

Echolocation signals of a beaked whale at Palmyra Atoll

Simone Baumann-Pickering,^{a)} Sean M. Wiggins, and Ethan H. Roth

Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0205

Marie A. Roch

Department of Computer Science, San Diego State University, 5500 Campanile Drive, San Diego, California, 92182-7720

Hans-Ulrich Schnitzler

Eberhard-Karls-Universität Tübingen, Zoologisches Institut, Abteilung Tierphysiologie, Auf der Morgenstelle 28, 72076 Tübingen, Germany

John A. Hildebrand

Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0205

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Acoustic recordings from Palmyra Atoll, northern Line Islands, central Pacific, showed upsweep frequency modulated pulses reminiscent of those produced by beaked whales. These signals had higher frequencies, broader bandwidths, longer pulse durations and shorter inter-pulse intervals than previously described pulses of Blainville's, Cuvier's and Gervais' beaked whales [Zimmer *et al.* (2005). *J. Acoust. Soc. Am.* **117**, 3919–3927; Johnson *et al.* (2006). *J. Exp. Biol.* **209**, 5038–5050; Gillespie *et al.* (2009). *J. Acoust. Soc. Am.* **125**, 3428–3433]. They were distinctly different temporally and spectrally from the unknown beaked whale at Cross Seamount, HI [McDonald *et al.* (2009). *J. Acoust. Soc. Am.* **125**, 624–627]. Genetics on beaked whale specimens found at Palmyra Atoll suggest the presence of a poorly known beaked whale species. *Mesoplodon sp.* might be the source of the FM pulses described in this paper. The Palmyra Atoll FM pulse peak frequency was at 44 kHz with a –10 dB bandwidth of 26 kHz. Mean pulse duration was 355 μ s and inter-pulse interval was 225 ms, with a bimodal distribution. Buzz sequences were detected with inter-pulse intervals below 20 ms and unmodulated spectra, with about 20 dB lower amplitude than prior FM pulses. These clicks had a 39 kHz bandwidth (–10 dB), peak frequency at 37 kHz, click duration 155 μ s, and inter-click interval between 4 and 10 ms.

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I. INTRODUCTION

Beaked whales are among the least known large mammals on the planet, as they are infrequently encountered in the field and difficult to identify (e.g., Pitman, 2008). They are pelagic, deep foraging divers with rather short surface intervals between dives (e.g., Tyack *et al.*, 2006). Many of the more than 20 species of beaked whales are known only from strandings and the study of skeletal material (Jefferson *et al.*, 2008). The *Mesoplodon* beaked whales are rarely seen alive although they are the most species rich cetacean genus (Pitman, 2008). The number of mesoplodont species is still increasing with two new species described as recently as 1991 and 2002 (Reyes *et al.*, 1991; Dalebout *et al.*, 2002).

Until a few years ago, the acoustic behavior of beaked whales was barely known, with descriptions being incomplete due to restrictions in recording bandwidths (e.g., Caldwell and Caldwell, 1971; Lynn and Reiss, 1992; Dawson *et al.*, 1998). There has been an increased investigation effort

after several mass strandings of beaked whales, which have been linked to anthropogenic noise during military sonar exercises (Simmonds and Lopez-Jurado, 1991; Frantzi, 1998; Jepson *et al.*, 2003). New acoustic technologies with a wide frequency range have made it possible to record the ultrasonic echolocation signals of beaked whales (e.g., Johnson and Tyack, 2003; Wiggins and Hildebrand, 2007). Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales are the more commonly encountered and best acoustically studied among this group of cetaceans (Johnson *et al.*, 2004; Madsen *et al.*, 2005; Zimmer *et al.*, 2005; Johnson *et al.*, 2006, 2008). Recent recordings of signals from Gervais' beaked whales reveal their acoustic signature (Gillespie *et al.*, 2009). All three species produce upsweep frequency modulated (FM) pulses, which are species and activity specific. Johnston *et al.* (2008) and McDonald *et al.* (2009) report an FM ultrasonic sound of unknown origin with beaked whale characteristics, discovered on a long-term broadband acoustic recording from Cross Seamount, HI. Other beaked whales within the genus *Hyperoodon* and *Berardius* also use short duration, broadband echolocation clicks but restrictions in sampling frequency do not allow for judgment whether these signals have a frequency sweep

^{a)}Author to whom correspondence should be addressed. On leave from: Eberhard-Karls-Universität Tübingen, Zoologisches Institut, Abteilung Tierphysiologie, Auf der Morgenstelle 28, 72076 Tübingen, Germany. Electronic mail: sbaumann@ucsd.edu

(Dawson *et al.*, 1998; Rogers and Brown, 1999; Hooker and Whitehead, 2002). So far we know Baird's, Arnoux's and Blainville's beaked whales also produce whistles (Dawson *et al.*, 1998; Rogers and Brown, 1999; Rankin and Barlow, 2007), while whistles from unidentified small beaked whales have been recorded in the Antarctic (J. A. Hildebrand, personal communication).

