individually; and (2) non-tourist session when tourists were absent and only the observer, trainers, and authorized staff were present in the pool area—during these sessions, all dolphins freely swam through all areas of the pool. A typical day included five rounds each of tourist and non-tourist sessions but varied depending on the number of tourists present. The total observation time was approximately 42 h. Sounds were recorded on the hydrophone at a depth of 2 m in both tourist and non-tourist sessions, while the observers stayed at designated viewing areas about 3 m from the edge of the pool.

Behavioural Data Collection

Behavioural data was continuously recorded by video camera concurrently with the acoustic recordings. According to preliminary observations, various behaviours exhibited in both tourist and non-tourist sessions generally fell into nine categories: (1) *Feeding* – dolphins consumed food items; (2) *Interaction* – dolphins engaged in physical contacts with the tourists or trainers—tourists were allowed to touch all body parts except the genital area; (3) *Jumping* – dolphins aerially jumped with partial or whole body displayed; (4) *Playing* – dolphins interacted with artificial objects such as balls and flying discs; (5) *Socializing* – dolphins socialized with one another, including swimming alongside each other and having physical contact—any signs of aggressive or sexual orientations were excluded;

(6) *Swimming* – dolphins swam individually; (7) *Tourist Encounter* – the dolphins spontaneously swam toward the tourists while they were entering or leaving the pool area, as well as while they were exchanging/relocating the stations within the pool during SWD; (8) *Water Spitting* – dolphins spit water—although this is natural behaviour, it was never displayed unless the animals were directed to do so by their trainers; and (9) *Sexual Arousal* – male dolphins were made to ejaculate by the dolphinarium's veterinarian—this husbandry behaviour was trained to collect the sperm, and it was conducted in a private session where only the veterinarian and the observer were allowed to be present within the pool. From these behaviours, only feeding, jumping, and playing were trained behaviours; dolphins were ordered by hand signals from the trainers to perform each behaviour. Additional behaviours were observed beyond these and will be described in the results. All experiments and observations were granted permission by the dolphinarium and were conducted under direct supervision of an authorized veterinarian. This research was approved by Chulalongkorn University Institutional Animal Care and Use Committees (IACUC) (Protocol Number 1423004).

Acoustic Data Analysis

The acoustic data was digitized as spectrograms and waveforms using Adobe *Audition*® CC, Version 6.0, and *Praat*, Version 5.3.66. Sound data was then divided into three main categories: (1) clicks, (2) pulsed sounds, and (3) whistles. Only good signals, based on individual signal qualities where all parameters of the spectral contour (spectrogram shape) were distinctly measurable, were used for further numerical analysis. After initial characterization, clicks and pulsed sounds were further analyzed statistically based on the following parameters: duration, click/pulse rate, repetition rate, frequency range, minimum frequency, maximum frequency, dominant frequency, inter-click interval (ICI), and number of harmonic structures within pulses. For whistles, the start frequency, end frequency, number of harmonics, and frequency modulation were also measured in addition to the other metrics described. However, each whistle type was classified based on the spectrogram shape only.

Statistical Analysis

All statistical analysis was performed in *Statgraphics*® (Centurion XV.II). The multiple comparison test (Dwass, 1960) or the Kruskal-Wallis test (Kruskal & Wallis, 1952) were used to test whether there was a difference for each parameter within each sound type due to a low

dolphin number ($N = 3$). The paired t test was used to determine if there were differences of vocalization rates (number/min) in each sound type between tourist and non-tourist sessions.

Behavioural Data Analysis

The video-recorded behavioural data were visually analyzed together with the acoustic data. Each behaviour associated with a vocalization was determined by time-lapsing the behaviours and the recorded vocalizations.

Results

We obtained a total of 6,749 vocalization samples, which consisted of clicks ($n = 3,898$), pulsed sounds ($n = 2,807$), and whistles ($n = 44$) from over 40 h of acoustic recording. All of the values reported below are in the form of range (mean \pm standard deviation [SD]).

Clicks

Individual clicks were found in series of clicks commonly referred to as *click trains*. Clicks were broadband in frequency with a range from 0.3 to above 22 kHz. The minimum frequency was 0.3 to 18.7 kHz (6.9 ± 2.3). Each click train consisted of 2 to 702 clicks (59.5 ± 75.9), with a repetition rate of 1 to 882 clicks/s (37.4 ± 38.2). The duration of click trains was incredibly wide in range from 8 ms to 19 s (1.9 ± 2.3 s). Clicks were recorded mostly during feeding, followed by socializing and swimming. Clicks were produced significantly more often during the tourist sessions ($p < 0.05$).

