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ORIGINAL ARTICLE

Commerson's dolphins (*Cephalorhynchus commersonii*) can relax acoustic crypsis

Morgan J. Martin[1,2] · **Sara Torres Ortiz**[1,3] · **M. Vanesa Reyes Reyes**[4,5] · **Alexander Marino**[4] · **Miguel Iñíguez Bessega**[4,6] · **Magnus Wahlberg**[1]

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Abstract

Toothed whales use powerful ultrasonic biosonar pulses (i.e. clicks) for echolocation. Underwater acoustic recordings have suggested that the majority of toothed whale species can be grouped acoustically as either producing broadband clicks or narrowband high-frequency (NBHF) clicks. Recently, it has been shown that Heaviside's dolphins, *Cephalorhynchus heavisidii*, emit NBHF clicks for echolocation but also clicks of lower frequency and broader bandwidth for communication. Here, we use acoustic recorders and drone video footage to reinforce previous findings that Commerson's dolphins (*C. commersonii*) produce signals similar to Heaviside's dolphins. We reveal that they use clicks with a lower frequency and broader bandwidth in the form of click trains and burst-pulses. These sounds were not recorded in the presence of smaller groups of Commerson's dolphins, indicating that they may fulfil a communication function in larger groups. Also, we utilised a novel combination of drone video footage paired with underwater acoustic recordings to estimate the source level of echolocation clicks produced by Commerson's dolphins. In addition, we compare the acoustic signals produced by Commerson's and Heaviside's dolphins to identify inter-specific similarities and differences. Spectral differences were found in NBHF click trains, buzzes and burst-pulses between species; however, bandwidth and duration parameters were not significantly different for broadband click trains. Our findings make it likely that all four species of the *Cephalorhynchus* genus have the ability to generate both signal types, and further challenges the evolutionary concept of NBHF signal production.

Significance statement

This study confirms the presence of a duel echolocation click (i.e. biosonar) strategy in Commerson's dolphins, making them the second species of their genus known to produce two types of biosonar. We provide an in-depth quantitative analysis of Commerson's dolphin acoustic signal types, and include a comparison of signal types between Commerson's dolphins and the other species known to produce two types of biosonar, the Heaviside's dolphin. In addition, this is the first study to combine drone footage with underwater acoustic recordings to measure the source level of toothed whale echolocation signals. We use this novel technique to provide source levels measured from Commerson's dolphin echolocation clicks which are comparable to published values for this species calculated using an expensive and complicated array of hydrophones. Thus, we provide a simpler and more cost effective way to study sounds produced by marine mammals.

Keywords Acoustic crypsis · Biosonar · Cetacean · Communication · UAV · Echolocation

Morgan J. Martin and Sara Torres Ortiz contributed equally to this work.

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✉ Morgan J. Martin
mjmartin@sandiego.edu

1 Department of Biology, Marine Biological Research Center, University of Southern Denmark, Kerteminde, Denmark

2 Wildlife Conservation Society Canada, c/o Department of Biology, University of Victoria, Victoria, BC, Canada

3 Max Planck Institute for Ornithology, Seewiesen, Germany

4 Fundación Cethus, Olivos, Prov. Buenos Aires, Argentina

5 Whale and Dolphin Conservation (WDC), Chippenham, Wiltshire, UK

6 Whale and Dolphin Conservation (WDC) NA, Plymouth, MA 02360, United States

Introduction

Animals need to maintain a balance between social communication and remaining inconspicuous from potential predators. Prey animals achieve this balance by using unique modes of communication, such as signals which are difficult for predators to detect or locate (e.g. high-pitched or low amplitude sounds; Payne 1971; Holy and Guo 2005; Nakano et al. 2010), or by restricting their social interactions to locations or time periods where they are less likely to be detected by predators (e.g. sea birds breeding on high cliffs or on isolated islands; Schreiber and Burger 2001).

In the aquatic environment, where sound is the most effective way to transmit information, cetaceans (whales, dolphins and porpoises) rely on sound as the primary medium for orientation, foraging and communication (Tyack 1998). Odontocetes (toothed whales) produce a variety of sounds, most of which can be broadly classified into three categories: biosonar pulses (echolocation clicks), burst-pulses which are composed of clicks produced in a rapid series and tonal whistles (Herman and Tavolga 1980). Burst-pulses and whistles typically are used in communication (Janik 2009), while echolocation clicks primarily are used for orientation and navigation (Au 1993).

Toothed whales are grouped into four acoustic categories by the type of echolocation clicks they emit: (1) broadband clicks, which are produced by most toothed whales; (2) narrowband high-frequency (NBHF) clicks, which are produced by 13 species of small toothed whales; (3) multi-pulsed low-frequency sperm whale clicks and (4) frequency-modulated beaked whale clicks (Wahlberg et al. 2011; Fenton et al. 2014). Broadband clicks are short and intense transient pulses containing energy ranging from around 10 to 150 kHz, with broad bandwidths of tens of kHz (Au 1993). In contrast, NBHF clicks are transient pulses that are longer in duration, weaker in amplitude, with energy above 100 kHz which is contained within a narrower bandwidth (Au 1997). NBHF-clicking toothed whales echolocate and communicate at frequencies above the ~110 kHz hearing limit of one of their main predators, the killer whale (*Orcinus orca*) (Szymanski et al. 1999; Branstetter et al. 2017). Avoiding predation through an acoustically cryptic strategy has become a commonly accepted explanation for the adaptation and use of NBHF signals (Andersen and Amundin 1976; Madsen et al. 2005; Morisaka and Connor 2007; Clausen et al. 2011; Morisaka 2012; Kyhn et al. 2013; Martin et al. 2018a; Sørensen et al. 2018).

Martin et al. (2018a) recently showed that Heaviside's dolphins (*Cephalorhynchus heavisidii*) can produce both NBHF and clicks that are lower frequency and broader bandwidth, with most of the latter occurring in the form of burst-pulse communication signals (Martin et al. 2018a, 2019). The authors concluded that Heaviside's dolphins maintain acoustic crypsis during navigation and foraging using NBHF clicks but switch to a riskier, lower-frequency broadband signal in order to communicate over greater distances (Martin et al. 2018a). The switch in signal production from NBHF to broadband signals was termed 'relaxing acoustic crypsis' as the broadband signals would make the dolphins easier to acoustically detect by predatory killer whales (Martin et al. 2018a). Currently, it is not understood if the Heaviside's dolphin is a curious exception to the otherwise seemingly clear division between NBHF and broadband clicking species, or if there are other species of *Cephalorhynchus* dolphins able to produce both types of pulsed signals.

An interesting species to examine for broadband click production is the Commerson's dolphin (*Cephalorhynchus commersonii*). This species is a close relative to the Heaviside's dolphin and inhabits coastal waters of southern South America and the Kerguelen Islands. Commerson's dolphins are one of the smallest cetacean species (length < 1.5 m) and are typically found in small groups (< 5 individuals, mode = 2; Iñíguez et al. 2001; Reyes Reyes et al. 2016). Several authors have reported on the acoustic signals produced by Commerson's dolphins in the wild and in captivity (Watkins and Schevill 1980; Kamminga and Wiersma 1981, 1982; Shochi et al. 1982; Evans et al. 1988; Hatakeyama et al. 1988; Dziedzic and De Buffrenil 1989; Kyhn et al. 2010; Yoshida et al. 2014; Reyes Reyes et al. 2015; Reyes Reyes et al. 2016). All of these studies which utilised full bandwidth recording equipment reported this species to produce NBHF signals, and only Reyes Reyes et al. (2016) cited the presence of any potential broadband signals. Reyes Reyes et al. (2016) reported a small number of sporadic broadband clicks (i.e. not in the form of echolocation click trains or burst-pulses). Furthermore, Commerson's dolphin burst-pulse signals are reported to be comprised exclusively of NBHF clicks (Yoshida et al. 2014). In light of the preliminary findings by Reyes Reyes et al. (2016), additonal acoustic research on Commerson's dolphins is needed to reliably conclude if this species can produce both NBHF and broadband clicks.

The aim of this study was to collect acoustic recordings of Commerson's dolphins in the wild performing natural behaviours using high-frequency recording hydrophones to determine if this species can produce broadband signals in the form of click trains or burst-pulses in addition to previously reported NBHF signals. Unmanned Aerial Vehicle (UAV or drone) video footage was recorded concurrently with underwater acoustic recordings to identify animal surface behaviour and its relationship with the function of sound production. In addition, the combined drone video footage and underwater recordings were used, for the first time to our knowledge, to estimate source levels of echolocation signals produced by a toothed whale. Our results show that some Commerson's dolphin click trains and burst-pulses indeed do consist entirely of broadband clicks, indicating that this species can relax acoustic crypsis in a similar manner as Heaviside's dolphins.

