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Description and clustering of echolocation signals of Commerson's dolphins (Cephalorhynchus commersonii) in Bahía San Julián, Argentina

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Commerson's dolphins (Cephalorhynchus commersonii) inhabit coastal waters of Southern South America and Kerguelen Islands. Limited information exists about the acoustic repertoire of this species in the wild. Here, echolocation signals from free-ranging Commerson's dolphins were recorded in Bahía San Julián, Argentina. Signal parameters were calculated and a cluster analysis was made on 3180 regular clicks. Three clusters were obtained based on peak frequency (129, 137, and 173 kHz) and 3 dB bandwidth (8, 6, and 5 kHz). The 428 buzz clicks were analyzed separately. They consisted of clicks emitted with a median interclick interval of 3.5 ms, peak frequency at 131 kHz, 3 dB bandwidth of 9 kHz, 10 dB bandwidth of 18 kHz, and duration of 56 μs. Buzz clicks were significantly shorter and with a lower peak frequency and a broader bandwidth than most of the regular clicks. This study provided the first description of different echolocation signals, including on- and off-axis signals, recorded from Commerson's dolphins in the wild, most likely as a result of animals at several distances and orientations to the recording device. This information could be useful while doing passive acoustic monitoring. © 2015 Acoustical Society of America. [http://dx.doi.org/10.1121/1.4929899]

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I. INTRODUCTION

Toothed whales rely mostly on sounds for orientation and foraging. They have evolved a biosonar system, called echolocation, which allows them to explore their surroundings by emitting short duration, ultrasonic pulses and listening to the echoes that return from ensonified objects (Au, 1993). In this way, they manage to locate and capture prey, and also to orient themselves.

Echolocation signals can be broadly divided into four different types: (1) broadband clicks, which are produced by most dolphins, (2) narrowband high-frequency (NBHF) clicks (Au, 1993), which are commonly produced by porpoises, some small dolphins, and pygmy sperm whales, (3) multi-pulsed low-frequency sperm whale clicks (Møhl et al., 2003), and (4) frequency-modulated clicks of beaked whales (Zimmer et al., 2005). Several odontocete species produce clicks with species-specific characteristics (Soldevilla et al., 2008; Madsen et al., 2005; Zimmer et al., 2005; Akamatsu et al., 1998; Kamminga et al., 1996) and therefore passive acoustics could be useful to identify cetacean species. In addition, passive acoustic surveys overcome some limitations of traditional visual surveys as they allow the detection of submerged animals and the detection range is often larger (Barlow and Taylor, 2005; Swartz et al., 2003; Clark and Fristrup, 1997). However, to be able to effectively conduct passive acoustic monitoring, previous information about the vocalizations of the focus species is required.

Commerson's dolphins are small dolphins that inhabit exclusively the Southern hemisphere. Two subspecies are geographically and genetically isolated presenting differences in the pigmentation and morphology of the animals (Robineau et al., 2007). Cephalorhynchus commersonii kerguelenensis (Robineau et al., 2007) inhabits the coastal waters of the Kerguelen Islands (Indian Ocean). Dziedzic and de Buffrenil (1989) described NBHF clicks with a peak frequency at 116 kHz for this subspecies.

Most Commerson's dolphins belong to the subspecies Cephalorhynchus commersonii commersonii (Lacépède 1804), and are distributed in temperate coastal waters of southern South America, around Islas Malvinas/Falkland Islands, and in the Drake Passage (Goodall, 1994; Rice,

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1998). Along the southern coast of Argentina, this species is found in cold inshore waters, bays, harbours, and river mouths. Between September and May, a population of Commerson's dolphins socializes, breeds, forages, rests, and commutes in Bahía San Julián (Iñíguez *et al.*, 2000).

Limited information exists about the acoustic repertoire of this species in the wild. Two studies that were conducted in the open sea off the Islas Malvinas/Falkland Islands area showed that the echolocation signals produced by Commerson's dolphins consisted of stereotyped NBHF clicks with a peak frequency around 133 kHz (Evans *et al.*, 1988; Kyhn *et al.*, 2010) and a half-power bandwidth (3 dB bandwidth) of 21 kHz (Kyhn *et al.*, 2010).

The aim of this work is to describe as much of the repertoire of echolocation signals of Commerson's dolphins in the wild as possible.

II. MATERIALS AND METHODS

A. Study area and recording device

The study area, Bahía San Julián, Argentina (49°14′S, 67°36′W, Fig. 1), consists of shallow waters with a maximum depth of 35 m and an area of 238 km². Underwater sound recordings were collected on 35 sessions during austral summer 2011, 2012, and 2013, spring 2011 and 2013, and autumn 2012 and 2013. The duration of each session ranged between 0.3 and 2 h.

