Species-specific beaked whale echolocation signals

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Beaked whale echolocation signals are mostly frequency-modulated (FM) upsweep pulses and appear to be species specific. Evolutionary processes of niche separation may have driven differentiation of beaked whale signals used for spatial orientation and foraging. FM pulses of eight species of beaked whales were identified, as well as five distinct pulse types of unknown species, but presumed to be from beaked whales. Current evidence suggests these five distinct but unidentified FM pulse types are also species-specific and are each produced by a separate species. There may be a relationship between adult body length and center frequency with smaller whales producing higher frequency signals. This could be due to anatomical and physiological restraints or it could be an evolutionary adaption for detection of smaller prey for smaller whales with higher resolution using higher frequencies. The disadvantage of higher frequencies is a shorter detection range. Whales echolocating with the highest frequencies, or broadband, likely lower source level signals also use a higher repetition rate, which might compensate for the shorter detection range. Habitat modeling with acoustic detections should give further insights into how niches and prey may have shaped species-specific FM pulse types.
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I. INTRODUCTION

Beaked whales are among the most poorly known groups of large mammals (Pitman, 2002; Jefferson *et al.*, 2008). They are difficult to study due to their offshore, pelagic habitat, and elusive behavior with prolonged deep dives and short surface intervals (e.g., Tyack *et al.*, 2006). Over the past decade, research has shown that most beaked whales use a species-specific frequency modulated (FM) upswept echolocation pulses to forage and sense their environment. Based on recordings from animal-attached, suction-cup acoustic archival tags and from towed hydrophones during concurrent visual surveys, acoustic descriptions have been made for FM pulses from Baird's (*Berardius bairdii*) (Dawson *et al.*, 1998; Baumann-Pickering *et al.*, 2013b), Arnoux's (*Berardius arnuxii*) (Rogers and Brown, 1999), Blainville's (*Mesoplodon densirostris*) (Johnson *et al.*, 2004; Madsen *et al.*, 2005; Johnson *et al.*, 2006; Aguilar de Soto *et al.*, 2012), Cuvier's (*Ziphius cavirostris*) (Zimmer *et al.*, 2005; Zimmer *et al.*, 2008), Gervais' (*M. europaeus*) (Gillespie *et al.*, 2009), Longman's (*Indopacetus pacificus*) (Rankin *et al.*, 2011), Deraniyagala's (*M. hotaula* or *M. ginkgodens hotaula*) beaked whales (Baumann-Pickering *et al.*, 2010), and Northern bottlenose whales (*Hyperoodon ampullatus*) (Wahlberg *et al.*, 2011). Likewise, Stejneger's beaked whale (*M. stejnegeri*) FM pulses were recorded with bottom-moored autonomous acoustic instruments and linked to the species based on geographic location and exclusion of other species (Baumann-Pickering *et al.*, 2013a). However, species-identified acoustic recordings do not yet exist for Perrin's (*M. perrini*), pygmy (*M. peruvianus*), Hubbs' (*M. carlhubbsi*), and ginkgo-toothed (*M. ginkgodens*) beaked whales in the North Pacific, and True's beaked whales (*M. mirus*) in the North Atlantic. Because their FM pulses can be discriminated to species level based on their spectral and temporal characteristics, long-term passive acoustic monitoring has taken a lead role in beaked whale research providing detailed information on the daily, seasonal, and geographical occurrence of this elusive group of animals.

The distinctiveness of beaked whale echolocation calls has an analog to those of echolocating bats. Bats are also known to produce species-specific echolocation calls, which have been shaped through adaptation and convergent evolution (Jones and Holderied, 2007). Bat spectral and temporal call properties are strongly optimized for navigation and foraging in the species' ecological niches (e.g., Schnitzler *et al.*, 2003; Siemers and Schnitzler, 2004). These specialized niche adaptations have convergently evolved multiple times within bats (Jones and Teeling, 2006; Teeling, 2009). Cases of convergent evolution are relevant to our understanding of natural selection. Bat and odontocete echolocation differ in many aspects, most importantly in the way the signal is produced. However, at a gene sequence level, such as for the hearing gene *Prestin*, convergent evolution has occurred in unrelated lineages of echolocating bats as well as echolocating dolphins, closely grouping these phylogenetically distant echolocating mammals (Li *et al.*, 2010; Liu *et al.*, 2010).

