RESEARCH ARTICLE

Discrimination of fast click-series produced by tagged Risso's dolphins (*Grampus griseus*) for echolocation or communication

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ABSTRACT

Early studies that categorized odontocete pulsed sounds had few means of discriminating signals used for biosonar-based foraging from those used for communication. This capability to identify the function of sounds is important for understanding and interpreting behavior; it is also essential for monitoring and mitigating potential disturbance from human activities. Archival tags were placed on free-ranging *Grampus griseus* to quantify and discriminate between pulsed sounds used for echolocation-based foraging and those used for communication. Two types of rapid click-series pulsed sounds, buzzes and burst pulses, were identified as produced by the tagged dolphins and classified using a Gaussian mixture model based on their duration, association with jerk (i.e. rapid change of acceleration) and temporal association with click trains. Buzzes followed regular echolocation clicks and coincided with a strong jerk signal from accelerometers on the tag. They consisted of series averaging 359±210 clicks (mean±s.d.) with an increasing repetition rate and relatively low amplitude. Burst pulses consisted of relatively short click series averaging 45±54 clicks with decreasing repetition rate and longer inter-click interval that were less likely to be associated with regular echolocation and the jerk signal. These results suggest that the longer, relatively lower amplitude, jerk-associated buzzes are used in this species to capture prey, mostly during the bottom phase of foraging dives, as seen in other odontocetes. In contrast, the shorter, isolated burst pulses that are generally emitted by the dolphins while at or near the surface are used outside of a direct, known foraging context.

KEY WORDS: Biosonar, Pulsed sound, Buzz, Burst pulse, Jerk, Foraging behavior

INTRODUCTION

Toothed whales (odontocetes) have evolved extraordinary capabilities to use sound as a main sensory cue (Au, 1993; Tyack, 1999). They use sound to communicate and echolocate, emitting directional pulses of high-frequency sound and listening for echoes to build an acoustic scene of prey and landmarks using an active echolocation sense (Madsen and Surlykke, 2013). Our understanding of the echolocation behavior of toothed whales is gradually increasing (Miller et al., 2004; Madsen et al., 2005; Wisniewska et al., 2016; Clausen et al., 2011), but is limited by the challenges of studying the acoustic behavior of free-ranging marine animals that often vocalize at depth and out of sight. Many toothed whales have sophisticated communication systems, but study of their vocal behavior is hampered by problems in identifying which animal makes a sound and which animals respond to these calls. These problems in linking individual acoustic signals with function in these taxa have largely prevented the contextualization and functional discrimination of pulsed sounds, which may be used for either echolocation or communication. This information, however, is essential to quantify foraging and social behavior and to assess potential impacts of disturbance from human activities.

Grampus griseus (G. Cuvier 1812) is a deep-diving social delphinid for which a diversity of vocalizations has been described, yet with little insight about functionality. The vocal repertoire of this species includes whistles, grunts, chirps, echolocation clicks (pulses), rapid series of clicks that have been described as barks, buzzes and isolated burst-pulses, and a combination of whistles and pulses, called whistle-burst pulses (Kruse et al., 1999; Corkeron and Van Parijs, 2001; Madsen et al., 2004; S. Neves, Acoustic behavior of Risso's dolphins, *Grampus griseus*, in the Canary Islands, Spain, PhD Thesis, University of St Andrews, St Andrews, 2012). Rapid increases in the click rate at the end of echolocation click sequences have been interpreted as attempts to capture prey, coined 'buzzes' in several echolocating species of bats (Griffin et al., 1960) and odontocetes (Miller et al., 1995; Miller et al., 2004; Johnson et al., 2006). A buzz represents the terminal phase of the biosonar-based foraging process, which basically consists of echo-guided search, approach and capture phases (Griffin, 1958). When closing in on targets during buzzes, echolocating toothed whales consistently reduce the inter-click interval (ICI) and output levels of clicks (Morozov et al., 1972; Au, 1993; Miller et al., 1995; Johnson et al., 2006; DeRuiter et al., 2009; Wisniewska et al., 2016). Moreover, buzzes are routinely associated with increased maneuvering and/or changes in the body acceleration rate ('jerk') (Johnson et al., 2004; Miller et al., 2004; Aguilar Soto et al., 2011), likely resulting from fast movements in pursuit of prey. Alternatively, short bursts of high-repetition-rate clicks have been proposed to function in communication (Aguilar Soto et al., 2011; S. Neves, Acoustic behavior of Risso's dolphins, *Grampus griseus*, in the Canary Islands, Spain, PhD Thesis, University of St Andrews, St Andrews, 2012), agonistic interactions (Miller et al., 1995; Blomqvist and Amundin, 2004; Lammers et al., 2006; Clausen et al., 2011) and long-range detection (Finneran, 2013) in this species as well as in

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List of abbreviations

AoA	angle of arrival
CEE	controlled exposure experiment
DTAG	digital tag
ICI	inter-click interval
IPSI	inter-pulsed sound interval
RMS	root mean square

other odontocetes. To date, *Grampus* buzzes have not been unambiguously defined (Corkeron and Van Parijs, 2001).

Digital tags (DTAGs) (Johnson and Tyack, 2003) that record audio and movement data provide a unique capability to collect acoustic and behavioral information simultaneously from a vocalizing individual, which improves our ability to infer when echolocation or communication takes place (Johnson et al., 2009; Wisniewska et al., 2016). A major challenge in tagging studies of whale vocal behavior is to identify which sounds are produced by the tagged individual and which are produced by nearby conspecifics. For larger odontocete species, usage of a combination of acoustic cues, such as a characteristic low-frequency component and a relatively stable amplitude and angle of arrival of the clicks at the two hydrophones on the tag, has proven reliable to identify click sequences produced by tagged individuals (Zimmer et al., 2005; Johnson et al., 2006). Here, we applied these techniques to data collected from *Grampus* to distinguish pulsed sounds produced by the tagged animal, so as to later contextualize their acoustic behavior. We hypothesize that: (1) *Grampus* 'buzzes' are preceded by regular echolocation click trains, with adjustment of the click output and movement pattern consistent with attempts to capture prey; and (2) 'burst-pulse' sounds that do not directly follow echolocation click trains and lack the acoustic and motor changes associated with prey capture are more likely than buzzes to cluster in social contexts. Using concurrent acoustic and motion-sensing tag data, we provide the first quantification of *Grampus* foraging buzzes and discriminate them from burst-pulse sounds in this species.