Materials and methods

Field site and data collection

During December 2019 and January 2020, data were collected from wild Commerson's dolphins near the mouth of San Julián Bay within the Parque Interjurisdiccional Marino Makenke (PIMM), Argentina. The PIMM covers the sea region beyond the mouth of San Julián Bay, from La Mina Beach (49° 8′ 30″ S, 67° 37′ 00″ W) to the area of Lobería Makenke (49° 51' 54.05" S, 67° 47' 1.83" W). San Julián Bay is 22 km long and varies 1–8 km in width, with a mouth connected to the Atlantic Ocean (Fig. 1). The bay has a maximum depth of 35 m and includes a wide shallow area at its base. The semidiurnal tidal difference is up to 8.9 m but is normally within 6.1 m. The sea surface temperature is around 5 °C (winter) to 14 °C (summer), and salinity is 33–34 ppt (Falabella et al. 2009; SHN 2009; Martin et al. 2015). The waters are turbid (visibility < 1 m), dependent on the tidal flux and wind conditions. Between September and May each year, Commerson's dolphins utilise San Julián Bay for foraging, socialising and breeding (Iñíguez et al. 2001). During January, Commerson's dolphins have been observed aggregating in large groups off the mouth of San Julián Bay (Iñíguez et al. 2001).

Underwater acoustic recordings of Commerson's dolphin vocalisations were made under calm weather conditions (Beaufort sea state ≤ 2) using two high-frequency recording data loggers (SoundTrap 300 HF; Ocean Instruments, New Zealand) deployed at 2 m depth on the port and starboard sides of a 6.5 m rigid-hull inflatable motorised boat. Sound was digitised at a sampling rate of 576 kHz with a 16-bit resolution, and settings were configured to include high gain (+12 dB). The SoundTraps' clipping levels were 176 and 178 dB re 1 μPa peak with a flat frequency response from 20 Hz to 150 kHz ± 3 dB. The data loggers contain a built-in 1-pole anti-aliasing filter at 150 kHz. Recordings were stored as compressed 30-min SUD files on the SoundTraps.

When an individual or group of dolphins was sighted, the research boat would attempt to approach with minimal disturbance. Once in the vicinity of dolphins (~100 m distance), the boat engine and echosounder were turned off and the hydrophones were deployed. A group was defined as two or more dolphins in close proximity (< 50 m radius to the next individual), generally carrying out the same activity. Behaviour and focal group information were collected concurrently with acoustic recordings. Surface behaviour was recorded both visually by an observer on board the boat and with a DJI Phantom 4 pro V2 drone (www.dji.com/phantom-4-pro-v2). A visual survey group-follow with a scan sampling protocol (Altmann 1974; Mann 1999) was used to record surface behaviour along with group size, group composition (presence or absence of calves), group spacing and estimated distance from the hydrophones. Additional focal notes were recorded ad libitum. Definitions of behavioural states and events were adapted from Henderson et al. (2012) and Herzing (1996). The drone was used to assist the boat-based observers to locate and maintain focal groups, record high-quality video footage of encountered dolphin groups to provide information on behaviour and distance from the hydrophones and to monitor other dolphin groups present in the bay. For large focal groups (i.e. ≥ 20 individuals), group size was estimated from

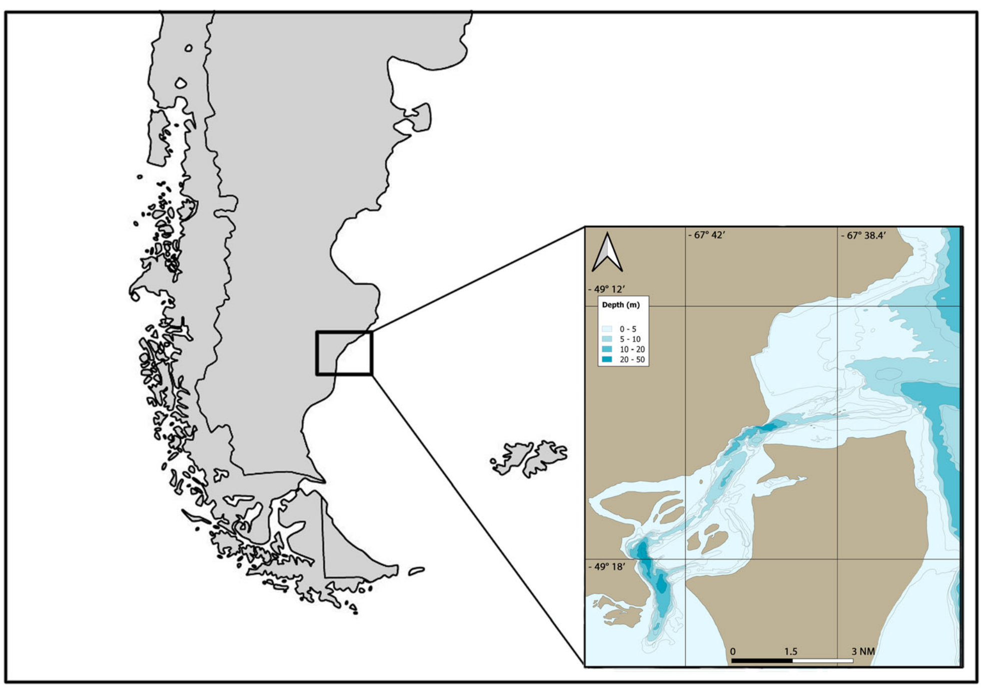

Fig. 1 Map of southern South America. Insert indicates the location of the study site, San Julián Bay, Argentina

the drone footage by counting the number of animals at the surface, which is likely an underestimate of the true number present in the focal group. Data were recorded over a range of group compositions (adults only, adults with juveniles or adults with mother and calf pair). Adults have a distinct black and white pattern, juveniles are medium-sized animals with a clear light grey rather than white pigmentation on the sides and back and calves have a distinguishing dark brown to grey colour pattern (Goodall et al. 1988). Calves were encountered during this study, and all dolphins presumed to be non-calves or non-adults based on size and colouration were considered to be juveniles.

The drone was launched and operated from the research boat by a licensed pilot (STO) under the Danish Transport, Construction and Housing Authority permit number 5032864. The drone pilot followed focal groups with the drone at an altitude of 10–25 m while simultaneously recording video footage for a maximum duration of 25 min before requiring a battery replacement. If a focal follow was in progress, the drone battery was changed before it required a replacement, and the drone was relaunched to continue recording the focal group. Video footage was collected using the built-in real-time camera output from the drone together with an Apple IPAD Mini™ and the DJI Go application. Videos were recorded at 4 K (3,840 × 2160 pixels) with a video frame rate of 50 frames per second. No animals were touched or harmed during this study, and it was not possible to record data blind because our study involved focal animals in the field.

Acoustic data extraction

Recordings made within a visually estimated 100 m range of dolphins were selected for analysis. Acoustic signals produced by Commerson's dolphins were identified through visual inspection of a spectrogram display in Adobe Audition CC (Adobe Systems Inc.). Commerson's dolphin NBHF echolocation clicks have been previously described (e.g. Kyhn et al. 2010; Reyes Reyes et al. 2015), and therefore only a subset was selected here for signal parameter analysis. Following the methods of Martin et al. (2018a), we defined three functional groups of signals based on signal context and interclick intervals (ICI, calculated as the time between subsequent clicks; Au 1993). Click trains were defined as series of clicks with ICI exceeding 13 ms. Such click trains are likely to be echolocation signals produced by the animals. A subset of click trains was composed of lower-frequency, broader-bandwidth signals than previously described for this species, and we therefore divided click trains into NBHF click trains and broadband click trains through visual inspection of spectrograms (Fig. 2). Foraging buzzes are used during prey capture by echolocating animals (Griffin et al. 1960; Miller et al. 1995), including NBHF species (Reyes Reyes et al. 2015; Wisniewska et al. 2016; Martin et al. 2019). These were defined as click series with ICIs decreasing from onset of approximately 13 to < 5 ms, which were preceded by a slower click train (e.g. DeRuiter et al. 2009). Since buzzes occurred at the end of a click train, we defined the start of a buzz as the point when the ICI first decreased below 13 ms and the end of the buzz as the point where the click train ended or where the ICI increased to greater than 13 ms. Finally, we defined burst-pulse signals as discrete, isolated series of high repetition rate clicks that began, persisted and generally ended with interclick intervals less than 10 ms following Lammers et al. (2004). A subset of burst-pulses was composed of broader-bandwidth signals than previously described for this species (Yoshida et al. 2014), and we therefore divided burst-pulses into NBHF and broadband categories by inspecting spectrograms. We defined a Commerson's dolphin broadband signal as a signal containing energy below 80 kHz. Only distinguishable, high-quality pulsed signals measuring more than 10 dB above the background noise measured immediately before the signal were selected for further analysis. Each acoustic signal selected for analysis was extracted from a single SoundTrap recorder to avoid pseudo-replication; however, both SoundTrap recorders were involved in the choice and extraction of data.