Clicks were divided into two types based on differences in the repetition rate or ICI patterns within the train: (1) clicks with constant ICI and (2) clicks with fluctuating ICI (Figure 1). Co-analysis of video recordings revealed that clicks with constant ICI were usually used for orientation and common navigation to locate unknown objects or the surrounding environment; clicks with fluctuating ICI were used while dolphins were approaching targets such as fish thrown by the trainers during feeding or artificial objects and tourists. Clicks with fluctuating ICI usually started with a high repetition rate followed by a low repetition rate and then ended with a high repetition rate (Figure 1).

Pulsed Sounds

Pulsed sounds consisted of both narrow- and broadband frequencies. There were five types of pulsed sounds (Figure 2; Table 1): (1) Crack, (2) Creak, (3) Raspberry, (4) Scrabble, and (5) Squeak. Pulsed sounds were different from each other primarily in pulse rate and repetition rate, followed by minimum frequency and ICI.

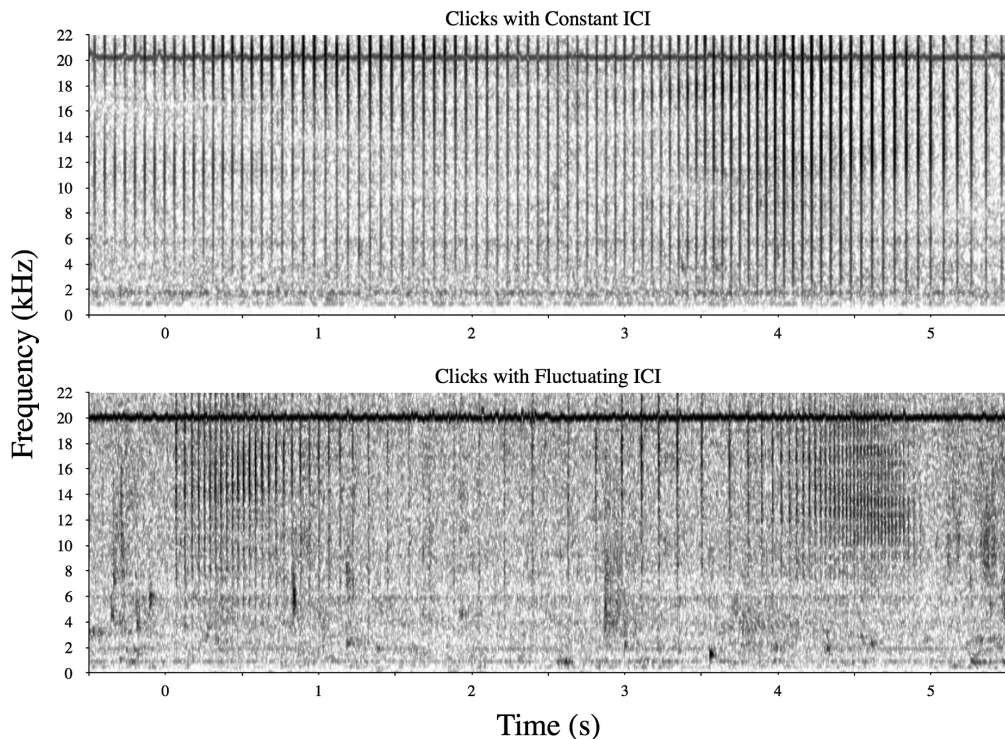


Figure 1. Spectrogram representations of two types of clicks produced by captive Irrawaddy dolphins (*Orcaella brevirostris*): (1) clicks with constant inter-click intervals (ICI) and (2) clicks with fluctuating ICI (The intense narrowband frequencies at 20 kHz were anomalies produced by our recording system.)

Dolphins produced significantly more pulsed sounds during the tourist session ($p < 0.05$).

Crack—Cracks (Figure 2), a newly described pulsed sound, had a unique sound like a door creaking and were short broadband pulses with a frequency range from 0.1 to above 22 kHz. Cracks consisted of 1 to 192 pulses (17.9 ± 16), with a repetition rate of 1 to 477 pulses/s (69.9 ± 35.5). Cracks had low minimum frequencies at 0.1 to 16 kHz (1.7 ± 1.1), short durations lasting from 7 ms to 3.5 s (0.3 ± 0.3 s), and narrow ICIs of 1 to 395 ms (17.4 ± 31.7). Cracks also had a fluctuating ICI within a pulse, which is similar to clicks with fluctuating ICIs, but no distinct ICI patterns could be determined. Cracks ($n = 1,900$) were heard the most compared to other pulsed sounds and were emitted significantly more often when tourists were present in the pool area ($p < 0.05$), particularly when the dolphins were playing with balls and flying discs, and during tourist encounters. Cracks were also produced simultaneously along with various behaviours such as interactions

with humans, feeding, jumping, swimming, and even when being ejaculated.