MATERIALS AND METHODS
Data collection and analysis
DTAGs were deployed on 15 wild adult *Grampus* in the Channel Islands National Marine Sanctuary off California, USA, in field efforts during the summers of 2011, 2013 and 2014. Ten out of the 15 dolphins included in this study were tagged as part of a behavioral response study and were exposed to playbacks of acoustic stimuli, but analyzing responses to these controlled exposure experiments (CEEs) is beyond the scope of this paper. Therefore, here we only use behavioral data recorded before the onset of CEEs. The first 15 min of each DTAG recording were also excluded from the analysis, to remove data potentially affected by the tagging procedure. The CEE data and data recorded immediately post-tagging were excluded to limit the data analyzed here to that which is considered to represent the natural undisturbed behavior of *Grampus*. Because all animals were tagged when they were in a traveling or social behavioral state, this likely represents a very conservative time period for animals to have returned to pre-tagging behavior, roughly equivalent to two to three dive cycles. Nine DTAGs were used in this study. Two of them were deployed on four occasions on different dolphins. Individuals were identified with the aid of photos of their dorsal fin and scar pattern, and none of the individuals were tagged more than once.

Tags were attached to the back of the dolphins using a 6-m-long hand-held pole from a 7-m-long rigid-hulled inflatable boat. The tags were programmed to detach at local sunset and were located using radio tracking equipment. Acoustic data were sampled in stereo with 16 bit resolution at 240 kHz except for the first tag (gg11_216a), where a 120 kHz sampling rate was used. Pressure sensor data and data from tri-axial accelerometers and magnetometers were sampled at 200 Hz per channel. Pressure data were decimated to 20 Hz and accelerometer data to 50 Hz for analysis. DTAG sensor data were calibrated for temperature and orientation offset and converted into depth, pitch, roll and heading of the tagged animal following methods described in Johnson and Tyack (2003). The acoustic sensitivity of the DTAG hydrophones was estimated at -178 dB re. 1 V µPa^{-1} by calibration of one DTAG used in this study, which was deployed on four individuals. The differences in sensitivity from tag to tag are expected to be on the same order of the variation due to tag placement, body shading or group spread. Acoustic and sensor data analysis was carried out in MATLAB R2016a (MathWorks, Natick, MA, USA) using the DTAG toolbox (soundtags.st-andrews.ac.uk) and custom-made scripts.

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Echolocation clicks
For some odontocete species, clicks produced by the tagged individual and recorded on the tag can be distinguished using their unique low-frequency component (<15 kHz), which is absent for clicks produced by other (nearby) individuals (Johnson et al., 2006; Zimmer et al., 2005). Moreover, clicks produced by the tagged individual are recorded on the tag with a consistent angle of arrival (AoA), while clicks from other individuals echolocating nearby show larger fluctuations of this parameter as the other animal moves with respect to the tagged dolphin (Johnson et al., 2006). Clicks produced by the tagged dolphins were extracted using a supervised energy detector (findclicks function, DTAG toolbox), following the techniques of Zimmer et al. (2005) and Johnson et al. (2006). *Grampus* echolocation clicks are short transients of 30 µs duration with a peak frequency of 45 kHz and a -3 dB bandwidth of 30 kHz (Madsen et al., 2004). The energy detector was set up with a 5–15 kHz band-pass filter and a -40 dB level re. max received level detection threshold on the extracted envelope of the one-channel filtered signal in order to capture the low-frequency component of focal clicks. A plot of click AoA versus time (Fig. 1) was examined to validate whether the clicks were produced by the tagged individual, based on whether they were recorded with a consistent AoA across the entire record, within ±20 deg evaluated in 10 s windows, on the tag hydrophones. This classification criterion is based on laboratory-based observations by Philips et al. (2002), who reported that *Grampus* move their head considerably during target approaches. Variation in the tagged dolphin click AoA within a few seconds, if present, would arise mostly from the tagged animal turning its head. Given that *Grampus* have secondarily fused cervical vertebrae (Howell, 1930; Flower, 1982; Narita and Kuratani, 2005), we acknowledge that any movement of the sound-producing structures relative to tag placement would have to involve either a movement of the entire head relative to the fused cervical vertebrae, or a movement of the thoracic spine, flexing such that the echolocation sound source is moving relative to the tag.