Acoustic feature extraction

To quantify temporal differences in repetition rate across signals, we used a click detection algorithm developed in MATLAB 2013B (The MathWorks Inc., USA). We first filtered the input signal with a six-pole Butterworth bandpass filter (20–250 kHz), calculated the signal envelope and extracted peaks in the envelope that were separated by more than 0.5 ms. Click detections were visually inspected and manually corrected for missed detections. Following the methods of Martin et al. (2018a), to compare signals with highly variable numbers of clicks, we calculated the 5^{th}, 50^{th} (median) and 95^{th} percentile ICI across each click series. To quantify temporal and spectral differences of component clicks, we extracted the highest amplitude click from each click series following the methods for on-axis click analysis (Madsen and Wahlberg 2007; Jensen et al. 2013). While these signals were recorded from an unknown aspect, the minute difference in the waveform and spectrum of NBHF clicks across varying off-axis angles means that spectral parameters are likely reasonably close to on-axis signals (Au et al. 1999; Madsen et al. 2005; Hansen et al. 2008; Koblitz et al. 2012). Individual signals were filtered in MATLAB with a four-pole Butterworth bandpass filter between 20 and 250 kHz. Individual click power spectra were calculated with a 512-point 50% Tukey window centred on the peak envelope of each click. Spectral and temporal click parameters were calculated according to methods for measuring on-axis click parameters (Au 1993; Madsen et al. 2004).

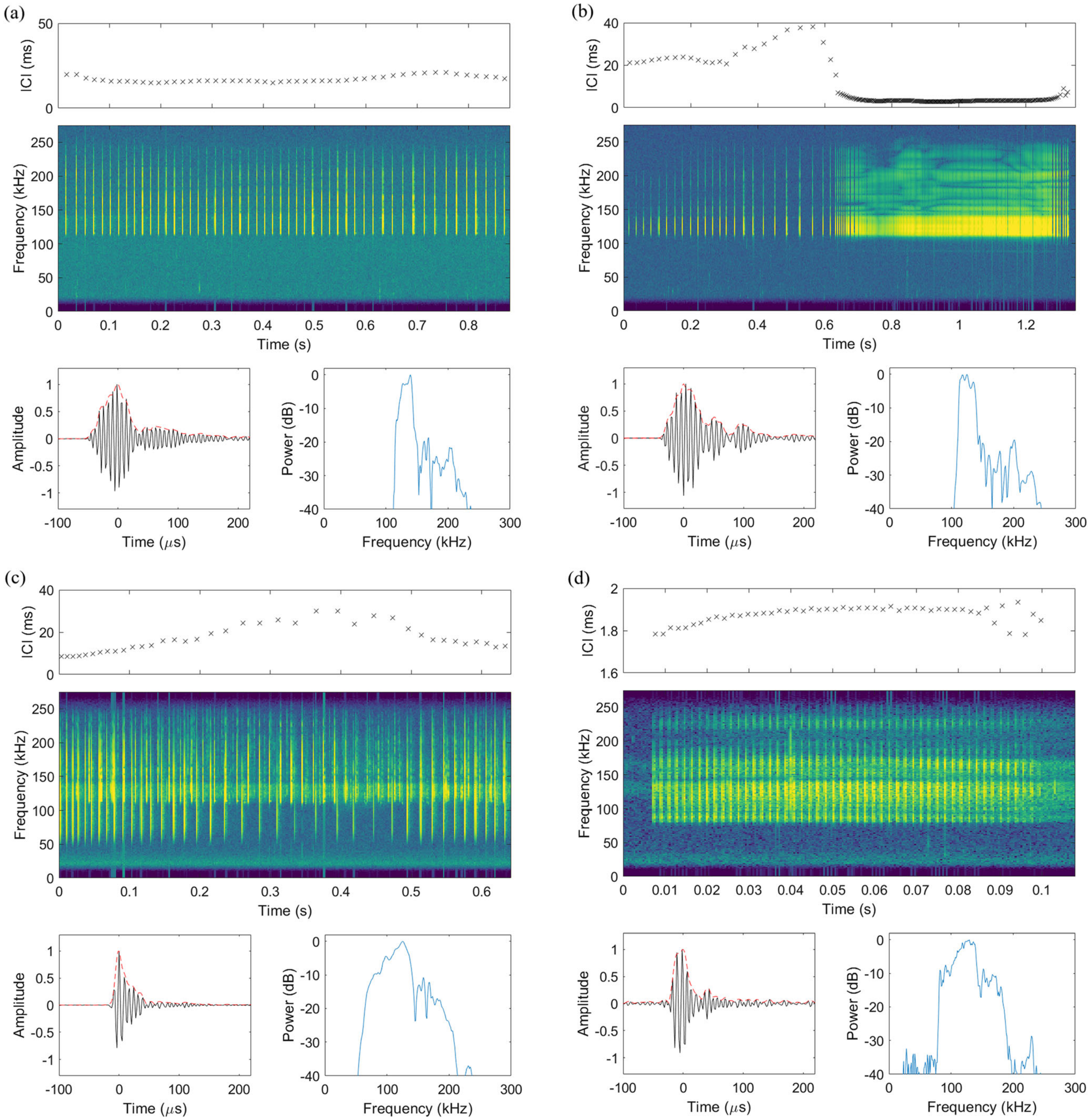

Fig. 2 Examples of Commerson's dolphin pulsed signal types: **a** narrowband high-frequency (NBHF) click train, **b** buzz, **c** broadband click train and **d** broadband burst-pulse. For each signal, the top panel represents the corresponding ICIs of the pulsed signal. Middle panel: spectrogram of the signal (512-pt. FFT, Hamming window, 50% overlap). Bottom left panel: normalised waveform (solid line) and envelope (dashed line) of a single click extracted from the pulsed signal shown in the middle panel (512-pt. rectangular window). Bottom right panel: normalised power spectrum of the extracted click (512-pt. rectangular window, 576 kHz sampling rate). NBHF click trains from other individuals can be seen overlapping the broadband click train in the spectrogram in '**c**'

Statistical analyses of acoustic data

All measured Commerson's dolphin signals were visually classified into the five proposed categories (NBHF click trains, broadband click trains, buzzes, NBHF burst-pulses and broadband burst-pulses) and then statistically evaluated to examine the ability to quantitatively distinguish pulsed signal types. Signal parameters, including spectral and temporal click parameters as well as interclick intervals, were compared across signal categories using non-parametric Kruskal-Wallis tests and subsequent Dunn's post hoc tests for pairwise comparisons in R version 3.4.2 (Fox and Weisberg 2011; Ogle

2017; R Core Team 2017). Further, all high-quality signals were evaluated with a principal component analysis (PCA) as it is robust to correlated variables using R (*prcomp*; R Core Team 2017). The PCA was used to identify the most influential parameters for signal classification. Nine parameter variables were included in the PCA: 5th, 50th (median) and 95th percentile ICIs, peak frequency, centroid frequency, −10 dB bandwidth, RMS bandwidth, Q-ratio (centroid frequency / RMS bandwidth) and − 10 dB click duration. All values were log transformed prior to the analysis. The Kaiser criterion was used to identify the number of principal components to retain and was determined by eigenvalues > 1.

An additional comparison was included to evaluate species level similarities or differences between the signal types produced by both Commerson's and Heaviside's dolphins. Martin et al. (2018a) utilised the same recording equipment (SoundTrap 300 HF) and measured identical signal parameters for Heaviside's dolphins, facilitating the ability to compare acoustic signals between species. Signal parameters from Heaviside's dolphins (Martin et al. 2018b, Supplemental Material Appendix S1) and signal parameters measured from Commerson's dolphins in this study (Online Resource 1) were included in a second PCA computed in R (*prcomp*; R Core Team 2017). All values were log transformed prior to the analysis. In addition, signal parameters from matching signal categories were compared statistically between species. Homogeneity of the variance between signal groups was assessed with Levene's tests in R. Groups which met the assumption of homogeneity of variance were compared using an independent two-sample *t* test, and groups with unequal variance were compared using a Welch's two-sample test. Statistical significance was determined at a threshold of 0.05.