Recordings were made under very calm weather conditions (low winds, Beaufort scale <2), using an omnidirectional, spherical hydrophone Reson TC 4033 (Teledyne RESON Inc., Thousand Oaks, CA) suspended from a semirigid boat or a pier. When recordings were made from the boat, the engine was turned off to deploy the hydrophone and start recording. Signals were digitized at a sampling rate of 500 kHz by Avisoft Ultrasound-Gate (Avisoft Bioacoustics e.K., Glienicke/Nordbahn, Germany) (connected with the Ultrasound-Gate charge amplifier), obtaining recordings with

frequencies ranging from 10 Hz up to 250 kHz. Data were stored as 1-min wav-files in a laptop.

Weather conditions, such as sea state, wind speed, and temperature were noted. A visual survey protocol was used to record surface behavior, age category, group size, and position of the observed animals (Mann, 1999). Three ages categories (adult, juvenile, and calf) were determined. Adults have a very distinct black and white pattern; juveniles are medium-sized animals with a light gray rather than white pigmentation on the sides and back; calves are distinguished by their dark brown to gray color pattern (Goodall *et al.*, 1988). No other marine mammals were sighted or detected acoustically at any time during the field trips.

B. Click analysis

Audio files were scanned using Ishmael 2.0 (Mellinger, 2001) and the occurrence of echolocation signals was logged. Only those files with clear echolocation signals were selected for further analysis. Files containing boat noise as well as clipped signals were discarded.

Signal analysis was performed with custom-written codes using MATLAB (Mathworks, Natick, MA). An algorithm to automatically detect and extract individual echolocation signals was developed. The algorithm consisted of two steps: the first one was a click detector to locate potential clicks in the time domain. Only echolocation signals with a signalto-noise ratio over 20 dB were picked. The second step consisted of a click extractor which was implemented on the data output from the first step to search for the start time of each click and extract the following 300 µs and previous 150 μ s before the onset of the click. The criterion for click onset was the first point at which the envelope (calculated as the absolute value of the Hilbert transformed version of the signal) was greater than the root of the mean squared amplitude of the signal. Extracted signals were classified as either regular or buzz clicks, based upon their production rate. A buzz was defined as a rapid series of clicks emitted at

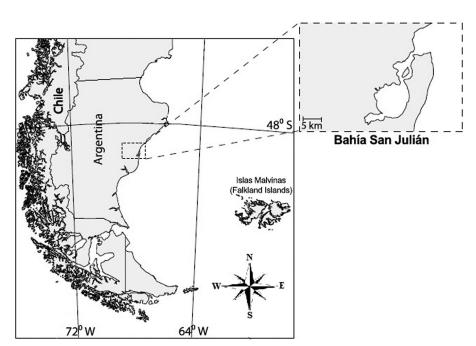


FIG. 1. Map of Southern South America. Insert box indicates study location at Bahía San Julián in Argentina.

intervals of 5 ms or less, while regular clicks were emitted at greater intervals.

To test the performance of the automatic detector, about 20% of the extracted signals were randomly selected and false positives were manually counted. Less than 6% of the detections were false positives.

To correct the received levels according to sensitivity of the recording system the inverse of the system transfer function was applied. The spectral characteristics of clicks were quantified for the 300 μ s following the start of each click by calculating a 512-point fast Fourier transform (FFT) with zero padding, rectangular window, and a fourth-order Butterworth bandpass filter between 25 and 240 kHz to eliminate the low frequency noise and aliasing. For each click, the following parameters were calculated according to Au (1993): peak frequency, centroid frequency (defined as the frequency dividing the spectrum in two halves of equal energy), 10 dB bandwidth (defined as the bandwidth at $-10 \, dB$ points below the maximum intensity), 3 dB bandwidth (defined as the bandwidth at $-3 \, dB$ points below the maximum intensity), and $10 \, dB$ duration (defined as time between $-10 \, dB$ points on the envelope computed by taking the absolute value of the analytical signal). Inter-click interval (ICI) was calculated as the difference between the start time of an echolocation signal and the start time of the previous one, and the median ICI was reported, with its corresponding quartiles.