The proportion of clicks reported by the detector algorithm but not produced by the tagged dolphin (false positive detection rate) was estimated by inspection of the AoA on a subset of data from three randomly selected tag records. We did not estimate the
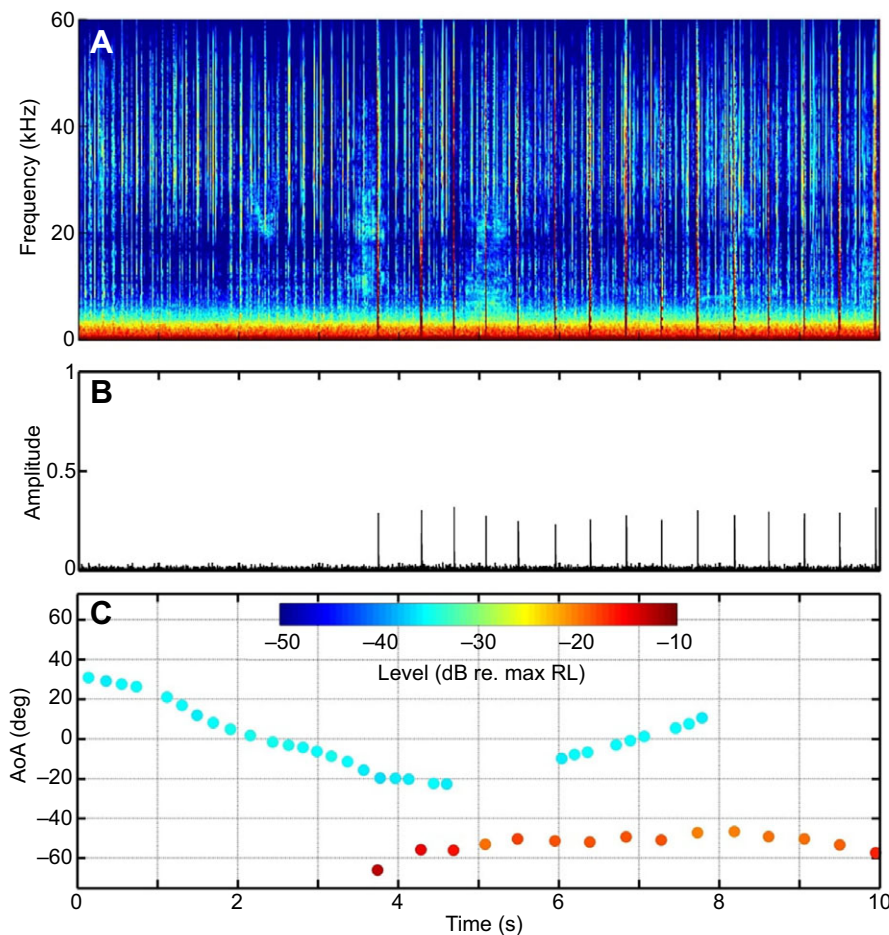
Fig. 1. Identification of echolocation clicks produced by tagged *Grampus griseus* and recorded on the tag. (A) Spectrogram [Hamming fast Fourier transform (FFT) length 1024, 512 overlap] of a 10 s audio sequence, (B) signal envelope (Hilbert transform), and (C) angle of arrival (AoA) of the clicks to the stereo tag hydrophones, colored by received level (RL). Click level is calculated as the peak value of the Hilbert transform for each click, in dB re. max RL. Lower dotted line in C is judged as clicks produced by the tagged dolphin based on their stable AoA (within ±20 deg, see Materials and methods for details), which remains relatively consistent across the tag record. Note the wider variation on the AoA of clicks not produced by the tagged individual (upper dotted line in C).

proportion of false negatives by the detector. A total of 14,815 detections were visually checked in sequences of 20 s duration starting at time 0 and at every 500 s thereafter (resulting in 23, 11 and 37 windows of 20 s for gg11_216a, gg13_190a and gg13_267a, respectively) (Fig. 1). Clicks were classified as 'tagged-dolphin' or 'untagged-dolphin' using the same AoA criterion as for tagged-dolphin click validation (variations up to ±20 deg in the AoA were accepted for tagged-dolphin clicks). Two types of false positive detections were expected: untagged-dolphin *Grampus* clicks and transients that were not *Grampus* clicks. We did not separate these two categories. The proportion of 'tagged-dolphin' and 'untagged-dolphin' clicks was determined from the ratio between the number of clicks reported by the observer per category and the total number of detections, for a given time window. Results indicate that the majority (94%) of detections corresponded to tagged-dolphin clicks with a 5% false positive rate (Table 1). This false detection rate is expected to remain relatively constant for buzzes and purported social sounds, as the energy content below 15 kHz should be consistent, independent of variations in the directionality, frequency band or off-axis angle of the recorded vocalizations.

Pulsed sounds

To maintain a nomenclature for vocalizations consistent with the cetacean literature, we used the term 'pulsed sound' for a rapid sequence of pulses (clicks). Pulsed sounds were distinguished from regular echolocation in tagged-dolphin click sequences by fitting a Gaussian mixture model (with two distributions) using the log-transformed ICIs following the method of Tolkamp and Kyriazakis

(1999) and the package mixtools (Benaglia et al., 2009) in R statistical software (R Foundation for Statistical Computing, Vienna, Austria) (Fig. 2). The fitted normal distributions had a mean±s.d. log(ICI) of −5.78±0.41 for pulsed sound clicks and a mean±s.d. log(ICI) of −1.94±0.71 for regular echolocation clicks. The mean ICI was 0.003 s for pulsed sound clicks and 0.143 s for the regular echolocation clicks. According to this model, the 99.5th percentile of pulsed sound clicks had an ICI of 0.0090 s whereas the 0.5th percentile of regular echolocation clicks had an ICI of 0.023 s. The point halfway between those two values (0.016 s) was taken as

Table 1. Clicks of tagged *Grampus griseus* identified by an energy detector and checked visually by the authors to estimate the proportion of detections corresponding to tagged-dolphin clicks

Tag record	Clicks selected by the detector and checked by the authors	Tagged-dolphin clicks (%) – correct classification by the detector	Untagged-dolphin clicks (%) – false positives identified by the detector
gg11_216a	4675	98	2
gg13_190a	2133	91	9
gg13_267a	8007	94	6

Clicks selected by the detector and checked by the authors: number of click detections checked. Tagged-dolphin clicks – correct classification by the detector: proportion of detections correctly classified by the detector as clicks produced by the tagged dolphin. Untagged-dolphin clicks – false positives identified by the detector: proportion of detections corresponding to clicks produced by other (nearby) dolphins or transients that are not *Grampus* clicks.
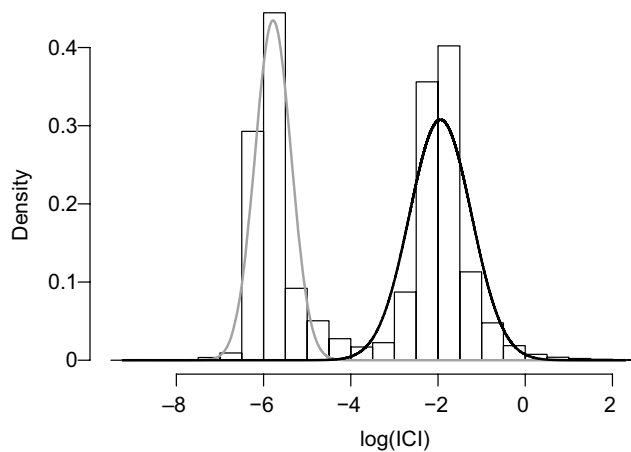
Fig. 2. Histogram of log-transformed inter-click intervals (ICIs) with fitted normal distributions overlaid, for clicks produced by 15 tagged *Grampus* (N=258,560 clicks). Clicks pertaining to regular echolocation (black fitted line) and pulsed sounds (gray fitted line) are separated into two groups using a threshold of 0.016 s, based on the point halfway between the 99.5th percentile of pulsed sound clicks and the 0.5th percentile of regular echolocation clicks.

a threshold to classify clicks as regular echolocation or pulsed sound. To discard potential individual differences in ICI patterns, data for each dolphin were checked visually. Vocalizations consisting of a simultaneous whistle and pulsed sound (Corkeron and Van Parijs, 2001) were identified on the recordings but not analyzed for this paper.