The echolocation signals of Blainville's and Cuvier's beaked whales are similar linear upsweep FM pulses of about 270 and 200 μ s duration, sweeping from 26 to 51 kHz and 31 to 54 kHz with center frequencies of 38 and 42 kHz, and inter-pulse intervals of 370 and 380 ms, respectively (Zimmer *et al.*, 2005; Johnson *et al.*, 2006). Source levels of up to 214 dB re 1 μ Pa at 1 m peak-to-peak (pp) have been reported for Cuvier's beaked whales (Zimmer *et al.*, 2005). Zimmer *et al.* (2005) measured a narrow beamwidth with directivity index of 30 dB and head scan rates of 25 deg/s for Cuvier's beaked whales. Gervais' beaked whales produce FM pulses of about 200 μ s duration with a dominant frequency in the range of 30 to 50 kHz and a mean inter-pulse interval of 270 ms. The beaked whale signals from Cross Seamount (Johnston *et al.*, 2008; McDonald *et al.*, 2009) swept in a different frequency range from 35 to above 100 kHz (the bandwidth limitation of the recording), with long pulse durations of about 990 μ s, and short inter-pulse intervals of 110 ms.

Most work on toothed whale echolocation has been with captive animals and has focused on target detection (e.g., Au, 1993; Kastelein *et al.*, 1999) and discrimination (e.g., Au, 1993; Kastelein *et al.*, 1997) while little is known about prey capture, particularly in the wild. A few recent studies show that the phases of prey capture in odontocetes (e.g., Miller *et al.*, 1995; Madsen *et al.*, 2002; Johnson *et al.*, 2004; Miller *et al.*, 2004; Akamatsu *et al.*, 2005; Madsen *et al.*, 2005; Johnson *et al.*, 2006, 2008; Jones *et al.*, 2008; Verfuß *et al.*, 2009) are very similar to those of prey capture in bats (e.g., Griffin *et al.*, 1960; Kalko and Schnitzler, 1989; Surlykke *et al.*, 1993; Schnitzler and Kalko, 1998; Miller and Surlykke, 2001; Schnitzler *et al.*, 2003; Melcón *et al.*, 2007). Vocalizing with long intervals is used to search for prey items while a group of signals with short intervals, the buzz, indicate prey capture attempts. Blainville's beaked whales (*Mesoplodon densirostris*) use FM echolocation pulses at 0.2–0.6 s inter-pulse intervals to detect and approach prey. At a distance to prey of about 3–4 m, they switch to a buzz with inter-pulse intervals around 10 ms, using lower energy unmodulated clicks for prey capture (Madsen *et al.* 2005; Johnson *et al.* 2006, 2008).

We describe the spectral and temporal characteristics of presumed beaked whale signals recorded with a towed hydrophone array and found on a yearlong seafloor acoustic recording at Palmyra Atoll. Based on preliminary analysis of two stranded specimens from Palmyra Atoll, Dalebout *et al.* (2007) suggested that the Palmyra Atoll beaked whales may represent yet another undescribed species. We show that the echolocation signals of the Palmyra Atoll beaked whale are similar to those of other whales in this family, which change their echolocation signal types and signal timing dependent upon behavioral context.

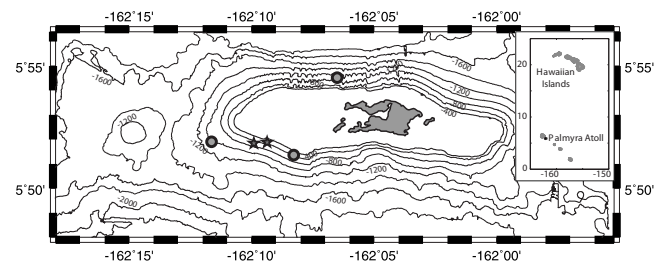


FIG. 1. Bathymetric map of Palmyra Atoll, with positions of HARPs indicated by stars and beaked whale sightings indicated by filled circles. Top right inset shows approximate location of Palmyra Atoll. Data courtesy of NOAA Coral Reef Ecosystem Division, Pacific Islands Fisheries Science Center and the Pacific Islands Benthic Habitat Mapping Center, SOEST, University of Hawaii. Coastline data courtesy of National Geophysical Data Center, NOAA Satellite and Information Service, WVS Coastline Database. Plotting with GMT by Paul Wessel and Walter H. F. Smith.