C. Statistical analysis

Regular clicks detected by the aforementioned algorithm were randomly partitioned into two parts. A nonhierarchical k-means clustering analysis was made on each subsample, using the peak frequency and the 3 dB bandwidth as variables. One of the reasons to use peak frequency is that clicks showed a consistent multiple peak structure and so the various clusters would emphasize either of these peaks. Besides, authors considered those parameters to be less sensitive to the animal's head orientation with respect to the hydrophone and to sound propagation path differences than other parameters—such as centroid frequency and duration. The analysis consists of partitioning the data into k clusters through an iterative process that minimizes the sum, over all clusters, of the within-cluster sums of the distances between each point to the centroid of the cluster. The number of replicates was set to 1000, so the clustering process was repeated over 1000 times, each with a new random set of initial cluster centroid positions, and the software returned the solution with the lowest value for within-cluster sums of point-tocentroid distances. The analysis was performed using the squared Euclidean distance, which had the greatest cophenetic correlation coefficient (c = 0.8) in comparison with other measures of distance. The cophenetic correlation for a cluster analysis is defined as the linear correlation coefficient between the distance of each point to every k cluster centroid, and the original distances used to construct those clusters, in this case squared Euclidean distance. Thus, it is a measure of how faithfully the clustering represents the dissimilarities among observations (Kaesler, 1970). The cophenetic correlation can be used to compare alternative cluster solutions obtained using different algorithms, such as two methods to compute the original distances between objects. The "elbow" method was used to choose an appropriate number of clusters. This method consists of looking at a plot of percentage of explained variance as a function of the number of clusters, and search for a distinctive break after which the curve levels off. It indicates whether there will be little improvement in the explained variability of the data by adding another cluster (Yan, 2005; Sugar *et al.*, 1999). The results showed in this paper proceeded from the first subset of clicks, while the second subsample of clicks was used to search for stability and validity of the results from the clustering of the first data set.

Buzz clicks were analyzed separately and since no distinct groups were recognized for buzz clicks, no clustering analysis was conducted. Instead, the median of the individual spectra for all the detected buzz clicks and the lower (Q1) and upper quartiles (Q3) of the distribution were calculated.

Kruskal Wallis and multiple comparison tests were used to search for significant differences between the parameters of the echolocation signals.

III. RESULTS

The number of recording sessions included in this analysis was 13. A total of 6887 regular clicks and 428 buzz clicks met all of our criteria for analysis. During the whole period of study, we had a sample of 129 sighted individuals (109 adults, 15 juveniles, and 5 calves), including re-sighted individuals. Distances from the recorded individuals to the hydrophone varied between about 1 and 300 m. Figure 2 depicts a typical click train produced by a Commerson's dolphin that was engaged in foraging activities. This train included regular clicks and a terminal buzz where ICIs fell below 5 ms [Fig. 2(c)].

A. Regular clicks

Regular clicks were produced with a median ICI of 36.4 ms (ranging from 6 to 472 ms). The cluster analysis included 3180 regular clicks. The selected number of clusters for the analysis was 3 since they explained 86% of the variability of the data and a fourth cluster would improve only in 4% the explained variance. Since the peak frequency and the 3 dB bandwidth within each cluster were not normally distributed, the medians, lower quartile (Q1) and upper quartile (Q3) were used to illustrate the distributions of the clicks within each cluster in a more reliable way (Fig. 3). Signal parameters of the three clusters are summarized in Table I. Clicks within each cluster differed significantly in peak and centroid frequency, bandwidth, and duration, except for duration of cluster 1, and 2 and 3 dB bandwidth of clusters 1 and 3 for which multiple comparison tests showed nonsignificant differences. Spectrograms of click trains showing a representative click of each cluster and its time series and spectrum are depicted in Figs. 4(a)-4(i). Also the signal parameters of all the regular clicks without dividing them into different clusters are presented in Table I, for comparison with buzz clicks and previous studies. All the clicks presented a subdominant frequency component at around

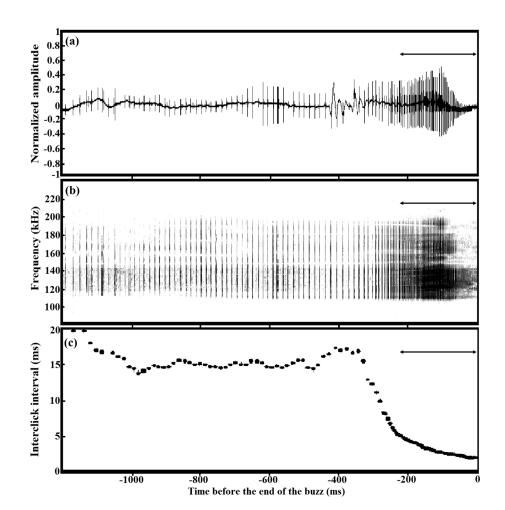


FIG. 2. (a) Normalized time series of a representative click train of a Commerson's dolphin while echolocating in the wild. The arrows indicate the buzz at the end of the train. (b) Spectrogram of the same click train (1024-point FFT, 0.002 s FFT length, 0% overlap, hamming window). (c) Corresponding ICIs along time.

160–180 kHz, with the exception of clicks in cluster 3 which had their peak frequency within this range of frequencies.