Classification

Using a multivariate Gaussian mixture model, pulsed sounds were classified into two classes, buzzes and burst pulses, on the basis of their associated jerk ratio (detailed below), the time since the last regular click, and the duration of the sound. Models were fitted using the package mixtools (Benaglia et al., 2009) in R statistical software. The derivative of acceleration, termed jerk, was computed as the absolute value of the difference of the triaxial acceleration signal divided by the sampling interval (sensu Simon et al., 2012). The RMS jerk, calculated as the square root of the mean of the squares of the jerk values, was estimated over the duration of the pulsed sounds and also over control intervals with the same duration starting prior to the onset of the sound. The ratio of the RMS jerk during the pulsed sound to RMS jerk during a preceding control interval was computed for each sound. To avoid having controls overlapping with sounds, sounds with a preceding inter-pulse sound interval (IPSI) less than two times the sound duration were compared against the control from the nearest preceding sound with an IPSI over this threshold. All controls started within 10 s prior to the onset of the sound. The time since last click was estimated as the time elapsed since the end of the last echolocation click recorded prior to the onset of the pulsed sound (in minutes). The duration of each pulsed sound was estimated as the time difference between the last and first clicks (in seconds). To assess whether this categorization separated sounds into two functional groups, we explored the acoustic properties and context of production associated with each pulsed sound type.

Acoustic properties

Click envelopes were produced by computing the Hilbert transform of the 5 kHz high-pass filtered one-channel audio signal. Average peak values of the clicks in buzzes and preceding clicks were

normalized by maximum click amplitude recorded in the 10 regular clicks prior to each sound and subtracted to obtain a relative measure of differences in click amplitude. The receiver placement may introduce some distortion in spectral content and amplitude of clicks recorded from the tagged dolphin. This is because clicks are recorded off-axis from a tag placed behind the sound-producing structures (Madsen et al., 2004), so the tag is capturing low-frequency energy likely associated with click production (Zimmer et al., 2005) and the animal's body may act as a sound-absorbing or -reflecting surface (Johnson et al., 2006). Moreover, several odontocetes adjust directionality of outgoing clicks (Moore et al., 2008; Wisniewska et al., 2012; Jensen et al., 2015). This would influence properties of recorded clicks and result in regular differences in the transfer function from outgoing to recorded clicks between different sound types, if the directionality adjustment is the same for different sound types. We expect these factors to have little impact on the discrimination of such sounds on the tag, although we acknowledge that the sounds recorded on the tag are not necessarily accurate representations of outgoing sounds. The pattern of adjustment of ICIs of pulsed sound clicks over time was explored using a Spearman rank correlation coefficient, pooling all pulsed sounds, and the sign of the slope of the first-order regression of the ICI, normalized by mean ICI for each pulsed sound. The above acoustic parameters were explored for a subset of 35 sounds of each of the two sound types (representing approximately 5% of buzzes and 20% of burst pulses) that were selected using a random permutation procedure. Only pulsed sounds for which the full click sequence could be identified were used in this analysis. Completeness of click sequences was confirmed by checking whether the click detector reported a click for every visually distinguishable peak in the envelope plot.

Dive context of sound production

To determine whether buzzes were concentrated in the bottom phase of the dives where foraging is expected, descent, bottom and ascent phases were identified in dives following a method modified from Hooker and Baird (2001). The descent phase of each dive was defined as the period from when the dolphin left the surface to the first time the depth exceeded 70% of maximum dive depth. This criterion was decided based on visual inspection of a random subset of 25% of dives and adjusting the percentage of maximum depth to cover the variation in depth (Bost et al., 2007) during the deepest part of most dives. The ascent phase started at the last time the depth exceeded the 70% of maximum dive depth and ended when the dolphin reached the surface. The bottom phase was defined as the period from the first to the last time the depth exceeded 70% of the maximum dive depth. Co-occurrence of pulsed sounds from tagged and non-tagged dolphins was assessed by visual inspection of 10 s window audio recordings centered at the onset of the sound produced by the tagged dolphin, from a random subsample of 20 sounds.

RESULTS

Overall, 49.4 h of audio and sensor pre-CEE data were analyzed from 127 complete dives exceeding 20 m depth. The mean (range) maximum depth was 128 m (20–566 m) and dive duration was 4.6 min (0.5–8.1 min). Overall, 258,560 clicks were identified as produced by the tagged dolphins. Tagged dolphins were clicking on average (mean±s.d.) for 70±20% of the time during each dive (Fig. 3). The first and last click in each dive was recorded at a mean (range) depth of 13 m (3–43 m) on descent and 24 m (4–164 m) on ascent, respectively.
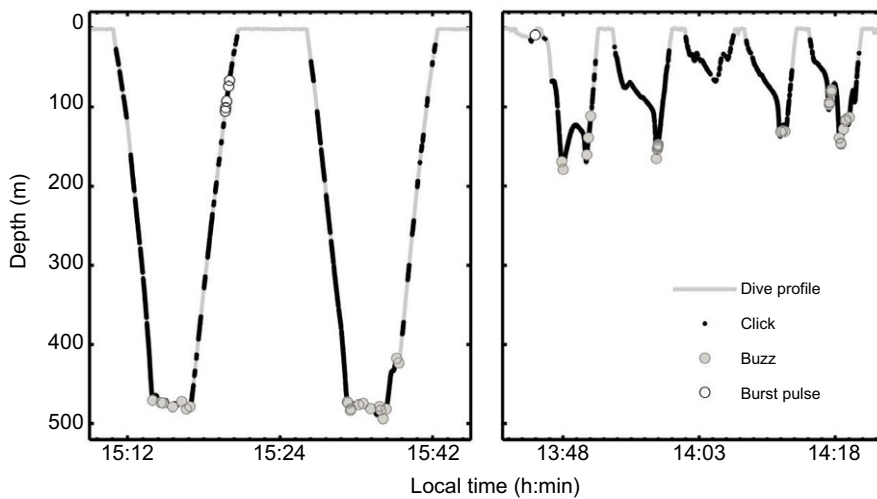
Fig. 3. Example of dive profiles and associated sounds, including click trains, buzz and burst pulses, recorded from *Grampus* tagged off California.