Creak—Creaks (Figure 2) were narrowband pulsed sounds with a continuous wave-like structure and sound similar to a buzzing sound. Creaks produced by captive Irrawaddy dolphins resembled those produced by wild Irrawaddy dolphins, which were first described by Kreb & Borsani (2004). Creaks were emitted in frequency ranges from 0.2 to above 22 kHz. Creaks consisted of 2 to 73 pulses (26.5 ± 16.3), with a high repetition rate of 16 to 842 pulses/s (136.6 ± 117.4), and were 4 ms to 1.6 s in duration (0.2 ± 0.2 s). The minimum frequency was 0.2 to 7.7 kHz (1.7 ± 0.9). Creaks looked similar to cracks, but the duration, pulse rate, and repetition rate were significantly different ($p < 0.05$). Creaks ($n = 458$) were produced in association with several behaviours such as interaction, playing, feeding, water spitting, and jumping during tourist sessions.

Raspberry—Raspberries (Figure 2) were broadband pulses with a frequency range from 0.1 to above 22 kHz. Raspberries consisted of 2

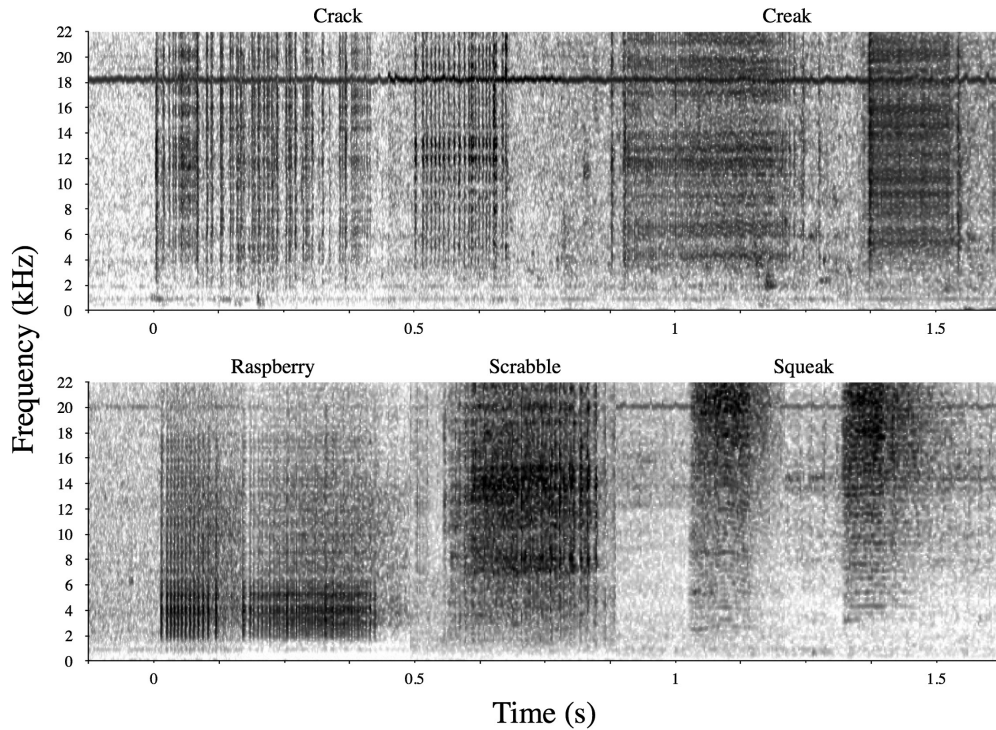


Figure 2. Spectrogram representations of five types of pulsed sounds produced by captive Irrawaddy dolphins: (1) Crack, (2) Creak, (3) Raspberry, (4) Scrabble, and (5) Squeak (The intense narrowband frequencies at 18 and 20 kHz were anomalies produced by our recording system.)