Pairing surface behaviour with acoustic recordings

An aim of this study was to examine the relationship between Commerson's dolphin surface and acoustic behaviour. An in-depth assessment of acoustic behaviour across a range of behavioural states was not possible due to the issue of attractive responsive movement toward the research boat. Commerson's dolphins are known to be attracted to moving vessels (Iñíguez and Tossenberger 2007); however, we did not anticipate the severity of responsive movement experienced during data collection. Thus, we report on recorded signal types with estimated group size and composition of encountered focal groups. During focal follows, drone footage and visual observer data were used to count the number of Commerson's dolphins observed at the surface in 2-min intervals. Drone video footage was synchronised in time with acoustic recordings from the port and starboard hydrophones using Audacity (Audacity Team) and OpenShot Video Editor (OpenShot Studios, LCC). Time synchronization of the drone video footage and acoustic recordings primarily was used to examine the relationship of broadband signals and group size and also in the analysis to estimate the source level of echolocation clicks. Synchronization was implemented by simultaneously recording a signal (a short series of taps on the hydrophone) while being filmed with the drone at the end of each session. Maximum synchronization error was 20 ms, since the drone video capture rate was 50 frames per second.

Relationship of broadband signals and group size

During the acoustic feature extraction, we noticed that broadband signals were present only in recordings collected from large aggregations of Commerson's dolphins (i.e. groups ≥ 20 individuals). Due to a low number of focal groups, a Fisher's exact test was used to study the relationship between group size and presence of broadband pulsed signals (click trains or burst-pulses) using R. Focal groups were binned into two categories based on group size observed in the drone footage, < 20 individuals and ≥ 20 individuals. Broadband click trains and broadband burst-pulses were assessed as present or absent in recordings from each focal group. Statistical significance was determined at a threshold of 0.05.

Estimation of source level

To estimate the source level (SL) of Commerson's dolphin echolocation clicks, sequences of drone video footage synchronised with the acoustic recordings from the port side SoundTrap were utilised from periods of calm weather conditions (Beaufort sea state ≤ 1). A measuring tape was attached to the port side of the boat, with a visible tape marker every 0.5 m to assist with verification of the precision of the distance measurements estimated from the drone video footage (Fig. 3). SL is defined as the sound pressure level of sound at 1 m from the source using 1 μPa as the reference pressure

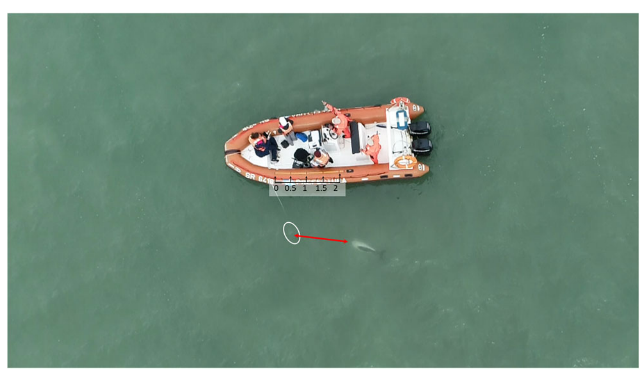

Fig. 3 Screenshot obtained from the Commerson's dolphin source level analysis using the software 'Porpoise Measure' and the drone video footage. The measuring tape located on the port side boat pontoon was used for calibration and calculation of the distance error, with markers placed every 0.5 m. The white circle represents the underwater location of the hydrophone and the red line is a distance measure from the hydrophone to the tip of the dolphin's rostrum

(Au 1993). SL is the result of the sum of the received level (RL) and the transmission loss (TL; Urick 1983) such that:

$$SL = RL + TL \quad (1)$$

Transmission loss for NBHF clicks is estimated assuming spherical spreading plus the attenuation caused by absorption (DeRuiter et al. 2010) such that:

$$TL = 20 \cdot \log_{10}(R) + \alpha R \quad (2)$$

where R is the distance to the emitter and α is a constant defined as the frequency dependent absorption (Francois and Garrison 1982). R was calculated as the distance from an animal's rostral tip to the hydrophone using the drone footage together with the custom programme, 'Porpoise Tracker' (https://github.com/henrikmidtiby/PorpoiseTracker). We estimated the error in distance range by measuring the measurement tape located on the port side of the boat 52 times from drone video sequences (Fig. 3). Echolocation clicks were selected during video sequences when only one animal was present. On-axis clicks were determined by correlating an on-axis head position (i.e. pointed directly toward the port side hydrophone) from the drone footage with the highest amplitude click in a given click train. SL was measured as peak-to-peak (that is, the difference between the highest and lowest amplitude; denoted $SL_{p\text{-}p}$) and root mean square (SL_{rms}) values (Au 1993; Madsen and Wahlberg 2007) within a time window defined by the −10 dB duration. Before the measurements were made, the average of the signal was subtracted from the signal to make sure the signal was centred around zero. All analyses were completed using MATLAB.

Results

We collected 6 h 22 min of acoustic recordings and 6 h 3 min of drone video footage from wild Commerson's dolphins located in PIMM, Argentina. Data were collected from 20 focal groups during 8 sampling days. Recording sessions during focal follows lasted between 2 and 54 min. Peale's dolphins (*Lagenorhynchus australis*) also occur in the study area; however, this species looks markedly different and did not commonly associate with Commerson's dolphins during the recording sessions. There were two occurrences where Peale's dolphins were sighted in the vicinity of the boat during focal follows of Commerson's dolphins, and the subsequent recordings and focal follows were removed from this analysis. No other cetaceans were visually sighted or detected acoustically during recording sessions, and with the supporting drone footage, it is highly unlikely there were other cetacean species in the area.

A total of 18 focal groups of Commerson's dolphins were selected for analysis. Group size varied from 1 to 68 individuals (median = 6, mode = 2). Four of the 18 focal groups were comprised of large aggregations (≥ 20 individuals) recorded over 3 days. Focal groups were comprised of adults and adults with juveniles and/or calves. The most frequently observed behaviours consisted of the dolphins being attracted to and investigating the boat, with some interactions lasting up to 30 min. While this provided the ability to record the animals at close distances, it precluded examining relationships between dolphin surface and acoustic behaviours across a variety of behavioural categories.

In total, 317 buzzes, 234 NBHF burst-pulses, 58 broadband burst-pulses and 42 broadband click trains were identified in the recordings. NBHF echolocation click trains were abundant throughout the recordings while other categories of pulsed signals were less common. Broadband click trains and broadband burst-pulse signals were composed of clicks with lower minimum frequency and broader bandwidth compared to typical NBHF signals (Fig. 2, Table 1). Q-ratios are an indicator of click type, and NBHF species produce echolocation clicks generally with Q-ratios > 10. The measured Commerson's dolphin NBHF click trains and buzz signals had Q-ratios > 10, whereas broadband click trains generally had Q-ratios < 6 and broadband burst-pulses had a median Q-ratio of 7 (Table 1).

For Commerson's dolphin measured signal parameters, the Kruskal-Wallis and Dunn's post hoc tests confirmed there were significant differences in both ICI parameters and spectral parameters across the five signal types (Table 2, Fig. 2). Results of the PCA showed that 46% of the variance in the first principle component (PC 1) was explained primarily by bandwidth-related parameters (Table 3, Fig. 4). The second principle component (PC 2) accounted for an additional 23% of the variance which was attributed to the click rate parameters (5^{th}, 50^{th} and 95^{th} percentile interclick intervals) (Table 3, Fig. 4).

Signal categories were compared between Commerson's and Heaviside's dolphins using independent *t* tests and Welch's tests. The measured signal parameters confirmed that there were few significant differences in click rate between species (Table 4). There were significant differences in several spectral parameters between species for NBHF click trains, buzzes and burst-pulses; however, bandwidth and duration were not significantly different for broadband click trains (Table 4, Fig. 5). The PCA results were similar to the Commerson's dolphin signal type comparison where 49% of the variance in PC 1 was explained primarily by bandwidth-related parameters (Table 5, Fig. 5). PC 2 accounted for an additional 27% of the variance which was attributed to the click rate parameters (Table 5, Fig. 5).