Pulsed sounds

A total of 890 pulsed sounds were identified in tagged-dolphin click sequences. From those, 82% were classified as buzzes (N=734) and 18% were classified as burst pulses (N=156). According to the fitted model, buzzes corresponded to sequences of high-repetition-rate clicks starting within 0.0036 min (0.22 s) of the last regular echolocation click, with an average duration of 1.1 s (Fig. 4). The mean ratio of the RMS rate of change of body acceleration (jerk)
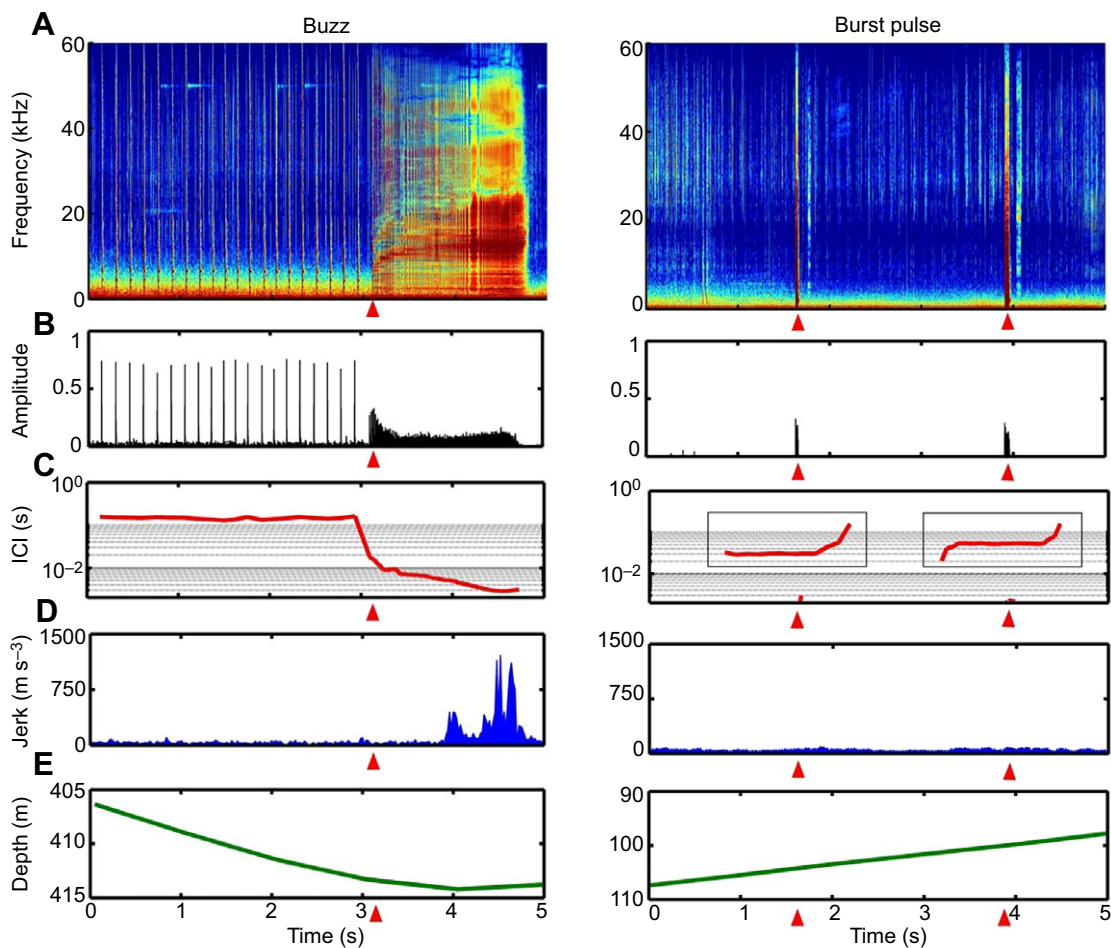

Fig. 4. Examples of a click train followed by a buzz (left) and two burst pulses (right) produced by a tagged *G. griseus*. The sounds were emitted by the same dolphin, diving at 414 and 100 m depth, respectively. (A) Spectrogram (Hamming FFT length 1024, 512 overlap), (B) signal envelope (Hilbert transform), (C) inter-click interval (ICI), (D) rate of change in acceleration (jerk) and (E) depth of the dolphin when emitting the sound. Note the downward adjustment of ICI during buzz clicks in comparison to the upward ICI pattern of burst pulses (inner boxes in C with different time scale). The jerk peaks occurring near the end of the buzz are absent during burst pulses (D).

measured during buzzes and control intervals of the same duration prior to the onset of the sound was 3.1. Burst pulses consisted of sequences of high-repetition-rate clicks starting on average 13 min after the end of regular echolocation with an average duration of 0.83 s. The mean jerk ratio associated with burst pulses was 1.3 (Fig. 4). Tables S1 and S2 give the fitted model variance–covariance matrices for burst pulses and buzzes, respectively.

Acoustic properties
Buzzes consisted of click series with a median±s.d. of 359±210 clicks with an ICI of 3.6±0.6 ms (Fig. 4). The amplitude of buzz clicks was on average 10–20 dB lower than the average amplitude of clicks in the preceding click train. The median slope of the first-order regression of the normalized ICIs for each buzz was −11±16 µs per click (Spearman correlation between time and ICI, $r=-0.63$, $P<0.001$, $N=35$ buzzes). Burst pulses comprised on average 45±54 clicks with an ICI of 5.3±4.9 ms (Fig. 4). The median slope of the first-order regression of the ICI values for each burst pulse was +4±0.03 µs per click (Spearman correlation between ICI and time $r=0.42$, $P<0.001$, $N=35$ burst pulses).