Table 1. Descriptive statistics for acoustic parameters of captive Irrawaddy dolphin (*Orcaella brevirostris*) pulsed sounds ($n = 2,807$) with range and mean \pm SD, including the associated behaviours

Category	Number	Duration (s)	Pulse rate (pulses)	Repetition rate (pulses/s)	Inter-click interval (ms)	Frequency range (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Behaviour
Crack	1,900	< 0.1 - 3.5 (0.3 \pm 0.3)	1 - 192 (17.9 \pm 16.0)	1 - 477 (69.9 \pm 35.5)	1 - 395 (17.4 \pm 31.7)	0.1 - > 22	0.1 - 16 (1.7 \pm 1.1)	> 22	F, I, J, P, S, SA, So, TE, W
Creak	458	< 0.1 - 1.6 (0.2 \pm 0.2)	2 - 73 (26.5 \pm 16.3)	16 - 842 (136.6 \pm 117.4)	--	0.2 - > 22	0.2 - 7.7 (1.7 \pm 0.9)	> 22	F, I, J, P, TE, W
Raspberry	380	< 0.1 - 1.4 (0.3 \pm 0.2)	2 - 57 (15.9 \pm 10.3)	15 - 347 (64.3 \pm 35.1)	1 - 210 (8.6 \pm 16.1)	0.1 - > 22	0.1 - 8.7 (1.5 \pm 0.7)	> 22	F, I, J, P, So, TE, W
Scrabble	66	< 0.1 - 1.8 (0.3 \pm 0.2)	4 - 200 (31.1 \pm 24.3)	29 - 181 (91.4 \pm 28.9)	1 - 9 (1.9 \pm 1.7)	0.5 - > 22	0.5 - 3.5 (1.6 \pm 0.8)	> 22	I, P, SA, TE
Squeak	3	0.1 - 0.5 (0.3 \pm 0.1)	52 - 62 (56 \pm 5.3)	147 - 278 (232.7 \pm 74.0)	--	0.1 - > 22	0.1 - 0.2 (0.1 \pm 0.06)	> 22	A

Behaviours: A = aggression, F = feeding, I = interaction/physical contact, J = jumping, P = playing, S = swimming, SA = sexual arousal, So = socializing, TE = tourist-encounter, and W = water spitting