II. MATERIALS AND METHODS

A. Data collection

Our study area is the off-reef of Palmyra Atoll, extending in longitude west to east from 162° 15' W to 161° 57' W and in latitude north to south from 5° 57.6' N to 5° 49.2' N (Fig. 1). During two field seasons from September 18 to October 13, 2007, and October 14 to November 2, 2008 we conducted visual and acoustic surveys off the 26 ft Davis boat, *Zenobia*. During our daytime surveys we circumnavigated the atoll choosing a route dependant on sea conditions and mostly within 0.5 to 4 km of the reef edge. We maintained a constant watch with two to three observers. The small boat and heavy swell largely precluded use of binoculars for searching. When we detected animals we approached them for identification, school size estimation, photography and acoustic recordings. Recordings were obtained using a towed four-channel hydrophone array, streamed on 80 m of cable behind the boat. Depending on the animals' behavior, the array was either towed with speeds ranging between 1 and 8 kn, which resulted in a hydrophone water depth of 10–15 m, or deployed as a stationary array with a maximum depth of 80 m. The array was equipped with HS150 hydrophones (Sonar Research & Development Ltd., Beverley, UK), which had a sensitivity of -205 dB re V/μ Pa and a flat frequency response of ± 1 dB over the analysis range of 8 to 85 kHz. The hydrophones were connected to custom-built preamplifiers band-pass filter electronic circuit boards. The circuit boards were designed to flatten the ambient ocean noise, which resulted in a nonlinear frequency response that provided greater gain at higher frequencies where ambient noise levels are lower and sound attenuation is higher (for a detailed description of the circuit board properties see Wiggins and Hildebrand, 2007). Data were digitally sampled with a MOTU Traveler (Mark of the Unicorn, Cambridge, MA) at a sampling frequency of 192 kHz and recorded directly to a computer hard-disk drive with the software ISH-MAEL (Mellinger, Oregon State University, Newport).

Parallel to this effort, an autonomous high-frequency acoustic recording package (HARP) was placed on a steep slope off Palmyra Atoll's western terrace (Fig. 1). The HARP design differed from what was described in Wiggins and Hildebrand, 2007 as it was in a mooring configuration with

the hydrophone floating at about 20 m above the seafloor. It recorded from October 19, 2006 until March 23, 2007 and from April 9, 2007 until September 18, 2007. The recording gap of 16 days between the two deployments corresponded to servicing of batteries and hard drives. During the first deployment the HARP was located at 05° 51.85' N 162° 09.91' W in 650 m water depth. It was then deployed about 1 km east of the initial location at 05° 51.88' N 162° 09.36' W in 550 m depth. The recorder was set to a sampling frequency of 200 kHz and duty cycled with an on duration of 5 min every 20 min. On the HARP we used an omni-directional transducer (ITC-1042, ITC, Santa Barbara, CA), which had an approximately flat (± 2 dB) frequency response from 10 Hz to 100 kHz with a hydrophone sensitivity of -200 dB re V/ μ Pa. It was connected to a custom-built preamplifier board with band-pass filter and designed to follow the reciprocal of ocean ambient noise in order to maximize the dynamic range of the recorder (Wiggins and Hildebrand, 2007). All hydrophones and associated electronics were calibrated. The frequency responses of systems were compensated for during analysis.

B. Signal processing

Signal processing was performed using custom-made routines in MATLAB (Mathworks, Natick, MA). Beaked whale type sweep signals were detected on array and HARP recordings. These signals had, in comparison to delphinid clicks, longer durations and an upswep frequency. One sequence of 1 min 20 s with 109 pulses was detected on the array recordings of fall 2008. Sixty-five sequences out of 575 sequences with beaked whale type sweeps on the yearlong HARP recordings were selected for further analysis. Sequences were selected when a larger number of signals were well detectable above noise. In addition to swept pulses there were a few calling bouts with differing signal pattern and structure categorized as buzz clicks, based upon their faster repetition rate and spectral properties. All sequences were digitally filtered with a 10-pole Butterworth band-pass filter. The low cutoff frequency was at 8 kHz for FM pulse sequences. Buzz clicks had a much lower sound pressure level and therefore the low cutoff frequency was raised to 16 kHz in these sequences to improve the signal-to-noise ratio. The high cutoff frequency was at 85 kHz for both signal types to prevent analysis of possibly aliased parts of the recorded signal.

FM pulses and buzz clicks were automatically selected using a two-step approach. The first step used time-domain cross-correlation of a typical echolocation pulse to detect signals. Cross-correlation gave the degree of linear relationship between an example pulse as the model and the data set to be analyzed. The threshold for cross-correlation was set low with about 2% missed pulses and missed pulses were of low signal-to-noise ratio. There was accordingly a high false alarm rate. These automatic selections were manually scanned and all false detections were deleted. A 2.5 ms time series window was roughly defined around the detected FM pulses, and a 2 ms window around the detected buzz clicks. The second automatic selection step determined the exact

start and end point of the FM pulses and buzz clicks. The finer resolution click detection algorithm (Soldevilla *et al.*, 2008) using the Teager energy operator (Kaiser, 1990) was applied. By processing three consecutive signal samples, the Teager energy operator provides nearly instantaneous energy tracking. The Teager energy operator of a discrete signal is defined as

$$\Psi[x(n)] = x^2[n] - x[n+1]x[n-1], \quad (1)$$

with n standing for the sample number. The usefulness of the Teager energy operator was successfully demonstrated for the detection of sperm whale regular and creak clicks (Kandia and Stylianou, 2006). In our analysis, we empirically chose a noise floor at the 40th percentile of energy for each click. Points that had a Teager energy 100 times greater than the preceding noise floor and were less than 500 μ s apart, were grouped as one click. In case of multiple clicks per 15 ms of data, the signal with the highest Teager energy was chosen for analysis. To find the complete click including reverberations, start and end points were determined as the first and last points that were three times greater than the noise floor of a ten-point running mean of the Teager energy. Additionally, as a comparison, the 98% energy duration was calculated such that the calculated start and end of a pulse or buzz click was at the point t in time at which the integral of the energy ($p^2(t)dt$) increased or decreased, respectively, no more than 1% as t increased (Au, 1993).