B. Buzz clicks

Buzzes consisted of clicks emitted with a median ICI of 3.5 ms (ranging from 1.6 to 5 ms). The time series and

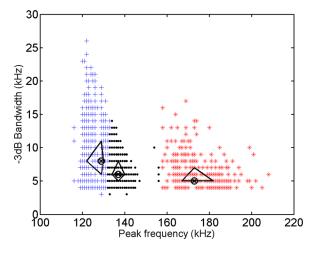


FIG. 3. (Color online) Peak frequency (kHz) of regular clicks within each cluster against the 3 dB bandwidth (kHz). Clicks within cluster 1 are represented by spots, cluster 2 by pluses, and cluster 3 by asterisks. The medians of each cluster are represented by a cross within a circle and the area inside the lines include clicks between the lower quartiles (Q1) and upper quartiles (Q3) of the distributions of the two parameters for each cluster.

spectrum of a single buzz click are represented in Figs. 5(a) and 5(b), respectively. Figure 5(c) depicts the median spectrum of all buzz clicks analyzed with its lower and upper quartile. Median peak frequency was at 131 kHz $(Q1=129\,\mathrm{kHz};\ Q3=140\,\mathrm{kHz})$ with a median 3 dB bandwidth of $9\,\mathrm{kHz}$ ($Q1=5\,\mathrm{kHz};\ Q3=12\,\mathrm{kHz})$, and $10\,\mathrm{dB}$ bandwidth of $18\,\mathrm{kHz}$ ($Q1=8\,\mathrm{kHz};\ Q3=20\,\mathrm{kHz}$). The median duration of buzz clicks was $56\,\mu\mathrm{s}$ ($Q1=52\,\mu\mathrm{s};\ Q3=64\,\mu\mathrm{s}$). A subdominant component at $160-180\,\mathrm{kHz}$ was also present in the spectra of buzz clicks.

IV. DISCUSSION

This paper intends to describe variability in the spectral content of echolocation signals of Commerson's dolphins in the wild when using passive acoustic monitoring and the position and orientation of the animals with respect to the recording device is unknown. In particular, we found that there is variability in the regular clicks that can be grouped into three different clusters.

A. Clusters

Given that in a non-hierarchical cluster analysis the number of clusters needs to be predetermined, the selection of this number requires the application of some criteria. For this study, regular clicks were divided into three clusters because adding a fourth cluster would not lead to a significant increase of the variability explained by the model. The

TABLE I. Median (Med), lower quartile (Q1), and upper quartile (Q3) of regular click characteristics of Commerson's dolphins.

Sample size	Cluster 1 1751			Cluster 2 1114			Cluster 3 315		
	Peak frequency (kHz)	137	134	140	129	122	130	173	167
Centroid frequency (kHz)	141	137	146	136	133	140	163	155	171
3 dB bandwidth (kHz)	6	5	8	8	6	11	5	5	7
10 dB bandwidth (kHz)	9	7	12	15	13	21	11	8	16
10 dB duration (μs)	80	66	108	76	66	100	74	60	104

presence of three clusters does not mean that Commerson's dolphins actively produce three different types of regular clicks. However, this method could be useful to identify and classify echolocation clicks of the species recorded in the wild while doing passive acoustic monitoring in the future.

Kyhn et al. (2010) showed high classification probability of Commerson's dolphin's echolocation signals using centroid frequencies when comparing two different species producing NBHF clicks. However, in this study different types of clicks within the same species were compared without any previous classification criterion such as different species, individuals, or behavior, so the methods used in the aforementioned paper do not fully apply here. Additionally,

peak frequency and 3 dB bandwidth were used in this study because they were considered to be less sensitive than other parameters to the animal's head orientation with respect to the hydrophone and to sound propagation path differences.

The dataset was split into two subsets, and each of them was thereafter analyzed separately using the same parameters. The two solutions' cluster centroids did not differ significantly, so it can be presumed that the three means clustering analysis has a high degree of stability. Furthermore, other parameters that were not included in the cluster analysis, such as central frequency, 10 dB bandwidth, and duration also differ significantly among clusters, which validates our clustering analysis and confirms that the three clusters are distinct groups.