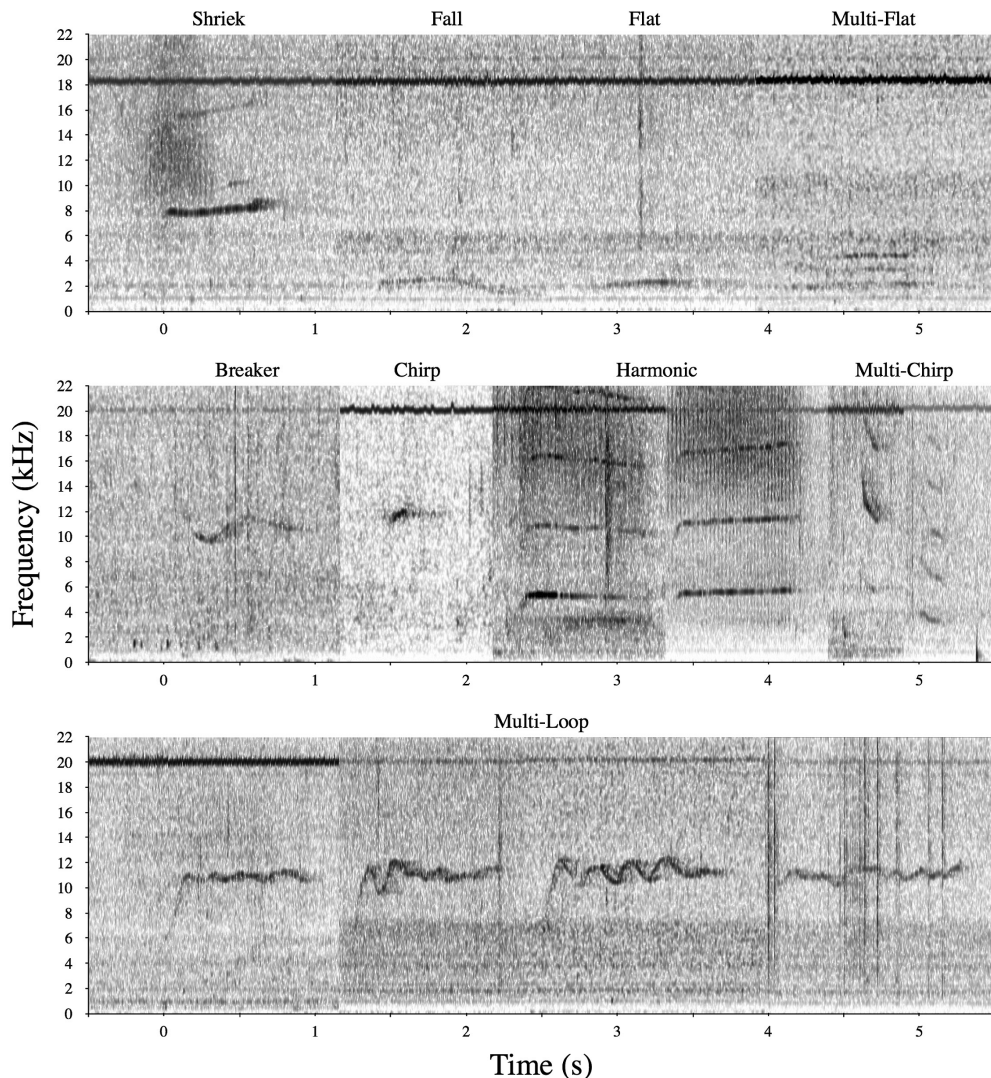


Figure 3. Spectrogram representations of nine types of whistles produced by captive Irrawaddy dolphins: (1) Shriek, (2) Fall, (3) Flat, (4) Multi-Flat, (5) Breaker, (6) Chirp, (7) Harmonic, (8) Multi-Chirp, and (9) Multi-Loop (The intense narrowband frequencies at 18 and 20 kHz were anomalies produced by our recording system.)

to 57 pulses (15.9 ± 10.3), with a repetition rate of 15 to 347 pulses/s (64.3 ± 35.1). Raspberries had ICIs ranging from 1 to 210 ms (8.6 ± 16.1), with a minimum frequency at 0.1 to 8.7 kHz (1.5 ± 0.7) and a duration of 30 ms to 1.4 s (0.3 ± 0.2 s). The ICIs of raspberries differed from those in other pulsed sounds by two main characteristics: (1) they were broadband signals with constant ICIs (which varied among individuals) and (2) they were shorter than other pulsed sounds, with the exception of scrabbles. Raspberries also

had significant differences in two acoustic parameters: (1) pulse rate and (2) repetition rate ($p < 0.05$). Raspberries ($n = 380$) were recorded mostly during tourist encounters and were also recorded along with the following behaviours: interaction, jumping, playing, water spitting, and feeding. The name *raspberry* was previously referred to a type of pulsed sounds produced by several delphinids (Herzing, 2000); however, there was no description of any acoustic parameter in the study, except the less than 1 s of the duration. Thus, we opted to use

Table 2. Descriptive statistics for acoustic parameters of captive Irrawaddy dolphin whistles ($n = 44$) with value given as mean \pm SD, including the associated behaviours

Category	Number	Duration (s)	Frequency range (kHz)	Start frequency (kHz)	End frequency (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Behaviour
Breaker	1	0.9	9.6 - 12.1	12.1	10.3	9.6	12.1	I
Chirp	1	0.1	11.2 - 12	11.2	12	11.2	12	S
Fall	5	0.5 - 1.5 (1.1 \pm 0.4)	1.1 - 2.7	1.1 - 2.3 (2.0 \pm 0.5)	1.2 - 1.5 (1.4 \pm 0.2)	1.1 - 2.7 (1.6 \pm 0.7)	1.3 - 2.6 (2.3 \pm 0.6)	S
Flat	3	0.3 - 1.6 (0.9 \pm 0.7)	1.9 - 3.7	1.9 - 3.7 (2.9 \pm 0.9)	2.3 - 3.5 (3.0 \pm 0.6)	1.9 - 3.7 (2.9 \pm 0.9)	2.4 - 3.6 (3.2 \pm 0.7)	S
Harmonic	3	0.4 - 0.8 (0.6 \pm 0.2)	4.7 - 22	4.7 - 4.9 (4.8 \pm 0.1)	5.3 - 10.3 (7.2 \pm 2.7)	4.7 - 4.9 (4.8 \pm 0.1)	17.5 - 22 (20.5 \pm 2.6)	S
Multi-Chirp	2	0.1 - 0.2 (0.1 \pm 0.04)	3.8 - 20.6	3.8 - 14.8 (9.3 \pm 7.8)	6.3 - 11.5 (8.9 \pm 3.7)	3.4 - 5.7 (4.6 \pm 1.6)	17.6 - 20.6 (19.1 \pm 2.1)	I, S
Multi-Flat	12	0.2 - 0.7 (0.4 \pm 0.1)	1.8 - 6.1	1.8 - 4.8 (3.5 \pm 0.8)	2.2 - 5 (3.5 \pm 0.9)	1.8 - 3.7 (2.5 \pm 0.5)	4 - 6.1 (5.0 \pm 0.6)	S
Multi-Loop	16	0.7-1.3 (0.9 \pm 0.3)	2.3 - 12.3	2.3-10.9 (7.4 \pm 2.5)	8.9 - 11.7 (10.9 \pm 0.6)	2.3 - 11.7 (7.4 \pm 2.5)	11.2 - 12.3 (11.8 \pm 0.4)	I, Re, S
Shriek	1	0.7	7.5 - 16.7	7.5	8.6	7.5	16.7	R

Behaviours: I = interaction/physical contact, R = riding/rode by trainer, Re = regrouping, and S = swimming

this name for the pulsed sound described above to describe its rasp-like-sound characteristic.