Dive context of production
The majority (95%) of buzzes were produced in dives at a mean depth of 120±16 m (Fig. 5), when the tagged dolphins were near the bottom of their dive. Overall, 75% of buzzes occurred during the bottom phase, 17% during the ascent, and 7% during the descent of dives (Table 2). Burst pulses were mostly emitted by the tagged dolphins while at the surface (Fig. 5). A small proportion of burst pulses were recorded in dives, most during the ascent, at a mean depth of 63±2 m (Fig. 5, Table 2). All tagged-dolphin burst pulses were recorded when burst pulses from other dolphins were evident on spectrograms within 5 s either from the start or end of a tagged-dolphin burst pulse. None of the tagged-dolphin buzzes occurred within 5 s of a burst pulse from an untagged dolphin. Only 15% of tagged-dolphin buzzes were observed to co-occur within 5 s of a buzz produced by an untagged dolphin.

DISCUSSION
This study provides the first quantification and functional discrimination of *Grampus* pulsed sounds, buzzes and burst-pulses. This study relies on animal-borne tags that synchronously record vocalizations and animal movement, providing data that have

increased our ability to infer the behavioral context and function of free-ranging cetacean vocalizations.

Identification of tagged-dolphin clicks
Because of the social nature of *Grampus*, sequences of clicks produced by tagged dolphins often overlap with those of nearby vocalizing conspecifics, and may be difficult to identify. Clicks produced by tagged dolphins and recorded on their own tag have a low-frequency component, allowing identification using an energy detector in a low-pass band. The 5% of false detections reported in the present study may be the result of some actual energy below 15 kHz in *Grampus* clicks that are not an artifact of tag location (Madsen et al., 2004), leading to some dolphin clicks not originating from the tagged dolphin being misclassified. The use of extra click attributes, particularly the click AoA to the hydrophones on the tag, in combination with energy content in a frequency range, seemed a reliable method to distinguish tagged-dolphin clicks from clicks of other nearby conspecifics (Johnson et al., 2006). The stability of the false positive rate across tagged dolphins suggests that the false positive rate is independent of social and behavioral context or tag placement, because tagged dolphins were associated with social groups of different sizes, dove to very different depths, and the tags were located on different parts of their body.

Echolocation
Tagged *Grampus* echolocated during most of the duration of each dive with a variable ICI, 0.15 s on average, but with several long pauses of up to 30 s. The mean ICI of *Grampus* clicks is consistent with long-range echolocation-based search behavior described in other odontocetes (Au, 1993; Madsen et al., 2002, 2005, 2013; Johnson et al., 2004; DeRuiter et al., 2009). Assuming that dolphins do not emit the next click until the echo from the target has been received and its information has been processed (Au, 1993), the mean ICI of *Grampus* click trains in the present study (0.15 s) suggests a maximum detection range of ICI/2×1500 m s^{-1}=112 m. The aforementioned assumption that dolphins do not click until they have processed information from the previous echo may be questioned, given evidence of multi-echo processing in bottlenose dolphins (Ivanov, 2004; Finneran et al., 2014). However, this detection range is similar to the approximately 100 m range estimated based on *Grampus* click source properties (Madsen et al., 2004). The relatively stable ICIs of the search clicks' preceding buzzes (Fig. 4B) suggest that *Grampus* do not employ a range-dependent reduction in ICI during their approach to the target
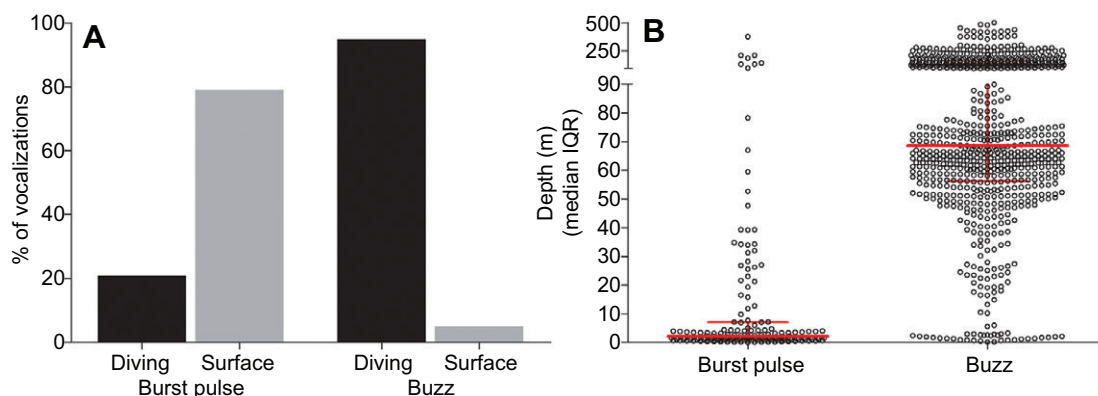

Fig. 5. Comparative of the context of production of pulsed sounds. Dive context (A) and depth of production (B) for buzz (*N*=734) and burst pulse (*N*=156) sounds recorded from 15 tagged *Grampus*. Histograms for burst pulses (left) and buzzes (right) emitted during diving (black) and surface periods (gray) represent pooled data from all tagged dolphins. IQR, interquartile range.