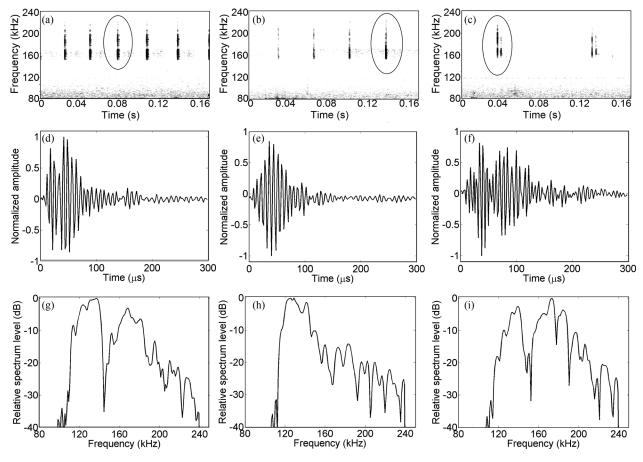


FIG. 4. Spectrogram of an echolocation click train (1024-point FFT, 0.002 s FFT length, 0% overlap, hamming window) showing a representative click (black circle), its time series and normalized spectrum (512-point FFT, 500 kHz sampling frequency, rectangular window) for each cluster. (a) and (d) cluster 1, (b) and (e) cluster 2, and (c) and (f) cluster 3.

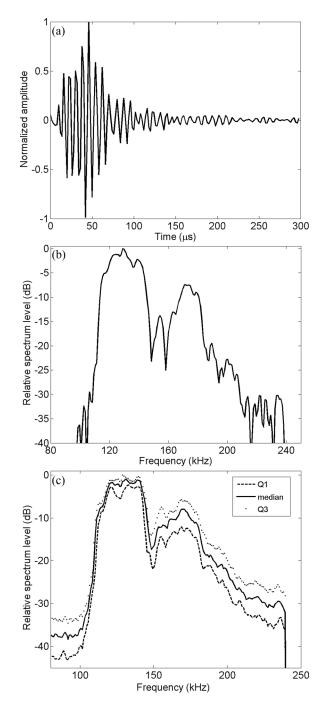


FIG. 5. (a) Normalized time series of a representative buzz click. (b) Normalized spectrum of a representative buzz click. (c) Normalized median spectrum with its lower (Q1) and upper quartile (Q3) of all buzz clicks analyzed (512-point FFT, $500\,\mathrm{kHz}$ sampling frequency, rectangular window).

B. Sources of variability in regular clicks

There are several sources of variability that could account for the differentiation of the clusters obtained in this study.

Is it possible that Commerson's dolphins produce different types of echolocation signals? We observed that many echolocation trains proceeding from a single animal are made up of more than one type of click, and the presence of different clusters was also evident in some occasions when two animals were swimming nearby, so both intra- and interindividual variability were found. There is some previous

evidence that some species of odontocetes can adjust the frequency spectrum of their echolocation signals in response to tasks or ambient conditions (Au *et al.*, 1985, 1995). However, the methodology used in this study did not allow us to test whether Commerson's dolphins produce different types of clicks, since we were not able to localize the source of the sounds nor identify clicks emitted on-axis.

Why can we not rule out other factors that influence the differences shown in the echolocation signals? With our experimental setup we cannot discriminate between clicks recorded on and off the acoustic axis of the animal. Given that echolocation signals are highly directional and suffer from distortion in the wave shape and spectral content as a function of the beam angle (Au, 1993; Madsen et al., 2004; Au et al., 2012a,b), clicks recorded off-axis likely differ from those recorded on-axis. Thus, the variability found in this study, or at least some of it, is probably an effect of the animal's head orientation with regard to the hydrophone instead of consisting of a change in sound production. While conducting passive acoustic monitoring with a single hydrophone the true orientation of the beam is unknown. Hence, since we are interested in describing as much as the repertoire of echolocation signals as possible, knowing possible types of regular clicks recorded from different angles to the hydrophone is useful.

Another source of variability could be the uncertain distance of the animal to the hydrophone. As higher frequencies attenuate faster due to a higher absorption (Urick, 1983), it is possible that differences in the spectral content of the recorded clicks are due to different positions of the animals.

C. Echolocation behavior

The recorded click trains sometimes end in a buzz, which contains clicks that are significantly shorter and with a lower peak frequency and broader bandwidth than most of the regular clicks. Click trains ending with a buzz have also been recorded in the field from several toothed whales and associated with presumed prey capture (Johnson et al., 2004; Miller et al., 2004; Aguilar de Soto et al., 2008). A reduction in pulse duration and increase in the spectral content have been previously described for buzzes produced by bats (Griffin et al., 1960; Kalko and Schnitzler, 1989; Melcón et al., 2007). Schnitzler and Kalko (2001) interpreted these characteristics along with the higher repetition rate as an adaptation for a greater precision in localization and tracking of moving prey before capture. Melcón et al. (2007) studied the echolocation behavior of vespertilionid bats and found that the information conveyed by a buzz often reaches the bat too late to guide the animal to a target prey. In such situations, they hypothesized that buzzes may help to evaluate unsuccessful attempts and to react properly (Melcón et al., 2009). In our study, the association between buzzes and foraging activities is supported by visual observations.