In order to calculate signal-to-noise ratios, a 5 ms time series window was roughly picked preceding every FM pulse and a 2.5 ms window preceding every buzz click. Spectra of each signal and preceding noise were calculated using 1.28 ms of data and a 256-point Hann window centered around the pulse or click and in the beginning of the noise sample.

For the calculation of received levels, peak-to-peak levels of each FM pulse or buzz click were measured and converted into decibel values. The system response was approximately flat (± 3 dB) across the frequency range of the signals. The dB value of the inverse of the system response at peak frequency was added. Click received levels are given over a band encompassing the click energy. To approximately represent click sound pressure levels on a plot of ambient noise levels, -10 dB bandwidths of pulses and buzz clicks were calculated according to the definition by Au (1993) and $10 \log$ (bandwidth) was added. Signal-to-noise ratios were calculated with rms signal levels and rms noise levels. For rms noise level calculation, the noise was digitally band-pass filtered with a 10-pole Butterworth filter and cut at 25 and 75 kHz, which was the frequency range representative of the signals. To use only good quality pulses and clicks for the signal description, potentially clipped signals were eliminated by allowing only signals with amplitudes up to 80% of the dynamic range of the recording system, which resulted in a cut-off received level of about 165 dB re 1 μ Pa at 1 m. Furthermore all FM pulses recorded on the HARP with a signal-to-noise ratio of less than 20 dB and HARP buzz clicks as well as array FM pulses with less than 10 dB were discarded.

Signal parameters are influenced by the distance and orientation of the vocalizing animal to the recording hydrophone. Lower frequencies are less attenuated over distance than higher frequencies. The following equation (Richardson *et al.*, 1995) was used to approximate the influence of attenuation:

$$\alpha = 0.036f^{1.5} \text{ dB/km}, \quad (2)$$

with f being frequency in kHz. At a distance of 100 m the 25–85 kHz band was attenuated 0.5–2.8 dB. Thus for short ranges the recorded spectra is similar in shape to the source spectra. At 1 km the attenuation will be 5–28 dB in the signal range and therefore distort the spectral characteristics especially in the high frequencies. The orientation of the whale to the recording device changes the signal properties as higher overall amplitudes, more high frequency energy and shorter duration signals are expected when the whale's vocal beam is on axis with the recorder (Au, 1993). To minimize these biases for the calculation of median signal parameters, only highest amplitude signals were used. FM pulses and buzz clicks from HARP data with received levels between 150 and 160 dB re 1 μPa (pp) were included, leaving 3924 and 113 signals, respectively. 52 FM pulses from the array recordings with received levels between 130 and 160 dB re 1 μPa (pp) were included. The frequency-related signal parameters peak and center frequency, -3 and -10 dB bandwidth were processed using methods from Au (1993). Modulation rate of FM pulses was measured by computing the instantaneous frequency over the pulse using the Hilbert transform (Bracewell, 2000). The instantaneous frequency data were fitted with linear least-squares equations. Errors in the instantaneous frequency due to noise in the data were eliminated by discarding frequency values below 25 kHz in the entire pulse and above 80 kHz in the first half of the pulse.

Notable signals recorded were buzz clicks on the HARP and FM pulses from one vocalizing animal in a continuous click train on the array. Median and percentile values were calculated for these inter-pulse intervals with non-parametric distribution. FM pulses on the HARP recording originated from echolocation vocalizations of one or more animals. Inter-pulse intervals smaller than 120 ms were discarded because they showed either a change in echolocation behavior due to the approach to a target by shortening the inter-pulse interval, or indicated the presence of two or more animals vocalizing at the same time. Inter-pulse intervals longer than 550 ms were discarded, as they appeared due to larger gaps between FM pulse bouts or missed pulses of low amplitude. A histogram of the inter-pulse interval was computed using a 10 ms bin width from which two peaks in distribution appeared. A Gaussian mixture model with two mixtures was fitted to the histogram to describe the two peaks (Huang *et al.*, 2001). Inter-pulse interval means and standard deviations were derived from the Gaussian model for each peak.

III. RESULTS

A. FM pulse echolocation signals

During our two fall field seasons in the waters surrounding Palmyra Atoll we typically had sea states between Beaufort 3 and 4 and would regularly encounter bottlenose



FIG. 2. Surfacing sequence mother-calf pair of *Mesoplodon sp.* at Palmyra Atoll.

dolphins (*Tursiops truncatus*), melon-headed whales (*Peponocephala electra*), Gray's spinner dolphins (*Stenella longirostris longirostris*), and once short-finned pilot whales (*Globicephala macrorhynchus*). We had a total of three encounters with beaked whales. During two of the three encounters the animals were identified to be of the genus *Mesoplodon*, yet of an unidentified species. One encounter was of a distant unidentified beaked whale. Both sightings in 2007 were of two animals as a group, in one case a *Mesoplodon sp.* mother-calf pair (Fig. 2), the other case was unidentified. In 2008 one single *Mesoplodon sp.* was observed breaching once within 10 m off the bow of the small research vessel before starting a dive in perpendicular swim direction to the cruising direction of the boat. This sighting took place during bad visibility due to strong rainfall and sea state Beaufort 3.