Table 2. Context of production of buzz and burst-pulse sounds recorded from tagged *Grampus* (*N*=15)

Dolphin	Record length (h)	Buzz					Burst pulse				
		N	S	D	Depth (m)	D/B/A	*N*	S	D	Depth (m)	D/B/A
gg11_216a	1.2	0	0	0	–	–	0	0	0	–	–
gg11_265a	2.5	91	0	91	87 (14)	4/79/16	14	1	13	32 (1)	2/36/43
gg11_269a	3.3	0	0	0	–	–	7	7	0	–	–
gg11_272a	5.1	0	0	0	–	–	2	2	0	–	–
gg13_190a	2.3	3	1	2	64 (2)	0/83/16	5	0	5	33 (1)	0/0/1
gg13_204b	1.8	2	0	2	122 (0)	0/100/0	1	1	0	34 (21)	5/15/80
gg13_230a	1.6	23	0	23	378 (35)	0/100/0	2	2	0	–	–
gg13_255a	2.4	0	0	0	–	–	0	0	0	–	–
gg13_261a	5.5	48	3	45	119 (14)	4/40/55	3	0	3	117 (1)	0/1/0
gg13_262a	5.0	261	0	261	58 (9)	6/87/6	0	0	0	–	–
gg13_262b	4.0	51	6	45	66 (6)	0/1/0	11	11	0	–	–
gg13_266b	1.7	34	0	34	112 (18)	17/61/20	88	82	6	21 (6)	36/23/40
gg13_267a	9.1	133	16	117	154 (48)	5/69/26	18	13	5	118 (0)	20/40/40
gg14_223a	1.9	71	6	65	81 (19)	13/57/29	4	1	3	32 (0)	0/0/1
gg14_253a	1.3	17	8	9	76 (15)	27/52/21	1	1	0	–	–
Total	49.4	734	40	694	120 (16)	7/75/17	156	121	35	63 (2)	11/32/56

Values are means for all sounds with the standard deviation in parentheses. Record length: duration (h) of the tag record or of the subsampled pre-exposure period starting 15 min after tag began recording, used for the analysis (see Materials and methods). *N*: total number of sounds recorded within the above time period. S: number of sounds recorded while the dolphin was in surface periods. D: number of sounds recorded in dives. Depth: depth (m) of the sounds recorded within dive periods. D/B/A: proportion of sounds performed in the descent, bottom and ascent dive phases, respectively.

prior to the buzz. Although this finding may reflect only the capture of certain prey types, this echolocation tactic is similar to that of some deep-diving odontocetes such as beaked whales (Madsen et al., 2005, 2013), but departs from that of sperm whales (Miller et al., 2004) and porpoises (DeRuiter et al., 2009), and other more closely related delphinids such as bottlenose dolphins (Au and Benoit-Bird, 2003) and pilot whales in deep foraging mode (Aguilar Soto et al., 2008).

A stable ICI during the search and approach phases has been interpreted by Madsen et al. (2005) as an echolocation strategy to organize the acoustic input of echoes from multiple simultaneous targets, while maintaining a long range for acoustic detections. *Grampus griseus* and Blainville's beaked whales (*Mesoplodon densirostris*) have been reported to forage on deep-water bottom-dwelling organisms, amongst other prey (Kruse et al., 1999; Blanco et al., 2006; Santos et al., 2007; Arranz et al., 2011). It is possible that both species may be feeding in comparable habitats, where stable ICIs would facilitate gathering concomitant biotic and abiotic cues to locate prey and to orient near the seabed. Further investigation will be needed to clarify the biological and ecological reasons behind this biosonar tactic, which appears to be shared across these deep-diving odontocetes, and to determine whether it has evolved in response to particular prey and/or habitat types where it is crucial to track multiple targets simultaneously.

Buzzes

Grampus griseus buzzes consisted of relatively long series of high-repetition-rate clicks produced shortly after regular echolocation clicks (<0.5 s) and coincided with strong changes in the acceleration rate, consistent with the dolphins maneuvering in pursuit of prey (Fig. 4). Attempts to capture prey have been associated with jerk signals in other aquatic predators (Johnson et al., 2004; Aguilar Soto et al., 2011; Ydesen et al., 2014) and are powerful indicators of the foraging functionality of associated pulsed sounds.

The acoustic adjustments during *Grampus* buzzes involve a reduced output level and pulse rate during the terminal phase of the foraging process. These characteristics parallel those described in bats (Griffin et al., 1960) and other odontocetes, such as bottlenose dolphins (Au and Benoit-Bird, 2003), porpoises (Linnenschmidt

et al., 2013), sperm whales (Miller et al., 2004) and beaked whales (Madsen et al., 2013). *Grampus griseus* buzzes have a stereotyped pattern of decreasing ICI as a function of time (−11 µs per click). This pattern of decreasing ICI during buzzes is consistent with the animal reducing the ICI as it closes in on one target, and matches the target range-dependent adjustments of buzz click rate described for porpoises (DeRuiter et al., 2009; Wisniewska et al., 2012) and beaked whales (Johnson et al., 2008). Assuming that the targeted prey is stationary, the estimated closing rate of *Grampus* during buzzes would be equal to 0.82 cm per click (average reduction of ICI per click/two-way travel time=0.000011 s×750 m s^{-1}), equivalent to 2.2 m s^{-1} (using 3.6 ms as the mean ICI of buzz clicks; Table 2). On average, buzzes consisted of 360 clicks. Therefore, presuming that the end of the buzz coincides with prey capture, *Grampus* start buzzing when they are approximately one body length (~3 m) from the target prey. This distance of one body length is consistent with the onset of the terminal phase of prey capture in all odontocetes studied (Miller et al., 1995; Akamatsu et al., 2005; Madsen et al., 2005; Aguilar Soto et al., 2008; Verfuss et al., 2009). The mean ICI of *Grampus* buzzes (3–4 ms) is shorter than that of larger odontocetes, such as Blainville's beaked whales (3–5 ms) and sperm whales (11 ms), consistent with an ICI scaled to the size of the animals, as suggested by Madsen and Surlykke (2013). Buzz clicks are produced at an average level of 15 dB lower than preceding click trains. This reduction is likely range dependent and related to a high signal-to-noise ratio of returned echoes when closing in on targets (Au and Benoit-Bird, 2003). Additionally, some studies suggest that the sound-producing organ may not be capable of producing high source levels at higher click rates (Madsen et al., 2005; Beedholm and Miller, 2007; Fenton et al., 2014), although there are also data that suggest the contrary (Branstetter et al., 2012).