Odontocetes that produce NBHF clicks are found in three different families and they all produce echolocation signals with peak frequencies above 120 kHz, 3 dB bandwidth of 6–22 kHz and 10 dB bandwidth of 15–34 kHz [e.g., Kogia breviceps, Phocoena phocoena, Cephalorhynchus

hectori, Pontoporia blainvillei (Madsen et al., 2005; Au, 1993; Kyhn et al., 2009; Melcón et al., 2012)]. All the echolocation signals described in this paper resemble the NBHF clicks. Besides, all the spectra had a strong notch at 150 kHz and a subdominant frequency at around 160-180 kHz, except for 10% of the regular clicks (cluster 3) which had the peak frequency within that range. The presence of a subdominant frequency centered at 160 kHz had been reported before for captive Commerson's dolphins and finless porpoises (Neophocaena phocaenoides) (Kamminga and Wiersma, 1982; Kamminga et al., 1986). Also, the broadband clicks of several species of dolphins have two distinct peaks in frequency (Au et al., 1985, 1995; Philips et al., 2002). In these species, the frequency peaks are apparently related to different sizes of the fatty bursae within the left and right phonic lips (Cranford et al., 2011). However, in Commerson's dolphins both bursae are roughly similar in size (Amundin and Cranford, 1990). It remains unknown how the two separate components in the spectrum are generated.

On some occasions the spectrum of some clicks contained frequencies beyond 250 kHz, which was the upper limit of the recording device (not considering saturated recordings). The same was reported for franciscana dolphins in the Río Negro estuary (Melcón *et al.*, 2012). These two species share a small size, inhabit coastal waters and enter river mouths, and produce clicks at frequencies above 100 kHz. The mechanism involved in sound production in these species, how they manage to reach so high frequencies, and whether they make use of the entire frequency spectrum of their signals is still unknown. However, due to the fast attenuation of frequencies above 250 kHz, the echoes produced from this higher portion of the spectrum could only convey information from targets at very short distances.

V. CONCLUSIONS

This paper provides the first description of different echolocation signals, including on- and off-axis signals, recorded from Commerson's dolphins in the wild. The described variability is most likely due to animals emitting sounds at several distances and orientations to the recording device. However, the possibility that Commerson's dolphins may change the spectral content of their clicks upon different situations or individuals cannot be ruled out, and could be the subject of future research under more controlled conditions. Regardless, these results provide us with useful information to better analyze the data proceeding from passive acoustic monitoring, especially in areas where other species like *Lagenorhynchus australis* and *C. eutropia*, which produce similar sounds, overlap with Commerson's dolphins.