Table 1 Biosonar parameters of pulsed signal types produced by Commerson's dolphins

	NBHF click train		NBHF buzz		NBHF burst-pulse		Broadband burst-pulse		Broadband click train	
	n=41		n=40		n=41		n=16		n=18	
Source parameters	Median	(5–95%)	Median	(5–95%)	Median	(5–95%)	Median	(5–95%)	Median	(5–95%)
ICI_{5th} (ms)*	21.9	(15.9–89.4)	7.4	(2.7–9.6)	1.7	(1.2–2.4)	1.6	(1.4–1.9)	13.2	(5.6–98.2)
ICI_{MED} (ms)*	27.6	(19.1–116.6)	9.1	(2.9–11.5)	1.8	(1.3–2.6)	1.7	(1.6–2.0)	36.3	(6.3–129.1)
ICI_{95th} (ms)*	45.5	(25.2–167.0)	12.1	(5.3–15.2)	1.9	(1.4–3.1)	1.8	(1.6–2.0)	84.8	(7.6–198.3)
F_P (kHz) $^+$	135.0	(124.9–138.4)	128.3	(122.5–140.6)	126.0	(117.0–139.5)	129.4	(113.1–135.8)	127.1	(119.7–135.2)
F_C (kHz) $^+$	133.4	(127.5–137.9)	133.0	(127.1–137.0)	133.2	(126.4–140.9)	129.3	(123.7–146.7)	131.9	(119.2–139.6)
BW_{3dB} (kHz) $^+$	13.5	(9.0–19.1)	16.9	(8.9–23.6)	20.3	(3.4–29.3)	24.2	(7.0–58.2)	14.6	(3.0–45.8)
BW_{10dB} (kHz) $^+$	23.6	(14.6–46.1)	29.8	(20.3–54.1)	48.4	(22.5–82.1)	59.6	(37.4–127.1)	78.2	(41.5–118.3)
BW_{RMS} (kHz) $^+$	10.5	(8.3–14.1)	12.5	(9.1–19.0)	15.1	(11.8–28.0)	18.0	(15.9–29.4)	23.6	(14.4–39.7)
R_{QRMS} $^+$	12.8	(9.6–16.0)	10.7	(7.2–14.3)	8.9	(5.0–11.2)	7.0	(5.1–8.3)	5.8	(3.5–8.6)
Dur_{10dB} (μs) $^+$	74.3	(59.6–94.1)	66.8	(53.6–93.1)	60.2	(43.9–91.7)	47.1	(30.8–66.5)	35.8	(20.0–50.2)

The median and 5^{th}—95^{th} percentile values are reported for each parameter. A subset of click trains was composed of lower-frequency, broader-bandwidth signals than previously described (Kyhn et al. 2010; Reyes Reyes et al. 2015), and we therefore divided click trains into NBHF click trains and broadband click trains. A subset of burst-pulses was composed of broader-bandwidth signals than previously described (Yoshida et al. 2014), and we therefore divided burst-pulses into NBHF and broadband categories

ICI_{5th} 5^{th} percentile interclick interval, ICI_{MED} median (50^{th}) percentile interclick interval, ICI_{95th} 95^{th} percentile interclick interval, F_P peak frequency, F_C centroid frequency, BW_{3dB} −3 dB bandwidth, BW_{10dB} −10 dB bandwidth, BW_{RMS} root mean square bandwidth, Q_{RMS} F_C/BW_{RMS}, Dur_{10dB} −10 dB click duration

*Parameters measured across a click series

$^+$ Parameters measured for an individual click

Relationship of broadband signals and group size

Results of the Fisher's exact test indicated a significant increase in the presence of broadband click trains in Commerson's dolphin groups containing ≥ 20 individuals with a prevalence of 50% (2/4), compared to 0% (0/14) in groups containing < 20 individuals ($P = 0.039$). Similarly, the Fisher's exact test indicated a significant increase in the

Table 2 Dunn's post hoc tests of measured parameters across Commerson's dolphin signal categories.

	ICI_{5th} P	ICI_{MED} P	ICI_{95th} P	F_P P	F_C P	BW_{RMS} P	BW_{10dB} P	Q_{RMS} P	Dur_{10dB} P
Signal type comparison									
NBHF Train: BB Train	0.1656	0.3219	0.4975	**0.0162**	0.2732	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
NBHF Train: Buzz	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.3768	0.6238	**0.0056**	**0.0130**	**0.0032**	0.0990
NBHF Train: NBHF Burst-pulse	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.0971	0.7890	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
NBHF Train: BB Burst-pulse	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.0902	0.2519	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Buzz: BB Train	**0.0312**	**0.0134**	**0.0069**	0.0659	0.5400	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Buzz: NBHF Burst-pulse	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.2817	0.6764	**0.0022**	**0.0028**	**0.0034**	**0.0230**
Buzz: BB Burst-pulse	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.3157	0.3324	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
NBHF Burst-pulse: BB Burst-pulse	0.9106	0.8378	0.6905	0.7303	0.2078	**0.0264**	**0.0328**	**0.0119**	**0.0173**
NBHF Burst-pulse: BB Train	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.3698	0.3277	**0.0053**	**0.0103**	**0.0025**	**<0.0001**
BB Burst-pulse: BB Train	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.4738	0.6835	0.6775	0.7307	0.6708	0.1631
Compact letter display									
BB Burst-pulse	a	a	a	ab	a	a	a	a	a
BB Train	b	b	b	a	a	a	a	a	a
Buzz	c	c	c	ab	a	b	b	b	b
NBHF Burst-pulse	a	a	a	ab	a	c	c	c	c
NBHF Train	b	b	b	b	a	d	d	d	b

All parameters were log-transformed before statistical analysis. In the 'Compact letter display', signal types sharing a letter are not significantly different (alpha = 0.05). P values below this threshold are shown in boldface

NBHF Train narrowband high-frequency click train, *BB Train* broadband click train, *NBHF Burst-pulse* narrowband high-frequency burst-pulse, *BB Burst-pulse* broadband burst-pulse, ICI_{5th} 5^{th} percentile interclick interval (ms), ICI_{MED} median (50^{th}) percentile interclick interval (ms), ICI_{95th} 95^{th} percentile interclick interval (ms), F_P peak frequency (kHz), F_C centroid frequency (kHz), BW_{RMS} root mean square bandwidth (kHz), BW_{10dB} −10 dB bandwidth (kHz), Q_{RMS} F_C/BW_{RMS}, Dur_{10dB} −10 dB click duration (μs)

Table 3 Principal component analysis (PCA) output of the nine measured parameter variables from 156 Commerson's dolphin signals

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Importance of components									
Standard deviation	2.034	1.452	1.204	0.817	0.609	0.476	0.184	0.084	0.000
Proportion of variance	0.460	0.234	0.161	0.074	0.041	0.025	0.004	0.001	0.000
Cumulative proportion	0.460	0.694	0.855	0.929	0.970	0.995	0.999	1.000	1.000
Loadings with rotation = (9 × 9)									
ICI_{5th}	−0.385	0.415	0.028	0.086	−0.009	−0.005	0.672	0.469	0.000
ICI_{MED}	−0.381	0.430	0.010	0.083	0.005	0.017	0.070	−0.811	0.000
ICI_{95th}	−0.374	0.434	−0.012	0.069	0.005	0.064	−0.735	0.351	0.000
F_P	−0.167	−0.078	0.641	−0.506	0.523	0.164	−0.002	0.000	0.000
F_C	−0.048	−0.108	0.731	0.341	−0.529	−0.220	−0.043	−0.002	0.078
BW_{RMS}	0.398	0.317	0.168	0.262	0.298	−0.244	−0.010	0.006	−0.704
BW_{10dB}	0.387	0.288	0.137	0.022	−0.239	0.830	0.041	−0.004	0.000
Q_{RMS}	−0.403	−0.328	−0.087	−0.224	−0.356	0.219	0.005	−0.006	−0.706
$Duration_{10dB}$	−0.257	−0.381	0.009	0.700	0.418	0.352	0.006	0.001	0.000

All parameter values were log-transformed prior to the PCA

ICI_{5th} 5th percentile interclick interval (ms), ICI_{MED} median (50th) percentile interclick interval (ms), ICI_{95th} 95th percentile interclick interval (ms), F_P peak frequency (kHz), F_C centroid frequency (kHz), BW_{RMS} root mean square bandwidth (kHz), BW_{10dB} −10 dB bandwidth (kHz), Q_{RMS} F_C/BW_{RMS}, Dur_{10dB} −10 dB click duration (μs)

presence of broadband burst-pulse signals in Commerson's dolphin groups containing ≥ 20 individuals with a prevalence of 75% (3/4), compared to 0% (0/14) in groups containing < 20 individuals ($P = 0.005$). Broadband click trains and broadband burst-pulses were recorded from focal groups which contained calves but also were recorded from groups where calves were absent. Thus, this study confirms that adult animals produce broadband signals, while it cannot be discarded that calves also may produce them.