Given these similarities in evolution, the goal of this article is to describe and compare beaked whale FM pulses and to discuss reasons for the species-specificity found in these signals with implications for possible niche separation in beaked whales similar to that found in bats.

II. METHODS

A. Data collection

Autonomous High-frequency Acoustic Recording Packages (HARPs) (Wiggins and Hildebrand, 2007) collected long-term acoustic data for this study at over 20 sites in the North Pacific and Gulf of Mexico (Fig. 1, Table I). HARPs at these different sites had a variety of recording durations from a few weeks to several months, and recording schedules ranged from continuous to 5 min of recording every 40 min. Recorders were deployed to seafloor depths between 700 and 1300 m, where ocean noise is low and beaked whales often echolocate to forage. HARPs were bottom-mounted, either in a seafloor-packaged configuration or as a mooring with the hydrophone 10 to 30 m above the seafloor. All HARPs were set to a sampling frequency of 200 kHz with 16-bit quantization. The recorders were equipped with an omni-directional sensor (ITC-1042, International Transducer Corporation, Santa Barbara, CA), which had an approximately flat (± 2 dB) hydrophone sensitivity from 10 Hz to 100 kHz of -200 dB re V/μPa. The sensor was connected to a custom-built preamplifier board and bandpass filter. The preamplifiers were designed to flatten the frequency response of the ambient ocean noise, which provided greater gain at higher frequencies where ambient noise levels are lower and sound attenuation is higher (Wiggins and Hildebrand, 2007). The calibrated system response was corrected for during analysis. Data for Longman's beaked whale were from towed array data described in Rankin *et al.* (2011).

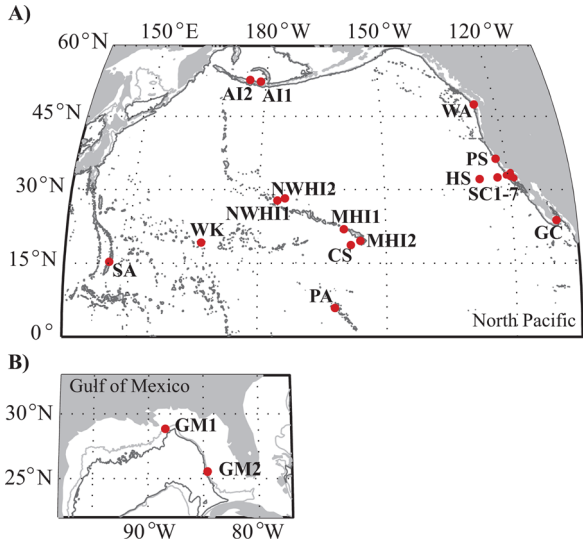

FIG. 1. (Color online) Location of HARPs in the North Pacific and Gulf of Mexico. AI = Aleutian Islands, SA = Saipan, WK = Wake Atoll, NWHI = Northwestern Hawaiian Islands, MHI = Main Hawaiian Islands, CS = Cross Seamount, PA = Palmyra Atoll, WA = Washington, PS = Point Sur, HS = Hoke Seamount, SC = Southern California, GC = Gulf of California, GM = Gulf of Mexico. 1000 m (thin) and 2000 m (bold) isobaths are shown.

TABLE I. Overview of HARP and array data (*) used for signal description. Regions indicate where data were collected, number in parentheses indicates if multiple sites in that geographic area had acoustic encounters. N = number of acoustic encounters; n = number of signals; AI = Aleutian Islands, SA = Saipan, NWHI = Northwestern Hawaiian Islands, MHI = Main Hawaiian Islands, CS = Cross Seamount, PA = Palmyra Atoll, WA = Washington, PS = Point Sur, HS = Hoke Seamount, SC = Southern California, GC = Gulf of California, GM = Gulf of Mexico.