Scrubble—Scrabbles (Figure 2), another newly described pulsed sound, were broadband pulses with a frequency range from 0.5 to above 22 kHz and a minimum frequency at 0.5 to 3.5 kHz (1.6 \pm 0.8). Scrabbles consisted of 4 to 200 pulses (31.1 \pm 24.3), with a repetition rate of 29 to 181 pulses/s (91.4 \pm 28.9) and a duration of 85 ms to 1.8 s (0.3 \pm 0.2 s). Generally, scrabbles looked similar to cracks; however, scrabbles had extremely narrow ICIs: 1 to 9 ms (1.9 \pm 1.7). Moreover, among the broadband types, scrabbles had the shortest ICI and highest pulse rate. Thus, we used these parameters to exclude scrabbles from the other pulsed sounds. Scrabbles ($n = 66$) were produced most often during playing, tourist encounter, and interaction activities.

Squeak—Squeaks (Figure 2) were narrowband signals that were clearly distinct from the other pulsed sounds as distinguished by their loud-trumpet-like sounds and unique spectral contours displayed by a complicated stacking of harmonic structures. Since squeaks occurred in a single loud burst of sound which may be referred to as *burst pulses* in many species (Herzing, 2000; Frankel, 2009), they were considered to be true burst-pulsed sounds for Irrawaddy dolphins. Squeaks were composed of multiple harmonics of narrowband frequency, with a very low minimum frequency of 0.1

to 0.2 kHz (0.1 \pm 0.06) and a bandwidth ranging from 0.1 to above 22 kHz. Each squeak consisted of 52 to 62 pulses (56 \pm 5.3), with a very high repetition rate of 147 to 278 pulses/s (232.7 \pm 74.0), and lasted between 0.1 and 0.5 s (0.3 \pm 0.1) in duration. Squeaks had the highest mean repetition rate compared to all pulsed sounds and the highest mean pulse rate among narrowband pulsed sounds. Only three squeaks were recorded. All were presented exclusively when aggressive behaviours were displayed; for example, in one instance, one dolphin swam quickly and charged another dolphin by leaping on it.

Whistles

Whistles were the least frequent sound type recorded with a total of only 44 samples. All whistles were narrowband, frequency-modulated sounds. Whistles were found to have diverse spectral contours that were categorized into the following nine types (Figure 3; Table 2)—all were newly described and named based on their spectrogram contours: (1) *Shriek* – a single horizontally straight whistle moving slightly upward at the end of the contour with one harmonic; (2) *Fall* – a single whistle with slightly ascending contour in the first half and descending in the second half of the contour; (3) *Flat* – a single low-frequency, horizontally straight whistle (1 to 4 kHz); (4) *Multi-Flat* – multiple horizontally straight whistles with low

frequency contours (1 to 7 kHz); (5) *Breaker* – a single whistle with an initially downward contour and two modulations; (6) *Chirp* – a very short single up-sweep whistle contour; (7) *Harmonic* – whistles with multiple harmonics, all with initially rising contours and then constantly slightly upward or downward at the end of the contour; (8) *Multi-Chirp* – very short multiple down-sweep harmonic contours; and (9) *Multi-Loop* – a single whistle starting with a rising contour with multiple (2 to 7) modulations.

Generally, the frequency of whistles ranged from 1.1 to 20.6 kHz (6.7 ± 4.4) and could extend to above 22 kHz for the harmonic whistle type. The duration was 0.1 to 1.6 s (0.7 ± 0.4). The start, end, minimum, and maximum frequencies also varied depending on the type of whistle as shown in Table 2. Most of the whistles were heard during non-tourist sessions while the dolphins were swimming; whereas only a few were heard when dolphins regrouped following SWD and when they swam with the trainers.

Discussion

Captive Irrawaddy dolphins, like other delphinids, produced three types of sound: (1) clicks, (2) pulsed sounds, and (3) whistles. This is the first study to capture all three sound categories (Frankel, 2009) within the frequency range audible to humans. The only previous captive study recorded only pulse trains (Kamminga et al., 1983). Herein, we discuss the similarities and differences of acoustic and physical behaviours of captive Irrawaddy dolphins compared to wild populations and other delphinid species.