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- Aguilar de Soto, N., Johnson, M. P., Madsen, P. T., Díaz, F., Domínguez, I., Brito, A., and Tyack, P. L. (2008). "Cheetahs of the deep sea: Deep foraging sprints in short finned pilot whales off Tenerife (Canary Islands)," J. Anim. Ecol. 77, 936–947.
- Akamatsu, T., Wang, D., Nakamura, K., and Wang, K. (1998). "Echolocation range of captive and free-ranging baiji (*Lipotes vexillifer*), finless porpoise (*Neophocaena phocaenoides*), and bottlenose dolphin (*Tursiops truncatus*)," J. Acoust. Soc. Am. 104, 2511–2516.
- Amundin, M., and Cranford, T. W. (1990). "Forehead anatomy of *Phocoena phocoena* and *Cephalorhynchus commersonii*: 3-dimensional computer reconstructions with emphasis on the nasal diverticula," in *Sensory Abilities of Cetaceans: Laboratory and Field Evidence*, edited by J. A. Thomas and R. A. Kastelein (Plenum Publishing Corp., New York), pp. 1–18.
- Au, W. W. L. (1993). The Sonar of Dolphins (Springer-Verlag, New York).
 Au, W. W. L., Branstetter, B., Moore, P. W., and Finneran, J. J. (2012a).
 "The biosonar field around an Atlantic bottlenose dolphin (*Tursiops truncatus*)," J. Acoust. Soc. Am. 131, 569–576.
- Au, W. W. L., Branstetter, B., Moore, P. W., and Finneran, J. J. (2012b). "Dolphin biosonar signals measured at extreme off-axis angles: Insights to sound propagation in the head," J. Acoust. Soc. Am. 132, 1199–1206.
- Au, W. W. L., Carder, D. A., Penner, R. H., and Scronce, B. L. (1985). "Demonstration of adaptation in beluga whale echolocation signals," J. Acoust. Soc. Am. 77, 726–730.
- Au, W. W. L., Pawloski, J. L., Nacjtigall, P. E., Blonz, M., and Gisner, R. C. (1995). "Echolocation signals and transmission beam pattern of a false killer whale (*Pseudorca crassidens*)," J. Acoust. Soc. Am. 98(1), 51–59.
- Barlow, J., and Taylor, B. L. (2005). "Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey," Mar. Mammal Sci. 21(3), 429–445.
- Clark, C. W., and Fristrup, K. M. (1997). "Whales 95: A combined visual and acoustic survey of blue and fin whales off Southern California," Rep. Int. Whal. Comm. 47, 583–600.
- Cranford, T. W., Elsberry, W. R., Van Bonn, W. G., Jeffress, J. A., Chaplin, M. S., Blackwood, D. J., Carder, D. A., Kamolnick, T., Todd, M. A., and Ridgway, S. H. (2011). "Observation and analysis of sonar signal generation in the bottlenose dolphin (*Tursiops truncatus*): Evidence for two sonar sources," J. Exp. Mar. Biol. Ecol. 407, 81–96.
- Dziedzic, A., and de Buffrenil, D. (1989). "Acoustic signals of the Commerson's dolphin, *Cephalorhynchus commersonii*, in the Kerguelen Islands," J. Mammal. 70, 449–452.
- Evans, W. E., Awbrey, F. T., and Hackbarth, H. (1988). "High frequency pulses produced by free-ranging Commerson's dolphin (*Cephalorhynchus commersonii*) compared to those of phocoenids," in *Biology of the Genus Cephalorhynchus. Rep. Int. Whal. Commn.* (*Special Issue 9*), edited by R. L. Brownell, Jr. and G. P. Donovan (Cambridge), pp. 173–181.
- Goodall, R. N. P. (1994). "Commerson's dolphin *Cephalorhynchus commersonii* (Lacépède, 1804)," in *Handbook of Marine Mammals. The First Book of Dolphins*, edited by S. H. Ridgway and R. Harrison (Academic, New York), pp. 241–267.
- Goodall, R. N. P., Galeazzi, A. R., Leatherwood, S., Miller, K. W., Cameron, I. S., Kastelein, R. K., and Sobral, A. P. (1988). "Studies on Commerson's dolphins, *Cephalorhynchus commersonii*, off Tierra del Fuego, 1976–1984, with a review of information on the species in the South Atlantic," Paper SC/36/SM8 presented to the IWC Scientific Committee.
- Griffin, D. R., Webster, F. A., and Michael, C. R. (1960). "The echolocation of flying insects by bats," Anim. Behav. 8, 141–154.
- Iñíguez, M. A., Tossenberger, V. P., and Tomsin, A. L. (2000).
 "Comportamiento y Biología de toninas overas (Cephalorhynchus commersonii) en la bahía San Julián, Pcia. Santa Cruz, Argentina" ["Behaviour and biology of Commerson's dolphins (Cephalorhynchus commersonii) in San Julián bay, Santa Cruz province, Argentina"], X Reunión de Trabajo de Especialistas en Mamíferos Marinos—III Congreso de SOLAMAC (Proceedings of the X Conferences on Specialists

- on Aquatic Mammals from South America and III SOLAMAC Congress) Buenos Aires, p. 62.
- Johnson, M., Madsen, P. T., Zimmer, W. M. X., Aguilar de Soto, N., and Tyack, P. L. (2004). "Beaked whales echolocate on prey," Proc. R. Soc. London, B. 271, s383–s386.
- Kaesler, R. L. (1970). "The cophenetic correlation coefficient in paleoecology," Geol. Soc. Am. Bulletin 81(4), 1261–1266.
- Kalko, E. K. V., and Schnitzler, H.-U. (1989). "The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentoni*," Behav. Ecol. Sociobiol. 24, 225–238.
- Kamminga, C., Cohen, S., and Silber, G. K. (1996). "Investigations on cetacean sonar XI: Intrinsic comparison of the wave shapes of some members of the *Phocoenidae* family," Aquat. Mamm. 22, 45–56.
- Kamminga, C., Kataoka, T., and Engelsma, F. J. (1986). "Investigation on cetacean sonar VII. Underwater sounds of *Neophocaena phocaenoides* of the Japanese coastal population," Aq. Mammals 12(2), 52–60.
- Kamminga, C., and Wiersma, H. (1982). "Investigation on cetacean sonar V. The true nature of the sonar sound of *Cephalorhynchus commersonii*," Aq. Mammals 9(3), 95–104.
- Kyhn, L. A., Jensen, F. H., Beedholm, K., Tougaard, J., Hansen, M., and Madsen, P. T. (2010). "Echolocation in sympatric Peale's dolphins (*Lagenorhynchus australis*) and Commerson's dolphins (*Cephalorhynchus commersonii*) producing narrow-band high-frequency clicks," J. Exp. Biol. 213, 1940–1949.
- Kyhn, L. A., Tougaard, J., Jensen, F. H., Wahlberg, M., Stone, G., Yoshinaga, A., Beedholm, K., and Madsen, P. T. (2009). "Feeding at a high pitch: Source parameters of narrow-band, high-frequency clicks from echolocating off-shore hourglass dolphins and coastal Hector's dolphins," J. Acoust. Soc. Am. 125(3), 1783–1791.
- Lacépède, B. G. E. (**1804**). *Histoire Naturelle des Cétacés* (París), Vol. 1, 396 pp.
- Madsen, P. T., Carder, D. A., Beedholm, K., and Ridgway, S. H. (2005). "Porpoise clicks from a sperm whales nose—Convergent evolution of 130 kHz pulses in toothed whale sonars?," Bioacoustics 15, 195–206.
- Madsen, P. T., Kerr, I., and Payne, R. (2004). "Echolocation clicks of two free-ranging, oceanic delphinids with different food preferences: False killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*," J. Exp. Biol. 207, 1811–1823.
- Mann, J. (1999). "Behavioral sampling methods for cetaceans: A review and critique," Mar. Mammal Sci. 15(1), 102–122.
- Melcón, M. L., Denzinger, A., and Schnitzler, H.-U. (2007). "Aerial hawking and landing: Approach behaviour in Natterer's bats, *Myotis nattereri* (Kuhl 1818)," J. Exp. Biol. 210, 4457–4464.
- Melcón, M. L., Failla, M., and Iñíguez, M. A. (2012). "Echolocation behavior of franciscana dolphins (*Pontoporia blainvillei*) in the wild," J. Acoust. Soc. Am. 131(6), EL448–EL453.