	N	n	Median n per N (min-max)	Regions
Baird's beaked whale	10	59 023	3481 (1131–12 812)	SC (4)
Longman's beaked whale	1*	312	–	NWHI
Blainville's beaked whale	11	9333	796 (94–4264)	MHI, NWHI, SA
Cuvier's beaked whale	22	46 629	1175 (15–16 287)	AI, MHI, HS, NWHI, SC (4)
BW40	8	3805	424 (15–1402)	NWHI, PS, SC (4)
Gervais' beaked whale	28	45 418	1104 (165–5485)	GM
BW43	6	3789	285 (24–2158)	HS, SC (2)
Deraniyagala's beaked whale	7	4887	810 (244–5199)	PA
BWG	6	1389	86 (36–640)	GM
BWC	9	3760	233 (31–2425)	CS, MHI, NWHI
Stejneger's beaked whale	15	24 412	1575 (35–6901)	AI (2), WA, SC (2)
BW70	8	8048	417 (80–3947)	GC

B. Signal processing

Signal processing was performed using the MATLAB (Mathworks, Natick, MA) based custom software program *Triton* (Wiggins and Hildebrand, 2007) and other MATLAB custom routines. Trained analysts (SBP, MAM, AES, ASB, KPBM) manually identified beaked whale type FM echolocation pulses in the HARP data. These signals had distinctive characteristics: Long duration compared to known delphinid clicks, a stable inter-pulse interval (IPI), and an upswept frequency modulation. Long-term spectral averages (LTSAs) were calculated for visual analysis of the long-term recordings and for indexing to finer-scale data for detailed analysis. LTSAs are long-term spectrograms with each time segment consisting of an average of 500 spectra. The averages were formed from power spectral densities of non-overlapped 10 ms Hann-windowed frames. The resulting long-term spectrograms have a resolution of 100 Hz in frequency and 5 s in time. When echolocation signals were notable in the LTSA, the sequence was inspected more closely (Fig. 2). IPIs were determined from 5 s time series, and the presence or absence of FM pulses was determined by examining the time series and spectrogram (Hann window, 60 samples/3.3 kHz bandwidth, 98% overlap) of 3 ms time segments. Start and end times of acoustic encounters were noted if beaked whale-like FM pulses were identified. Analysts initially labeled these acoustic encounters as having been produced by either one of the species whose echolocation signals are well known, one of the types of echolocation signal categories whose origin has not yet been determined (but described in this manuscript), or as unidentifiable with beaked whale echolocation signal characteristics.

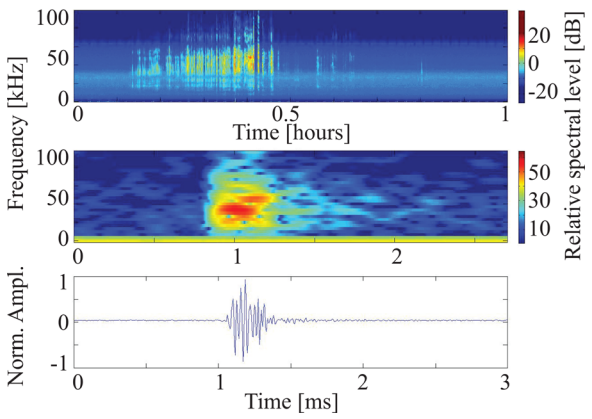

FIG. 2. (Color online) Example sequence of Cuvier's beaked whale acoustic encounter on 2/27/2009 at 22:39 in Southern California (33° 08.4 N 118° 52.8 W): (top) LTSA (5 s averages, 2000-points DFT, Hann window), (middle) example FM pulse in spectrogram (60-points DFT, 98% overlap, Hann window), and (bottom) waveform.