During the two *Mesoplodon sp.* encounters the towed hydrophone array was deployed and the boat was stopped until it drifted with the prevailing currents. Acoustic recordings were started after the animals had been spotted, carried out for 1.5 h and stopped after no resighting occurred. In both cases there had been a dolphin sighting (unidentified and bottlenose dolphin) about half an hour prior and about 5 km away from the sighting location. No further cetacean sighting was reported for either of the days after the beaked whale sighting. Only the recordings of the close encounter in fall 2008 had upsweep FM pulses immediately after the animal had breached and started to dive. A total of 109 FM pulses were detected but only 52 had a received sound pressure level between 130 and 160 dB re 1 μPa (pp) and were used for the array signal description (Table I). Signals had a -10 dB bandwidth of 39 kHz and a -3 dB bandwidth of 12 kHz. The center frequency was at 40 kHz and the peak frequency at 41 kHz. Linear fitting was used to describe modulation rates which resulted on average in 239 kHz/ms. Teager-energy pulse duration was 167 μs , while 98%-energy duration was 52 μs . Inter-pulse intervals had a median value of 79 ms.

The data analysis of the long-term HARP data showed upsweep FM pulses, which were similar to the array record-

TABLE I. Signal parameters of FM pulses and buzz clicks with received levels between 150 and 160 dB re 1 μ Pa (pp) for HARP recordings (FM pulses: $N=65$, $n=3924$, inter-pulse interval $n=8784$; buzz clicks: $N=2$, $n=131$, inter-click interval $n=291$). FM pulses with a received level between 130 and 160 dB re 1 μ Pa (pp) for array recording ($N=1$, pulse $n=52$, inter-pulse interval $n=109$); N =number of sequences, n =number of signals. Inter-pulse intervals for HARP are given as mean (μ) and standard deviation (σ).

Parameter	Unit	FM pulses (array)		FM pulses (HARP)		Buzz clicks (HARP)	
		Median	(10–90%)	Median	(10–90%)	Median	(10–90%)
Peak frequency	kHz	40.5	(34.5–48.5)	44.5	(39.8–50.8)	39.8	(25.0–46.1)
Center frequency	kHz	39.7	(27.2–44.8)	46.0	(41.5–51.3)	45.6	(39.5–52.3)
–3 dB bandwidth	kHz	12	(8.3–23.3)	12.5	(8.6–18.0)	13.3	(7.8–22.0)
–10 dB bandwidth	kHz	39.0	(23.0–52.5)	25.8	(17.2–35.9)	44.5	(20.8–60.9)
Teager-energy duration	μ s	167	(145–324)	355	(275–495)	155	(125–235)
98%-energy duration	μ s	52	(50–63)	130	(105–180)	70	(54–239)
First inter-pulse interval	ms	79	(70–180)	$\mu=225$ $\sigma=\pm 16$		5.3	(3.8–8.6)
Second inter-pulse interval	ms	$\mu=430$ $\sigma=\pm 35$	
Sweep rate	kHz/ms	239	(112–322)	253	(103–387)

ings. A total of 3924 FM pulses with a received level between 150 and 160 dB re 1 μ Pa (pp) were used for the HARP signal description (Table I). The –10 dB bandwidth was 26 kHz and the –3 dB bandwidth was 13 kHz. The center frequency was at 46 kHz and the peak frequency at 45 kHz (Fig. 3). Signal sweep rate was on average 253 kHz/ms. The Teager-energy pulse duration was 355 μ s and the 98%-energy duration was 130 μ s. Inter-pulse interval had a mean value of 225 ms.

FM pulse frequency values and received levels between 140 and 165 dB re 1 μ Pa (pp) had a distinct relationship [Fig. 4(A)]. The lower and upper limits of the –10 dB bandwidth had a standard deviation of approximately 5 to 6 kHz around means of 2 dB bin width. There was only a slight frequency variation of ± 2 kHz for the lower –10 dB mean

values over the range of received levels analyzed. The upper mean values rose from 54 kHz at low received level to 64 kHz with high received levels. Teager-energy pulse duration [Fig. 4(B)] was shortest with 330 μ s at a received level of around 140 dB re 1 μ Pa (pp) and was longer with higher received levels up to 165 dB re 1 μ Pa (pp) and 450 μ s. Standard deviations for pulse duration was between 80 and 115 μ s.

The inter-pulse interval had a bimodal distribution [Figs. 4(C) and 4(D)]. The vast majority (92%) of inter-pulse intervals were in the range of 120 and 340 ms with a mean of 225 ms and a standard deviation of 16 ms. There were also sequences with approximately double the primary inter-pulse interval, with a mean of 430 ms and a standard deviation of 35 ms (Fig. 5).