Clicks

As with other delphinid species, captive Irrawaddy dolphins altered their click characteristics while echolocating at different distances from their targets. The repetition rate or ICI patterns could reflect how the dolphins used clicks to assess the distance between their position and the positions of their targets, particularly clicks with fluctuating ICIs, which were regularly recorded while dolphins were approaching food items during feeding and objects (e.g., balls and flying discs) during playing behaviour.

In clicks with fluctuating ICIs (Figure 1), high repetition rate clicks at the beginning of the train were normally recorded when objects were initially introduced to the pool; this initial phase of the train generally possessed more energy, which would allow the signals to travel further through water to locate unknown objects (Au & Würsig, 2004). In these cases, the intervals between clicks were simultaneously adjusted

by emitting at rates that allowed the echo signals to return to the animals before the next click was emitted (Au & Benoit-Bird, 2003; Au & Würsig, 2004; Au, 2009). Therefore, this might explain why ICIs were decreasing while the dolphins were approaching the food items, which would be similar to the *decreasing type* clicks reported in captive Commerson's dolphins (*Cephalorhynchus commersonii*) (Yoshida et al., 2014).

Additionally, captive Irrawaddy dolphins did not use clicks as often as we expected despite the generally low visibility (2 m) within the pool. We suggest that the dolphins may have already memorized the entire small-and-non-complex geographic pool structure in which they have been living for 4 y and, therefore, relied less on echolocation.

Pulsed Sounds

Pulsed sounds produced by captive Irrawaddy dolphins were recorded mostly during tourist sessions ($n = 2,665$). These pulsed sounds were associated with various behaviours (Table 1), including aggression, sexual arousal, and tourist encounter.

Aggression—Squeaks (Figure 2) shared characteristic similarities to other burst-pulsed sounds produced by many delphinids, such as Hector's dolphins (*Cephalorhynchus hectori*) (Dawson, 1991), Australian snubfin dolphins (Van Parijs et al., 2000), bottlenose dolphins (Blomqvist & Amundin, 2004), spinner dolphins (*Stenella longirostris*) (Lammers et al., 2006), and dusky dolphins (*Lagenorhynchus obscurus*) (Au et al., 2010). Interestingly, it has been suggested that burst-pulsed sounds could be used by delphinids as a sonic weapon (Norris & Møhl, 1983; Marten et al., 1988). Furthermore, in consideration of the highly sensitive auditory system in delphinids (Au, 2009) combined with the fact that squeaks and burst-pulsed sounds were produced exclusively during aggression and socializing (Overstrom, 1983; Dawson, 1991; Blomqvist & Amundin, 2004; Lammers et al., 2006), it is possible that these pulsed sounds are intentionally used to cause auditory distress in the antagonists in addition to being used for expressing emotional states.

Sexual Arousal—Several delphinids have been reported to produce pulsed sounds during sexual behaviours. For example, the pulsed sound *pop* is used by bottlenose dolphins during courtship and/or dominant behaviours (Connor & Smolker, 1996), and *squawks* are used during sexual play (Herzing, 1996). Similarly, Atlantic spotted dolphins (*Stenella frontalis*) used the high-repetition-rate pulsed calls *buzz* and *squawk* during courtship and sexual play, respectively (Herzing, 1996). Excessive noises were also recorded in spinner dolphins during copulation (Silva et al.,

2005). Captive Irrawaddy dolphins often produced pulsed sounds while they were performing their trained ejaculation behaviours with the veterinarians. It may be that pulsed sounds, especially cracks (Figure 2), were produced to express sexual emotions.

Tourist Encounters—Behaviours during tourist encounters were the most interesting and unique behaviours recorded. All dolphins spontaneously swam toward the tourists and emitted every kind of pulsed sounds when tourists were entering or leaving the pool and/or rotating their stations within the pool during the SWD. The pulsed sounds were rapidly produced. None of these intense periods of pulsed sounds were heard except during these particular circumstances. Moreover, the dolphins usually interacted with the tourists voluntarily, and the animals continued to follow until all of the tourists left the pool area. These behaviours were similar to those reported in captive bottlenose dolphins, which showed frequent play behaviours and continued to voluntarily engage in activities with humans during dolphin interaction programs (Trone et al., 2005). Thus, these high activity periods during SWD potentially caused excitement for the dolphins, leading to high rates of vocalizations, specifically the pulsed sounds which were directly related to emotional expression and social interaction.