Estimation of source level

To estimate the source level of Commerson's dolphin NBHF echolocation clicks, we analysed 45 on-axis clicks from three video sequences extracted from three focal groups during which animals were slow swimming around the boat (Fig. 6). The three focal groups occurred on different survey days. For analysis, we only selected video sequences containing a single adult animal. The distance range error, calculated from the drone video footage using the measurement tape attached to the boat, resulted in a relative distance error of ± 10%. Using spherical spreading, this gave a transmission loss error and therefore a source level error of less than ± 1 dB. This calculation was derived from: $20 \cdot \log_{10}(R) - 20 \cdot \log_{10}(0.9R) = -20 \cdot \log_{10}(0.9) = -0.9$ dB. Recorded clicks were included from animals ranging 1.0–20.2 m from the port side hydrophone. The average distance between an individual dolphin and the hydrophone was 5.3 m (± 3.8 SD). The mean $SL_{p\text{-}p}$ (−10 dB) was 162 dB re 1 μPa p-p (± 7 SD; ± 1 dB range error) with a span of 148–185 dB. The mean SL_{rms} (−10 dB) was 150 dB re 1 μPa rms (± 7 SD; ± 1 dB range error) with a span of 135–173 dB. Click duration was 73 μs (± 10 SD), spanning 54–97 μs.

Discussion

We confirm that Commerson's dolphins produce a second type of click with a lower frequency emphasis and broader bandwidth than regular NBHF clicks. Some of the recorded burst-pulses and click trains were comprised purely of broadband echolocation clicks. The lower frequency emphasis broadens the transmission beam width and thereby makes these clicks more suitable for communication purposes compared to NBHF signals (sensu Martin et al. 2018a). Previously, NBHF biosonar signals were thought to have evolved to make the animal acoustically cryptic, thereby reducing predation risk by killer whales (Morisaka and Connor 2007). The recorded Commerson's dolphin broadband signals are well within the hearing range of killer whales (upper limit at approximately 110 kHz; Szymanski et al. 1999; Branstetter et al. 2017; Fig. 2). This could make these signals risky to produce, especially in the Argentine region of Patagonia where killer whales are known to predate on small cetaceans (Coscarella et al. 2015).

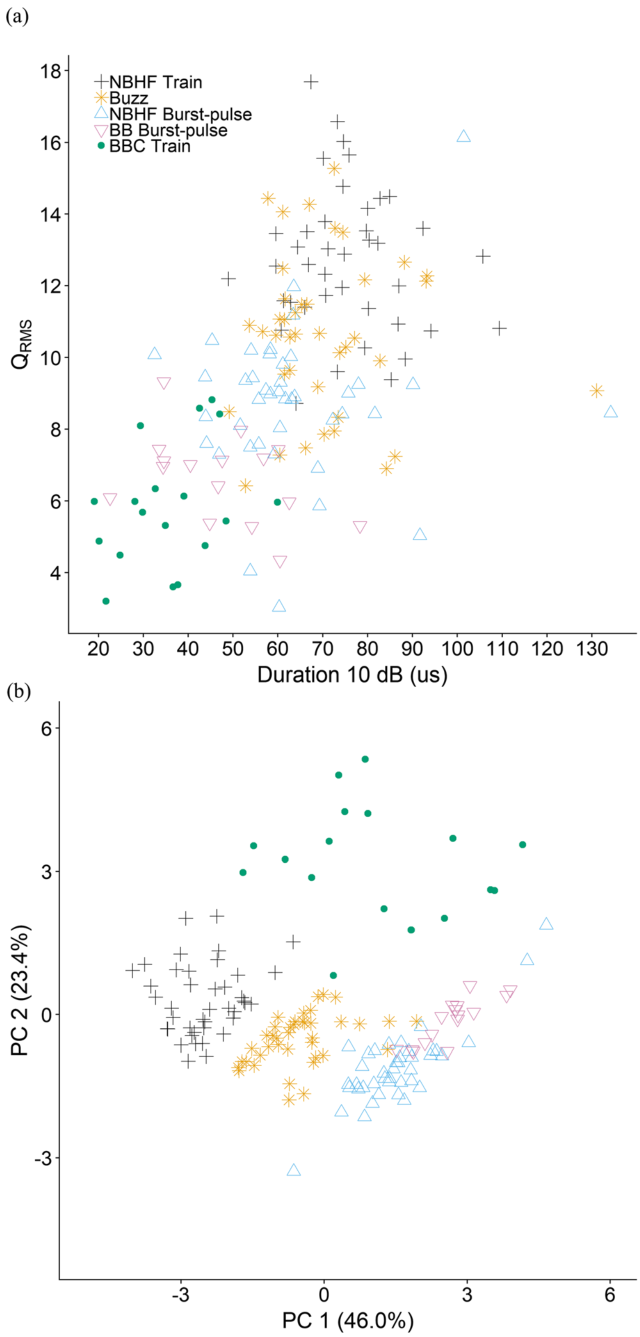

Fig. 4 Commerson's dolphin signal parameters and discrimination of signal types. Each data point represents one measured pulsed signal. 'NBHF Train' represents narrowband high-frequency click trains and 'BBC Train' represents broadband click trains. Burst-pulses are separated into NBHF and BB (broadband) categories. Panel display: **a** Q-ratio (centroid frequency/RMS bandwidth) as a function of click duration, and **b** principal component analysis of signal types including nine parameter variables. PC 1 primarily represents bandwidth (RMS and − 10 dB) and Q_{RMS} parameters. PC 2 represents click rate parameters (5th, 50th and 95th percentile interclick intervals)

There are similarities and differences between the Commerson's dolphin acoustic signals recorded during this study and Heaviside's dolphin acoustic signals reported in Martin et al. (2018b). Broadband signals from both species had similar bandwidth and duration (Table 4). NBHF click trains and buzzes were significantly different between species (Table 4). Our recordings of Commerson's dolphins had very similar parameters to previous studies for this species (Table 1; Kyhn et al. 2010; Reyes Reyes et al. 2015), indicating that the differences observed in Heaviside's dolphin signals may be due to interspecies related differences.

A notable spectral difference between the broadband pulses of Commerson's and Heaviside's dolphins is their minimum (i.e. lowest) frequency content. For Commerson's dolphins, 30% of analysed burst-pulse signals contained energy down to 75 kHz (Fig. 2), which is half an octave lower than the minimum frequency of burst-pulse signals reported for other NBHF species (100 kHz; Dawson 1991; Clausen et al. 2011; see also Yoshida et al. 2014 for recordings of Commerson's dolphins in captivity). However, more than 60% of all Heaviside's dolphin burst-pulse signals contained energy down to 50 kHz (Martin et al. 2018a). The fact that some of the Commerson's dolphin broadband click trains contained energy down to 50 kHz (Fig. 2) shows that this species is capable of producing broadband signals with minimum frequencies similar to those reported for Heaviside's dolphins. The observed significant differences in spectral parameters for Commerson's and Heaviside's dolphins could be attributed to the variability in the minimum frequency of broadband burst-pulses (Table 4). This could be due to inherent interspecific differences, behavioural context such as group effects on behaviour and/or geographic differences related to acoustic behaviour. We could not identify a plausible mechanism whereby different recording platforms (motorised boat in this study; kayak in Martin et al. 2018a, 2019) could have caused the observed species-specific differences.

Our findings indicate that Commerson's dolphins appear to produce broadband click trains and broadband burst-pulses when in large aggregations. Broadband sounds were not recorded in the presence of smaller groups of Commerson's dolphins, indicating that the broadband click trains and burst-pulses may fulfil a communication function in larger groups. This differs from broadband signal production reported for Heaviside's dolphin groups, where Martin and colleagues (2018a, 2019) did not encounter groups larger than 16 individuals, and broadband burst-pulses were commonly recorded from socializing groups comprised of at least four individuals. We did record NBHF burst-pulses (minimum frequency ~ 100 kHz; Table 1) from small and large groups of Commerson's dolphins. Based on the combined findings, we hypothesise that Commerson's dolphins occasionally may switch to a lower frequency, more broadband signal in large groups as a means to reduce acoustic masking from conspecifics. In addition, producing a lower frequency, more broadband signal has been shown to increase the volume ensonified by the signal compared to typical NBHF clicks (Martin et al. 2018a). However, it cannot be ruled out that possible

Table 4 Statistical tests of measured parameters across signal categories from Commerson's and Heaviside's dolphins

Signal type comparison	ICI_{5th} *P*	ICI_{MED} *P*	ICI_{95th} *P*	F_P *P*	F_C *P*	BW_{RMS} *P*	BW_{10dB} *P*	Q_{RMS} *P*	Dur_{10dB} *P*
Cc NBHF Train: Ch NBHF Train	**0.0240**	**0.0268**	0.1545	**0.0004**	**0.0198**	**0.0016**	**0.0011**	**0.0012**	**0.0002**
Cc Buzz: Ch Buzz	0.2047	0.1673	**0.0103**	**0.0001**	0.8584	**< 0.0001**	**0.0150**	**< 0.0001**	0.3819
Cc NBHF BP: Ch BP	0.1710	0.2118	0.5951	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
Cc BB BP: Ch BP	0.5427	0.7125	0.5282	**< 0.0001**	**0.0017**	**0.0004**	0.1882	**< 0.0001**	0.7151
Cc BB Train: Ch BB Train	0.7049	0.3427	0.3963	**0.0045**	**0.0005**	0.1397	0.5109	**0.0035**	0.9143