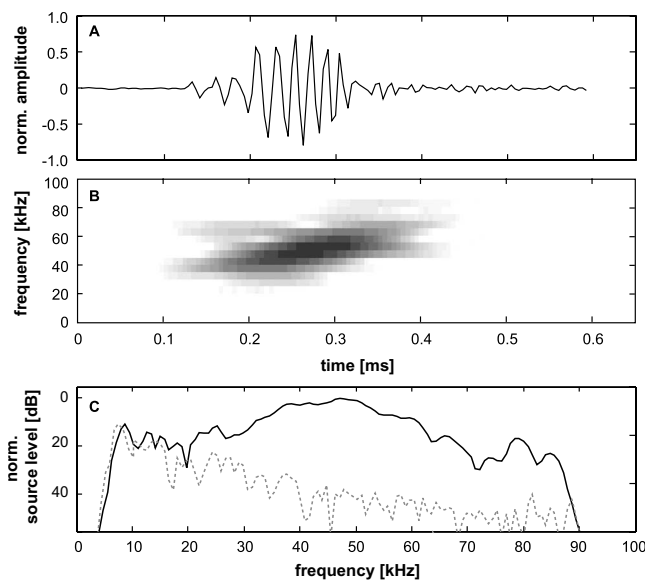


FIG. 3. Typical upsweep FM pulse recorded on the HARP at Palmyra Atoll. It represents the sum of 303 aligned pulses; all with a signal-to-noise ratio between 29 and 30 dB. (A) Waveform with normalized amplitude versus time, (B) spectrogram (Hann window, 40-point FFT, 98% overlap) with frequency versus time, and (C) spectra (Hann window, 256-point FFT) with normalized amplitude versus frequency. The continuous line represents the FM pulse; the dashed line shows the preceding noise floor.

B. Buzz sequences

Two buzz sequences with a total of 291 buzz clicks were detected and 131 of these were used for the signal description (Table I). The sequences were categorized as a buzz if a regularly spaced echolocation pulse sequence with inter-pulse intervals larger than 120 ms was followed by a sequence with clicks of less than 20 ms inter-click intervals. Buzz clicks were about 20 dB lower in amplitude than prior FM pulses. These clicks were not frequency modulated, with a –10 dB bandwidth of 45 kHz and a –3 dB bandwidth of 13 kHz. They had a center frequency of 45 kHz and a peak frequency of 40 kHz (Fig. 6). The Teager-energy duration was 155 μ s and the 98% energy duration was 70 μ s. The inter-click interval was between 4 and 10 ms. The two recorded buzz sequences differed from each other temporally (Fig. 7). They both had a series of regularly spaced FM pulses and then one shorter inter-pulse interval with FM pulse before changing the signal structure to buzz clicks and shortening the inter-click interval even more. One buzz sequence had continuously decreasing inter-click intervals starting at 10 ms and reducing it to a minimum of 3.5 ms. There was a long gap of about 700 ms before regular FM pulses were continued. The other buzz sequence started out

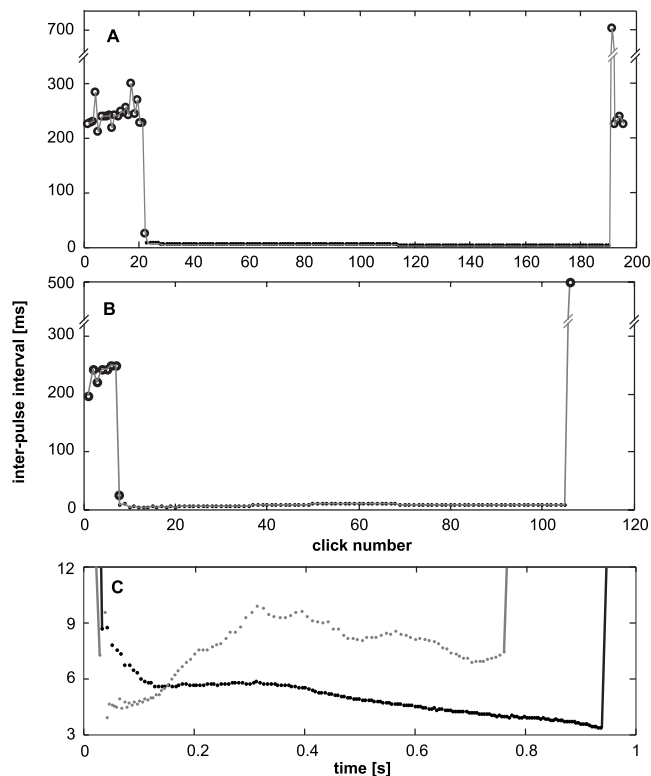


FIG. 7. [(A) and (B)] Change from regular pulses to clicks of buzzes in two sequences with shortening of inter-pulse intervals (open circles) before the buzz clicks to a minimum of 26 ms (A) and 24 ms (B) followed by inter-click intervals (points) between 10 and 4 ms. After the buzz there was a pause of 708 ms (A) and 499 ms (B) before echolocation pulses were resumed. (C) Detail of buzz inter-click intervals (points) versus time of sequence A (black) and B (gray). Lines in the beginning and end indicate long inter-pulse intervals.