The majority of buzzes were recorded while the tagged dolphins were near the bottom of the dive, where feeding is assumed to concentrate for animals that dive to forage (Houston and Carbone, 1992). Foraging buzzes have been associated with the deepest part of foraging dives in other odontocetes (Miller et al., 2004; Rasmussen et al., 2013). The shallowest maximum dive depth of dives (37 m) and the range of buzz depths (28 to 493 m) points at a

potentially large variation in prey type or prey location in the water column, and relatively shallow foraging depth for *Grampus* with respect to other deep-diving odontocetes foraging at comparable latitudes (Tyack et al., 2006; Watwood et al., 2006; Aguilar Soto et al., 2008; Arranz et al., 2011). As 5% of buzzes were recorded at or near the surface (<20 m depth; Fig. 5) and *Grampus* have been observed feeding near the surface in shallow areas (J.C., unpublished data), these buzzes likely represent foraging events. However, delphinids may also use echolocation and buzz sounds to investigate conspecifics (Herzing, 1996; Rasmussen et al., 2013), and buzzes occurring outside dive bouts, in a group context, may well be involved in social interactions. Upcoming analysis of the prevalence of surface buzzes in relation to the behavioral context (i.e. socializing, feeding) will help to clarify their functionality.

Burst pulses

Grampus griseus produced burst-pulse sounds with acoustic and kinematic features that differ from those of buzzes. Burst pulses consisted of high-repetition-rate series of clicks that were generally emitted after a long gap in clicking and lacked the typical jerk signature associated with buzzes. Most buzzes ended with a clear jerk signal on the accelerometers of the tag, which is interpreted as maneuvering to capture prey. The lack of such a jerk signal during burst pulses suggests that the burst pulse is not associated with the same kind of prey capture attempt. Echolocating animals closing in on prey tend to show a decrease in ICI, corresponding to the decreasing round-trip travel time to the target (Johnson et al., 2008; DeRuiter et al., 2009; Wisniewska et al., 2012). The increase in ICI for burst pulses therefore renders it unlikely that they were involved in echo-guided foraging.

Neves (S. Neves, Acoustic behavior of Risso's dolphins, *Grampus griseus*, in the Canary Islands, Spain, PhD Thesis, University of St Andrews, St Andrews, 2012) described burst-pulsed sounds from *Grampus* in recordings off Gran Canaria as short and isolated click sequences with ICIs of less than 4 ms that resemble the acoustic parameters of those reported here. These burst pulses were mostly found when dispersed dolphins reunited and their production rate increased proportionally with group size, which was interpreted as these sounds having a communicative function.

Communicative click sequences at varying pulse repetition rates have been described for several odontocete species (Weilgart and Whitehead, 1993; Blomqvist and Amundin, 2004; Lammers et al., 2006; Aguilar Soto et al., 2011; Clausen et al., 2011; Marrero et al., 2016). Captive bottlenose dolphins emit directional pulsed sounds in intraspecific agonistic interactions (Blomqvist and Amundin, 2004; Blomqvist, 2004). Sperm whales exchange patterned sequences of 'coda' clicks and produce 'squeal' and 'chirp' burst-pulse vocalizations that serve for communication (Watkins and Schevill, 1977; Weilgart and Whitehead, 1993; Madsen et al., 2002; Weir et al., 2007). Blainville's beaked whales produce isolated bursts of frequency-modulated clicks (ICI ~5 ms), called 'rasps' (Aguilar Soto et al., 2011). These rasps are produced just before or after the echo-guided prey search phase in the dives, and are thought to coordinate group dispersion and reunion. In the present study, burst pulses from tagged dolphins co-occurred with a burst pulse from another dolphin within 5 s, while only a small proportion of buzzes from tagged and other dolphins coincided in this time window. It is possible that the low source level (and perhaps high directionality) of buzzes from non-tagged dolphins may prevent them from being recorded on the tag. However, the prevalence of burst pulses from non-tagged dolphins recorded on the tags suggests

that these signals may be heard by conspecifics over a longer range compared with buzzes, and are therefore better suited to synchronize group activities. Although we cannot rule out that burst pulses may also be used for echolocation in a non-foraging context (i.e. long-range detection, navigation), the apparent difference from pulsed sounds used for prey capture (buzzes) and the indication of a social context of production suggest that burst pulses may have evolved to serve a communication function. *Grampus griseus* are social odontocetes, living in stable groups, like beaked, pilot and sperm whales, in which click communication may have developed as an effective way of transferring intra- or inter-specific information. Future analysis exploring how the production of burst-pulse signals vary according to social contexts, i.e. group spread, distance from others and transitions in behavior, i.e. traveling or resting to feeding or vice versa, will be valuable to address these questions.

Conclusions

Grampus griseus produce at least two types of pulsed sounds, buzzes and burst pulses. They produce buzzes during prey capture attempts with associated rapid changes in body acceleration (jerk) while foraging at depth. The absence of a downward adjustment of the ICI and jerk signature associated with burst pulses, together with the temporal pattern of occurrence and social context of production, suggest an alternative, non-foraging function for these sounds. The echolocation strategy of *Grampus* consists of a long-range biosonar search phase that rapidly switches to a terminal buzz when closing in on prey, similar to other deep-diving odontocetes, but different from the gradual reduction in ICI seen in most closely related species. Our data include some relatively shallow foraging depths for *Grampus* during daytime, an unusual foraging strategy for a deep diver. Future research on the diving and echolocation behavior of these teutophagous delphinids is important to improve our understanding of how small deep-diving odontocetes employ their biosonar to detect and capture prey in the wild, to investigate the space use and foraging ecology of this species, and to enable comparative studies across taxa. Further work is also needed to define the communicative function of burst-pulsed sounds, and to compare these with pulsed and other sounds used for communication in other species. In addition, the results presented here are relevant for applied studies because they provide detailed means of investigating potential behavioral responses of individuals to stimuli such as anthropogenic noise, as has been carried out and is ongoing within the Southern California Behavioral Response Study (Southall et al., 2012).

Author contributions
P.A. developed the concepts, analyzed the data and wrote the manuscript. S.L.D., F.V. and A.K.S. performed the experiments, analyzed the data and edited the manuscript. S.N. and F.V. analyzed the data and edited the manuscript. A.S.F., J.A.G., F.V., J.C., B.L.S. performed the experiments and edited the manuscript. P.L.T. developed the concepts, supervised the project and edited the manuscript.

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Data availability
Data are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.m0763.

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