Independent two-sample *t* tests were used when the variance between groups was equal (homogeneity) and Welch's two-sample tests were used when the variance between groups was not equal (heterogeneity). Statistical significance was set at a threshold of 0.05 and *P* values in boldface are significant. Signal parameters from Heaviside's dolphins were taken from Martin et al. (2018b Supplemental Material Appendix S1)

Cc Commerson's dolphin, *Ch* Heaviside's dolphin, *NBHF Train* narrowband high-frequency click train, *BB Train* broadband click train, *BP* burst-pulse, *NBHF BP* narrowband high-frequency burst-pulse, *BB BP* broadband burst-pulse, ICI_{5th} 5^{th} percentile interclick interval (ms), ICI_{MED} median (50^{th}) percentile interclick interval (ms), ICI_{95th} 95^{th} percentile interclick intervals (ms), F_P peak frequency (kHz), F_C centroid frequency (kHz), BW_{RMS} root mean square bandwidth (kHz), BW_{10dB} −10 dB bandwidth (kHz), Q_{RMS} F_C/BW_{RMS}, Dur_{10dB} −10 dB click duration (μs)

explanations to this broadband signal production could be linked to a specific behaviour (e.g. threat display, Blomqvist and Amundin 2004) or accidental by-product of excitement.

Acoustic masking occurs when sound (i.e. noise) interferes with an animal's ability to detect and interpret a sound (Fletcher and Munson 1937; Clark et al. 2009), and it has the greatest impact at frequencies similar to those of a species' own biologically important signals. The extent of masking can be influenced by a sound's frequency range, duration and amplitude. The modification of acoustic signals, including increasing the amplitude, repetition rate or shifting signal production to a different frequency range, in response to acoustic masking has been documented for a number of cetacean species (e.g. Lesage et al. 1999; Parks et al. 2007; Quick and Janik 2008; Heiler et al. 2016; Thode et al. 2020). For Commerson's dolphins, shifting signal production to a lower frequency and more broadband signal will likely alleviate some of the acoustic masking caused by a surplus of NBHF vocalizations by group members. Numerous NBHF signals producing potential acoustic masking can be observed in the

Table 5 Principal component analysis (PCA) output of the nine measured parameter variables from 156 Commerson's dolphin signals and 159 Heaviside's dolphin signals

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Importance of components									
Standard deviation	2.100	1.566	1.069	0.762	0.460	0.406	0.181	0.074	0.007
Proportion of variance	0.490	0.272	0.127	0.065	0.023	0.018	0.004	0.001	0.000
Cumulative proportion	0.490	0.762	0.889	0.954	0.977	0.996	0.999	1.000	1.000
Loadings with rotation=(9×9)									
ICI_{5th}	−0.312	0.471	−0.097	0.045	−0.035	−0.009	0.643	0.505	0.002
ICI_{MED}	−0.312	0.475	−0.106	0.055	−0.022	0.002	0.113	−0.806	0.000
ICI_{95th}	−0.309	0.472	−0.110	0.052	0.024	0.025	−0.756	0.309	−0.001
F_P	−0.275	−0.297	−0.533	−0.191	−0.630	0.343	−0.016	0.004	0.000
F_C	−0.238	−0.297	−0.616	0.199	0.464	−0.441	0.015	0.000	−0.159
BW_{RMS}	0.407	0.161	−0.293	0.372	−0.263	−0.267	−0.014	0.006	0.666
BW_{10dB}	0.382	0.167	−0.380	0.024	0.445	0.693	0.041	−0.003	0.000
Q_{RMS}	−0.423	−0.211	0.133	−0.296	0.342	0.148	0.013	−0.005	0.729
$Duration_{10dB}$	−0.294	−0.235	0.235	0.830	−0.027	0.336	0.007	0.003	0.000

All parameter values were log-transformed prior to the PCA. Signal parameters from Heaviside's dolphins were taken from Martin et al. (2018b Supplemental Material Appendix S1)

ICI_{5th} 5^{th} percentile interclick interval (ms), ICI_{MED} median (50^{th}) percentile interclick interval (ms), ICI_{95th} 95^{th} percentile interclick interval (ms), F_P peak frequency (kHz), F_C centroid frequency (kHz), BW_{RMS} root mean square bandwidth (kHz), BW_{10dB} −10 dB bandwidth (kHz), Q_{RMS} F_C/BW_{RMS}, Dur_{10dB} −10 dB click duration (μs)

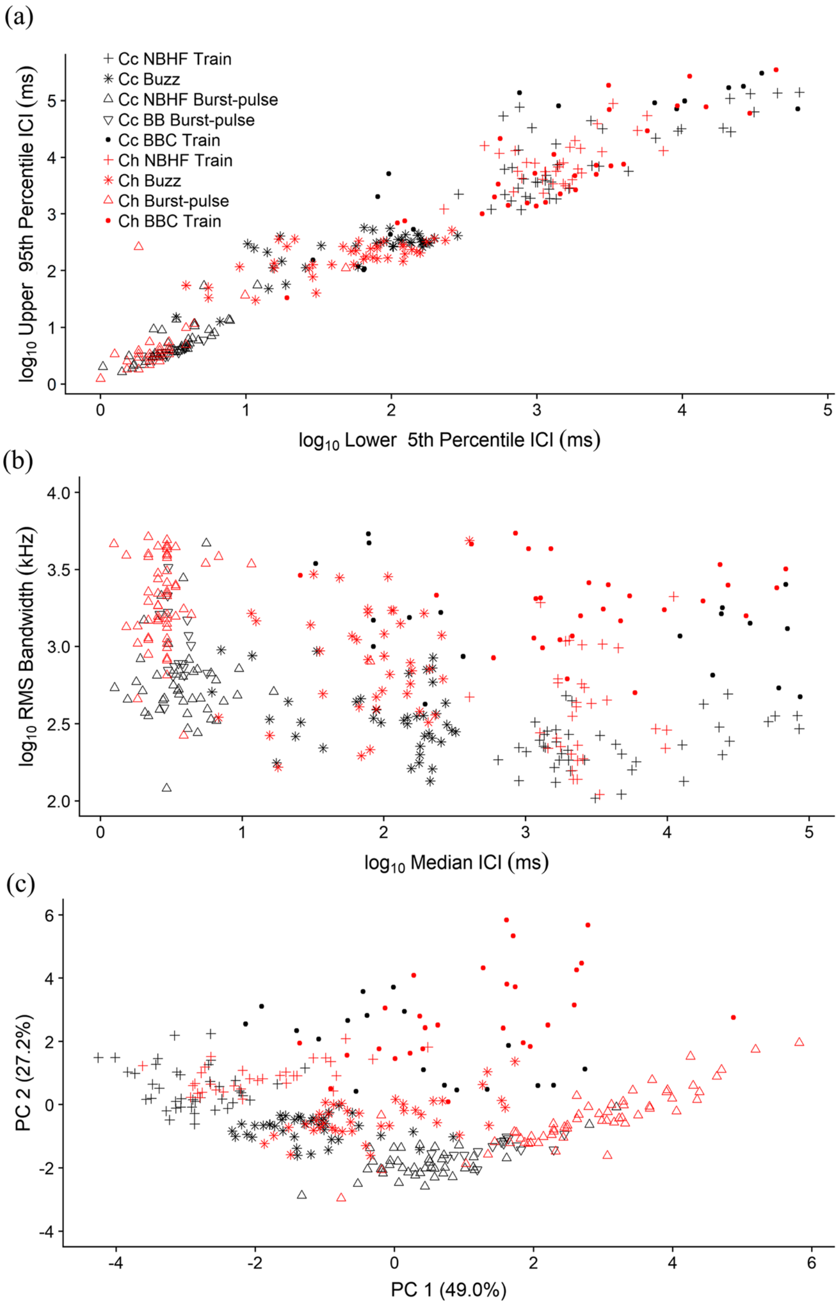

Fig. 5 Commerson's (Cc) and Heaviside's (Ch) dolphin signal parameters and discrimination of signal types. Each data point represents one measured pulsed signal. 'NBHF Train' represents narrowband high-frequency click trains and 'BBC Train' represents broadband click trains. Commerson's dolphin burst-pulses are separated into NBHF and BB (broadband) categories. Panel display: **a** log-transformed 95th percentile ICI as a function of log-transformed 5th percentile ICI, **b** log-transformed RMS bandwidth as a function of log-transformed median ICI and **c** principal component analysis of signal types including nine parameter variables. PC 1 primarily represents bandwidth (RMS and − 10 dB) and Q_{RMS} parameters. PC 2 represents click rate parameters (5th, 50th and 95th percentile interclick intervals). Signal parameters from Heaviside's dolphins were taken from Martin et al. (2018b Supplemental Material Appendix S1)

spectrogram in Fig. 2c where the broadband click train is overlapping several other dolphins' NBHF click trains. In addition, we provide drone video footage paired with acoustic recordings from a large Commerson's dolphin aggregation which contained broadband signals (Online Resource 2) to further support this idea.