Palmyra Atoll based on the known geographical distribution of mesoplodonts (MacLeod *et al.*, 2006; Jefferson *et al.*, 2008). Cookiecutter shark (*Isistius brasiliensis*) bites or tooth scrape marks of conspecifics did not leave characteristic white scars in this species, which makes them distinguishable in the field, at least from *M. densirostris* (trip report Pitman and Ballance). To distinguish *M. hotaula* from *M. ginkgodens* a biopsy sample would be necessary. In order to be certain about the precise species at Palmyra Atoll, more photos, particularly of adult males with their distinct tooth on each side of the lower jaw, and biopsy samples would be crucial.

It is probable that the unknown mesoplodont whale, presumably *M. hotaula*, produced the recorded sounds on the long-term data set as well as the array data. It has been the only confirmed species of beaked whale observed around the atoll and during the array recording. The FM pulses on the array recordings were possibly recorded from a caudal aspect as the animal descended on a dive which resulted in some clicks having low received levels and which could have a strong influence on both temporal and spectral properties of the recorded signals. In particular the bandwidth, center and peak frequency of on-axis signals is likely underestimated and the duration overestimated. Nevertheless, mean array and HARP signal spectra are very similar with more energy in the frequencies below 35 kHz for probably more off axis,

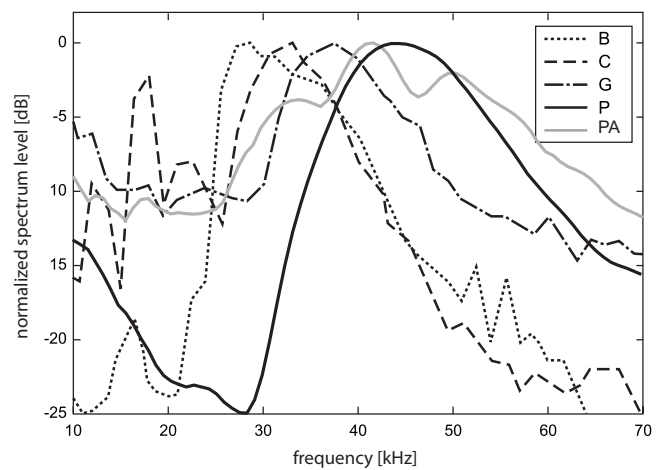


FIG. 8. Averaged power spectra for four beaked whale species (B=Blainville's beaked whale, C=Cuvier's beaked whale, G=Gervais' beaked whale, P=Palmyra beaked whale HARP, PA=Palmyra beaked whale array); data and graph adapted from Gillespie *et al.*, 2009.

low amplitude array signals (Fig. 8), resulting in discrepancies in median values (Table I). The beaked whale signals recorded in the presence of the *Mesoplodon sp.* of Palmyra Atoll and described here are unlike previously published FM pulse descriptions in their temporal and spectral properties. They are very different in all aspects to those found at Cross Seamount (Johnston *et al.*, 2008; McDonald *et al.*, 2009). Yet despite their differences, they have more similarity with those of Cuvier's, Blainville's and Gervais' beaked whales, but with higher peak and center frequencies, and shorter inter-pulse intervals (Table II, Fig. 8).

B. FM pulse echolocation signals

Beaked whale echolocation signals are known to be directional. Zimmer *et al.* (2005) reported for Cuvier's beaked whales a directivity index of 30 dB and head scan rates of 25 deg/s. With these beam characteristics only a few seconds of a continuous signal sequence with mostly on axis pulses would be detectable on a stationary recorder. Given the range of received levels and major pulse energy between 30 and 60 kHz, the maximum detection range of signals with high signal-to-noise ratio should approximately be around 3 km (Urlick, 1983) and clipping on the recorder appeared when

TABLE II. Comparison of FM pulse parameters of beaked whales.

	-10 dB bandwidth (kHz)	Center frequency (kHz)	Duration (μ s)	Inter-pulse interval (ms)
Blainville's beaked whale ^a	25	38	270	370
Cuvier's beaked whale ^b	23	42	200	380
Gervais' beaked whale ^c	~25	~45	200	270
"Palmyra" beaked whale (HARP)	26	46	355	225
"Cross Seamount" beaked whale ^d	>50	>70	985	110

^aJohnson *et al.*, 2006.

^bZimmer *et al.*, 2005.

^cGillespie *et al.*, 2009.