All presumed beaked whale acoustic encounters were reviewed in a second analysis step. Individual echolocation signals were automatically detected using a computer algorithm during time periods when FM pulses were manually detected (Soldevilla *et al.*, 2008). The individual FM pulse detections were digitally filtered with a 10-pole Butterworth band-pass filter with a pass-band between 5 and 95 kHz. Filtering was done on 800 samples centered on the echolocation signal. Spectra of each detected signal were calculated using 2.56 ms (512 samples) of Hann-windowed data centered on the signal. The frequency-related signal parameters peak, center frequency, and bandwidth were processed using methods from Au (1993). FM pulse duration was derived from the detector output and IPIs were calculated from the differences between FM pulse starts. All detected echolocation signals, independent of distance and orientation of the recorded animal with respect to the recorder, were included in the analysis. For each acoustic encounter, custom software for analyst-assisted signal discrimination displayed temporal and spectral characteristics of the encounter (Fig. 3). This consisted of histograms of peak frequency and IPI, their medians, and those of peak-to-peak received level, center frequency, and duration. Mean spectra of all pulses were plotted against the mean noise preceding each FM pulse [2.56 ms of noise (512 samples) with a 1.3 ms gap before the signal, bandpass filtered like the FM pulses] and additionally against an overlay of spectral templates from all FM pulse types. Spectral templates for signals of known origin were taken from literature. Finally, concatenated spectra of

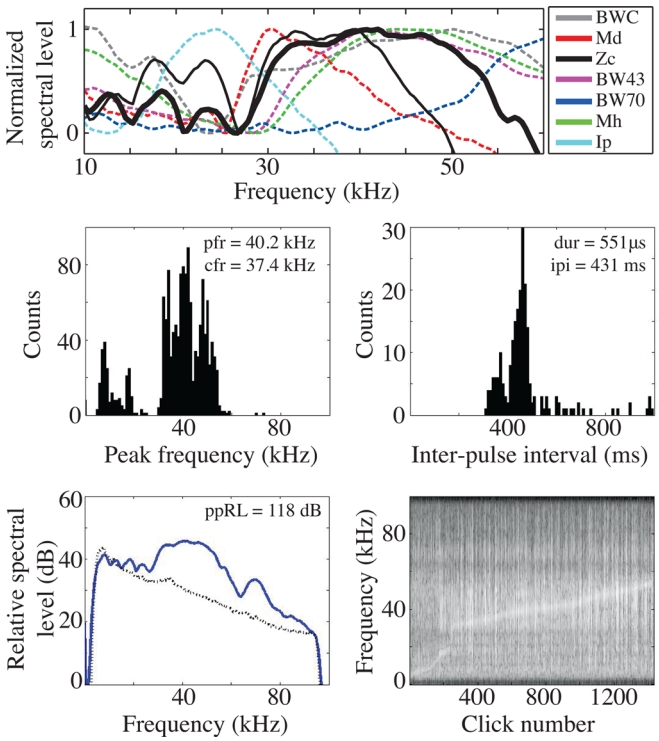

FIG. 3. (Color online) Example of software signal discrimination tool used to label an acoustic encounter consisting of 1431 Cuvier's beaked whale (Zc) FM pulses. (top) Mean spectra of all automatically detected FM pulses of the example encounter denoted by black bold line. Mean spectra of templates for all other FM pulse types are denoted as thin dashed lines with the exception of Zc, which is shown as a thin solid black line to highlight the similarity with the example encounter. (middle) Histograms of peak frequency (left, pfr) and IPI (right) with median values for pfr, center frequency (cfr), duration (dur), and IPI. (bottom) Mean spectra of encounter (left, solid line) and mean noise before each FM pulse (left, dashed line), with median peak-to-peak received level in dB re 1 μPa (ppRL) over all FM pulses in the encounter. Concatenated spectrogram of all FM pulses sorted by peak frequency showing variability (right).