Our findings that an additional *Cephalorhynchus* dolphin species produces broadband signals in the form of click trains and burst-pulses makes it highly likely that the two remaining species within the genus, Hector's dolphins (*C. hectori*) and Chilean dolphins (*C. eutropia*), also exhibit this acoustic behaviour. Based on the findings from Martin et al. (2018a) and this study, broadband signal production seems to occur when *Cephalorhynchus* dolphins are aggregated in large groups and/or exhibiting socializing behaviour. Broadband signals have not been described in detail in full bandwidth recordings in Hector's (Dawson 1988; Dawson and Thorpe 1990; Dawson 1991; Thorpe et al. 1991; Kyhn et al. 2009) or in Chilean dolphins (Götz et al. 2010), although very little acoustic research has been conducted on Chilean dolphins. Additional recordings are needed from both species before it is possible to conclude if they also can produce broadband signals.

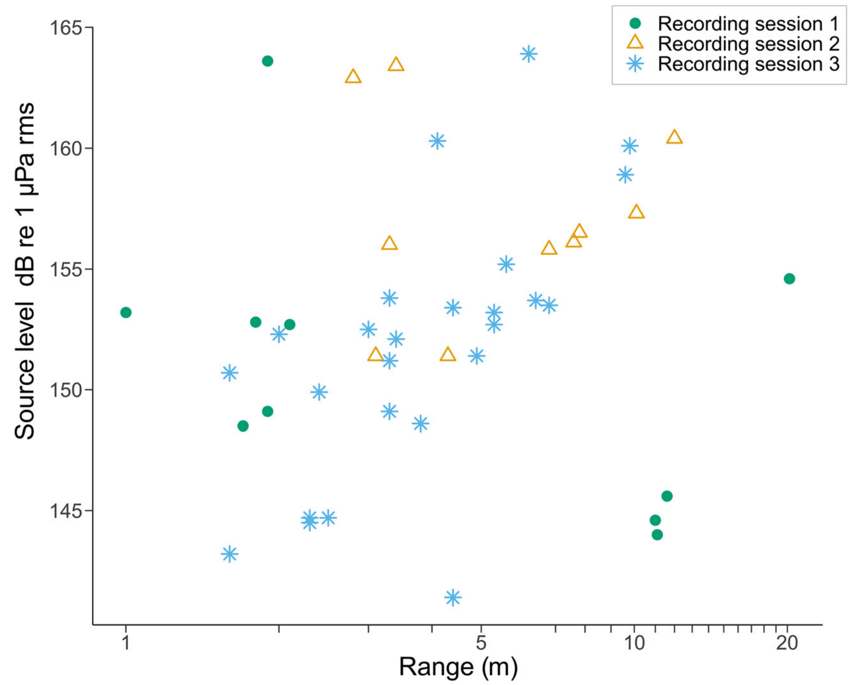

Fig. 6 Root mean square source level (SL_{rms}) of 45 Commerson's dolphin echolocation clicks as a function of range. SL_{rms} (dB re 1 µPa) is the RMS pressure calculated over the −10 dB duration of the signal. Echolocation clicks were extracted from three drone video sequences and are differentiated by shape and colour

Broadband click production from NBHF odontocetes may not only be restricted to the *Cephalorhynchus* genus. Cremer et al. (2017) reported that Franciscana dolphins (*Pontoporia blainvillei*) recorded off Brazil, albeit with a recording bandwidth restricted to 96 kHz, occasionally produce burst-pulses with an initial frequency content comparable to broadband burst-pulse signals described for Commerson's dolphins in this study. The recorded Franciscana dolphin burst-pulses only occurred during capture/tagging/release procedures, corresponding to an unusual, stressful situation (Cremer et al. 2017). In addition, Merkens et al. (2019) report the presence of dwarf or pygmy sperm whale (*Kogia* sp.) clicks that were more broadband than typical NBHF clicks recorded at depth off Hawaii. These findings support the possibility that broadband click production is not only an acoustic characteristic of the *Cephalorhynchus* genus, but characteristic of additional genera of NBHF species. Other coastal species of dolphins known to produce NBHF clicks, such as Peale's dolphin (*Lagenorhynchus australis*), could also be interesting to investigate for broadband signals.

The source levels measured in our study were on average 15–16 dB lower than those calculated for Commerson's dolphins using a six-element hydrophone array by Kyhn et al. (2010). Assuming the analysed clicks were recorded while the animal used its biosonar to investigate the recording gear, this variation partly can be explained by the difference in recording distances (mean = 20.7 m in Kyhn et al. 2010 vs. mean = 5.3 m in this study). Odontocetes typically reduce their source level when approaching an object (i.e. the hydrophone), generally following a $20 \cdot \log_{10}(R)$ relationship (Au and Benoit-Bird 2003). The average fourfold longer distances used to measure source levels in Kyhn et al. (2010) would therefore suggest that source levels would be around 12 dB higher compared to our data. The remaining 3–4 dB lower average source levels recorded in this study compared to Kyhn et al. (2010) may be explained by a difference in equipment methodology. Whereas Kyhn et al. (2010) used a linear hydrophone array to record clicks, we used a single recording unit. As clicks are highly directional, our method of securing that the dolphin was facing the data logger so the clicks could be recorded on-axis may be coarser than Kyhn et al.'s (2010) on-axis criteria from their array recordings. This could result in the inclusion of clicks in this study which were slightly off-axis and therefore having a lower source level.

By time syncing underwater acoustic recordings with the drone video, we obtained new insights into the source levels and functions of sounds produced by Commerson's dolphins. Our source level estimates are comparable to published source levels derived from hydrophone arrays for this species and other small NBHF cetaceans (Kyhn et al. 2009, 2010; Morisaka et al. 2011). To our knowledge, only one published study (Frouin-Mouy et al. 2020) has previously combined overhead visual observations from drones and underwater acoustic recordings to describe the acoustic behaviour and sound parameters of calls of cetaceans (gray whales, *Eschrichtius robustus*). This study is the first to measure source levels of echolocation signals from an odontocete using the combined drone and underwater recording method. This may be a more cost-efficient method to obtain source data from animals producing sound close to the surface than using hydrophone arrays.

Our findings suggest that Commerson's dolphins have a more complex communication system than previously thought. Spending sufficient time for fieldwork recording animals during all aspects of their behavioural repertoire, including foraging, socializing and resting, and across a range of group sizes seems crucial to fully describe their acoustic repertoire. This is important for correct species classification using passive acoustic monitoring and related density and abundance estimation (Caillat et al. 2013), as NBHF species are distributed globally and generally are sympatric with broadband toothed whale species (e.g. Heinrich et al. 2010). Results of this study will be useful for species identification from passive acoustic monitoring and toward a better understanding of how this species and perhaps genus communicate using a limited acoustic repertoire of pulsed signals.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-021-03035-y.

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Authors' contributions All authors contributed to the study conception and design. Data collection was performed by MJM, STO, MVRR, AM and MIB. Material preparation and analysis were performed by MJM, STO and MW. The first draft of the manuscript was written by MJM and STO and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and material All data generated or analysed during this study are included in this published article and its supplementary information files.

Code availability The progam 'Porpoise Tracker' used for collecting measurements from the drone footage is freely available on github: https://github.com/henrikmidtiby/PorpoiseTracker

Declarations

Ethics approval This research was conducted by the Fundación Cethus in collaboration with the University of Southern Denmark with permission from the Dirección General de Recursos Naturales – Province of Santa Cruz (Provision 013/19) and following the ethics guidelines from the University of Southern Denmark, under a permit from the Danish Animal Experiments Inspectorate, based on EU Directive 2010/63/EU. This is an observational study based on focal animal sampling where dolphins were observed from a distance and not touched or harmed in any way during data collection. The engine and echo sounder of the motor boat was turned off around dolphin groups to promote a quieter, less polluting and less disturbing environment.

Consent to participate All authors have provided their consent to participate in this research and related publication.

Consent for publication All authors have provided their consent to publish the results of this study.

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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