^dMcDonald *et al.*, 2009, personal communication.

animals approached to about 200 m. Due to the large range of distances and aspects of the vocalizing animal to the recorder one can assume a large variability in both temporal and especially spectral properties [Figs. 4(A) and 4(B)]. Looking at lower and upper frequency limits of the -10 dB bandwidth, spectral properties of FM pulse echolocation signals in relation to received levels are almost unaffected in the lower frequencies between 30 and 40 kHz yet higher frequencies increase with increasing received level from a mean of 54 to 64 kHz [Fig. 4(A)]. This frequency shift was most likely due to different distances of the vocalizing animal to the recorder, which attenuated higher frequencies more at larger range. A similar trend can be seen in the relationship of duration and received level [Fig. 4(B)]. With increasing received level the Teager-energy duration was getting longer, which is most likely not due to actually longer duration signals but due to a better signal-to-noise ratio. Teager-energy duration was used for this comparison as this paper describes clicks from random distances and axis orientations, which may be distorted in their wave forms and include reverberations caused by reflections within the head, the sound producing organs themselves, the external environment, or a combination of these (Au *et al.*, 1978; Soldevilla *et al.*, 2008; Lammers and Castellote, 2009). Energy duration as a measure of click duration has been widely used for the analysis of on-axis clicks; however, the Teager energy operator proved to be more appropriate for off-axis signals (Soldevilla *et al.*, 2008). Teager energy duration values were therefore higher than the 98% energy duration. The presentation of the full variety of recorded signals received with passive acoustic detection shows that both spectral and temporal mean values vary depending on the recording circumstances and quality of the signal and which part of the data is being used for mean value calculations.

C. Inter-pulse intervals

The Palmyra beaked whale had a large majority of the inter-pulse intervals on the HARP at 225 ± 16 ms [Fig. 4(C)]. Despite the automatic detection that also counted sequences with several animals vocalizing, which would result in shorter inter-pulse intervals, or dropped occasional low amplitude signals within a sequence, favoring longer intervals, the majority (92%) of inter-pulse intervals were within the distribution peak of the 225 ms inter-pulse interval. There was a second peak in the distribution of longer inter-pulse intervals from the HARP data produced by the Palmyra beaked whale [Fig. 4(D)] at 430 ± 35 ms, which was approximately double the value of the first and dominant mode. A methodological error due to dropped signals in the detection algorithm can be ruled out as lengthy sequences with long inter-pulse intervals were found [Fig. 5(B)]. We do not have a hypothesis for the use of a certain short or long inter-pulse interval, though the preference for these indicates a specialized way of sampling the acoustic scene.

Several species of beaked whales seem to have a species-specific inter-pulse interval (Zimmer *et al.*, 2005; Johnson *et al.*, 2006; McDonald *et al.*, 2009) while other delphinids do not show a species-specific inter-click interval

but adapt it to their echolocation task (e.g., Verfuß *et al.*, 2005, 2009). Generally, all echolocating odontocetes probably adjust their vocal behavior to environmental conditions and optimize their echolocation temporally to a certain habitat and prey, similar to what is known for insectivorous bats (e.g., Schnitzler *et al.*, 2003).

There have been two sequences in the yearlong acoustic data recorded by the bottom-moored recorder that had a terminal buzz after a series of regularly spaced FM pulses, which likely originated from this species of beaked whale. The low number could be either due to the strong directionality of the click with sound pressure levels 20 dB lower than FM pulses, or because the main foraging depth of the whales were at a different depth than the stationary recorder. Clicks with short inter-click intervals are either terminal buzzes during prey capture (e.g., Madsen *et al.*, 2005; Verfuß *et al.*, 2009) or burst pulses used in a social context (e.g., Lammers *et al.*, 2006). The sequences with short inter-click intervals described had a structure as expected for foraging namely with a series of regularly spaced pulses followed by a terminal buzz and therefore prey capture attempts are more likely than social calls. In several studies with beaked whales the emitted pulse and the returning echo were described through recordings obtained with a system attached to a diving and vocalizing animal. The inter-pulse intervals during search phase were generally much longer than the two-way travel time to the apparent target and inter-pulse intervals were in most cases stable before a terminal buzz started (Madsen *et al.*, 2005; Johnson *et al.*, 2008). Buzzes were characterized by inter-click intervals in the range of 3 to 10 ms (Johnson *et al.*, 2006). The use of stable inter-pulse intervals in beaked whales during prey capture before the terminal buzz was interpreted to be used for maintaining a broad view in a multi-target environment and low click rates would be beneficial for strong signals (Madsen *et al.*, 2005). The strong preference of the Palmyra beaked whale for a certain inter-pulse interval, while emitting FM pulses, and inter-click intervals below 10 ms during the buzz support this theory for another beaked whale species. The change in signal parameters from a longer duration FM pulse to broadband, short duration clicks during the buzz have previously been described for Blainville's beaked whales (Johnson *et al.*, 2006).

V. CONCLUSIONS

The echolocation signals of the mesoplodont beaked whale at Palmyra Atoll were spectrally and temporally different to previously published FM pulse beaked whale signals. The use of regularly spaced FM pulses and the switch to broadband clicks for the buzz, and with it probably prey capture, is a signal structural strategy already known for another beaked whale, *Mesoplodon densirostris*. Further investigations should include photographs of adult males and biopsy samples to test the hypothesis that this species is *Mesoplodon hotaula*. The signal description of this paper is the basis for future analysis of diel and seasonal patterns of this species. It will give us insight into the natural behavior of a beaked whale species in a pristine coral reef environment with little human impact.

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