Whistles

Even though little is known about the Irrawaddy dolphin's acoustic behaviour, they have been shown to produce whistles. In fact, both wild populations normally produced whistles about as often as they produced clicks and pulsed sounds (Van Parijs et al., 2000; Kreb & Borsani, 2004), except in isolated (and small) areas where Irrawaddy dolphins produced lower numbers of whistles (Kreb & Borsani, 2004). This reduction in whistles in confined areas is similar to what we observed in captive subjects in which only 44 whistles were produced compared to higher numbers of clicks (3,898) and pulsed sounds (2,807). The extremely low number of whistles could imply that, after years in captivity, the Irrawaddy dolphins did not mainly rely upon whistles to establish contact or convey identities; they no longer needed to do so. Also, it is possible that they genuinely produce low whistle rates in captivity, where space and social diversification are limited (only three individuals, all male); this may explain why Kamminga et al. (1983) were unable to capture whistles by this captive species. Nonetheless, comparative studies (e.g., with male-female compositions) would be necessary to ascertain the validity of this hypothesis.

Furthermore, there were two contradictions in whistling behaviours between captive Irrawaddy dolphins and other wild delphinids. First, no whistles were recorded during feeding at all despite the fact that whistles were often observed during socializing and foraging in other delphinids (Van Parijs et al., 2000; Kreb & Borsani, 2004; Au et al., 2010; May-Collado & Wartzok, 2010; Henderson et al., 2012; Andrade et al., 2015). We suggest this disparity is because live prey was not available in captivity; food was given to the dolphins directly, and there was an absence of group foraging/hunting behaviours which meant communication regarding feeding was likely unnecessary.

Second, numerous studies have shown that the whistling rate and the complexity of whistles are related to behavioural contexts and excitement level (Norris et al., 1994; Herzing, 1996; Frankel, 2009). Delphinids tend to produce less frequent and simpler whistles during low activity periods: swimming, travelling, and resting; and vice versa during high activity periods: foraging, socializing, fast movement, and aerial behaviours (Herzing, 1996; Azevedo et al., 2010; Díaz López, 2011). Wild Irrawaddy dolphins were reported to produce whistles most frequently when speed boats were present, followed by foraging and socializing (Kreb & Borsani, 2004). Yet, most of the whistles produced by our subjects were heard during non-tourist sessions in which the dolphins were typically swimming. Also, the complex multi-loop whistles with up to four to seven modulations and harmonic whistles were mostly recorded during low activity periods. Hence, captivity may alter the properties of the whistles over time or the various pulsed sounds have taken on the communication role for this species. So, rather than producing whistles during excitement and high energy behaviours, they produced the pulsed sounds.

Nevertheless, the presence of various types of whistles, from simple to complex contours, suggests these sounds play a role in communication and maintenance of group structure in captivity. Diverse types of whistles with routine uses of clicks and pulsed sounds demonstrated that some vocal repertoires are still preserved despite long-term habituation in captivity.

Summary

Captive Irrawaddy dolphins produced three sound categories, consisting of two types of clicks, five types of pulsed sounds, and nine types of whistles (Frankel, 2009). Broadband clicks were directly related to feeding and swimming behaviours in navigational contexts. Pulsed sounds were produced in both narrow- and broadband signals with very short durations, high repetition rates,

and high pulse rates. Pulsed sounds were associated with various behaviours related to social and communicative contexts. Whistles, which were narrowband signals with frequency modulations, had the highest diversity, although they were the least produced vocalization. Low whistling rates in captivity may imply that captive Irrawaddy dolphins do not rely on whistles as their only form of communication. Overall, vocalization rates were significantly higher during tourist sessions, where many exciting factors were present, leading to high rates of vocalizations, especially of pulsed sounds. Ultimately, captive Irrawaddy dolphins still have social interactions with each other, and some vocal repertoires are still preserved, even though the dolphins are habituated to, or even desensitized by, the dolphinarium where space and activity diversification are limited.

This study recorded clicks, pulsed sounds, and whistles below a frequency of 22 kHz, which does not include the complete bandwidth of this species. Further studies of a broadband recording system with a sample rate of at least 300 kHz would complement and extend the current study. Moreover, it is desirable to conduct more correlative studies of delphinid sounds and behaviours, both in captivity and in the wild. It would be interesting to compare turbid and clear captive environments and the differences between groups of only one sex and mixed sexes, as well as between small and large group sizes. Such studies would provide a foundation for evaluating the emotional state and vitality of delphinids that could enhance their welfare, which is especially important for endangered species such as the Irrawaddy dolphins.

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