- Melcón, M. L., Schnitzler, H.-U., and Denzinger, A. (2009). "Variability of the approach phase of landing echolocating greater mouse-eared bats," J. Comp. Physiol. A 195, 69–77.
- Mellinger, D. K. (2001). "Ishmael 1.0 User's Guide," NOAA Technical Memorandum OAR PMEL-120, available from NOAA/PMEL/OERD, 2115 SE OSU Drive, Newport, OR 97365-5258.
- Miller, P. J. O., Johnson, M. P., and Tyack, P. L. (2004). "Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture," Proc. R. Soc. London, B. 271, 2239–2247.
- Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A., and Lund, A. (2003). "The monopulsed nature of sperm whale clicks," J. Acoust. Soc. Am. 114(2), 1143–1154.
- Philips, J. D., Nachtigall, P. E., Au, W. W. L., Pawloski, J. L., and Roitblat, H. L. (2003). "Echolocation in the Risso's dolphin, *Grampus griseus*," J. Acoust. Soc. Am. 113(1), 605–616.
- Rice, D. W. (1998). "Marine mammals of the world: Systematics and distribution," Society for Marine Mammalogy, Special Publication Number 4 (D. Wartzok, ed.), Lawrence, KS.
- Robineau, D., Goodall, R. N. P., Pichler, F. B., and Baker, C. S. (2007). "Description of a new subspecies of Commerson's dolphin, *Cephalorhynchus commersonii* (Lacépède, 1804), inhabiting the coastal waters of the Kerguelen Islands," Mammalia 71, 172–180.
- Schnitzler, H.-U., and Kalko, E. K. V. (2001). "Echolocation by insecteating bats," Bioscience 51, 557–569.
- Soldevilla, M. S., Henderson, E. E., Campbell, G. S., Wiggins, S. M., Hildebrand, J. A., and Roch, M. A. (2008). "Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks," J. Acoust. Soc. Am. 124, 609–624.
- Sugar, C. A., Lenert, L. A., and Olshen, R. A. (1999). "An application of cluster analysis to health services research: Empirically defined health states for depression from the SF-12," Technical Report, Stanford University.
- Swartz, S. L., Cole, T., Mc Donald, M. A., Hildebrand, J. A., Oleson, E. M., Martinez, A., Clapham, P. J., Barlow, J., and Jones, M. L. (2003). "Acoustic and visual survey of humpback whale (*Megaptera novaean-gliae*) distribution in the eastern and southeastern Caribbean Sea," Caribbean J. Sci. 39(2), 195–208.
- Urick, R. J. (Editor.) (1983). Principles of Underwater Sound (McGraw-Hill, New York).
- Yan, M. (2005). "Methods of determining the number of clusters in a data set and a new clustering criterion," Ph.D. dissertation, Virginia Polytechnic Institute and State University.
- Zimmer, W. M. X., Johnson, M., Madsen, P. T., and Tyack, P. L. (2005).
 "Echolocation clicks of free-ranging Cuviers beaked whales (*Ziphius cavirostris*)," J. Acoust. Soc. Am. 117, 3919–3927.