echolocation pulses sorted by peak frequency were displayed. The analyst optionally browsed through plots of individual time series and spectrograms (2 ms data, 60-point DFT, 98% overlap) of echolocation signals detected within the acoustic encounter, sorted by peak-to-peak received level displaying high quality signals first. This led to a final judgment about the signal type label for each acoustic encounter and the analyst submitted a decision. The most relevant criteria on which the discrimination decisions were based, was the median IPI together with the overall shape of the mean spectra. The overlay of the mean spectra to be labeled over the spectral templates allowed for comparison of all spectral features, with special emphasis being made on smaller spectral peaks at frequencies below the main energy content and the slope at which the main energy content rose. Higher frequencies were used less in the decision process, as they were more susceptible to attenuation effects due to distance. In some cases, where the acoustic encounter was not labeled to belong to one of the distinct FM pulse types because of either low quality of the acoustic encounter, very few FM pulse detections, or spectral and temporal values that did not fit any of the defined FM pulse types, the acoustic encounter was labeled as a probable "unidentified beaked whale" (UBW). This label, being an inhomogeneous group and likely composed of a variety of FM pulse types, was not further analyzed. The decision upon a new FM pulse type with unknown origin was an iterative process by grouping good quality acoustic encounters with similar temporal and spectral values that were initially labeled UBW. These UBW pulses were then transitioned into a spectral template for the analyst-assisted signal discrimination software. All decisions on acoustic encounters with rare and new signal types were evaluated by at least two analysts and agreed upon.

A best-fit line and Pearson's linear correlation were used to test for a relationship between median center frequency and maximum body length to evaluate reasons for the species-specific signal features. Approximate measures for maximum body length were taken from Jefferson *et al.* (2008) and were estimated for Deraniyagala's beaked whale based on field encounters (SBP).

III. RESULTS

Data for Baird's (*Bb*), Blainville's (*Md*), Cuvier's (*Zc*), Gervais' (*Me*), Deraniyagala's (*Mh*) (Dalebout *et al.*, 2007; Baumann-Pickering *et al.*, 2010; Dalebout *et al.*, 2012), and Stejneger's beaked whale (*Ms*) (Table I) were recorded with HARPs. Towed-array recordings revealed echolocation signals of Longman's beaked whale (*Ip*) (Rankin *et al.*, 2011). Additionally, five distinct beaked whale-like FM pulse types of unknown origin were identified in HARP data, subsequently called BW40, BW43, and BW70 named after their dominant spectral content, as well as BWG (from the Gulf of Mexico) and BWC (from Cross Seamount).

The peak frequency of all FM pulse types ranged from as low as 16 kHz (Baird's beaked whales) to as high as 66 kHz (BW70) (Table II, Figs. 4–6). The example FM pulses per species (Fig. 4) and their associated parameter values and variability (Table II, Fig. 6) show that particularly Baird's but also Blainville's, Cuvier's, and the unknown BW40 FM pulse type have a smaller −10 dB bandwidth (8–12 kHz) in comparison to Longman's, Gervais', Deraniyagala's, Stejneger's, BW43, and BW70 FM pulse types (20–23 kHz). BWC and BWG FM pulse types have the broadest FM sweeps (26–31 kHz bandwidth). Mean spectra and concatenated spectrograms of some FM pulse types (Fig. 5) show consistent smaller spectral peaks below the main spectral energy. For species with peak and center frequencies in the 16–48 kHz range, corresponding IPIs tended to be between 190 and 440 ms. With higher spectral content, and for BWG and BWC with a very broad bandwidth, the IPI was considerably shorter, between 90 and 130 ms. The occurrence of additional echolocation signal types similar to those produced by dolphins, clicks with shorter duration over a broad frequency with no sweep, were another indicator for species discrimination (Table II). Signal duration was highly variable due to the inclusion of signals recorded from all angles of the echolocation beam and not very reliable for discrimination (Table II, Fig. 6).

There was a negative relationship of median center frequency (cf) and maximum body length (bl) (line of

TABLE II. Overview of signal parameters peak and center frequency, −10 dB bandwidth, duration, and inter-pulse interval (IPI) for all species given as median with 10th and 90th percentile in parentheses. For comparison, mean and standard deviation literature values of Northern bottlenose whale FM pulses were included (Wahlberg *et al.*, 2011). Column "Click" indicates whether an additional signal type similar to dolphin clicks has been observed during regular echolocation trains.

	Peak frequency (kHz)	Center frequency (kHz)	−10 dB bandwidth (kHz)	Duration (μs)	IPI (ms)	Click
Baird's beaked whale	16.4 (9.0, 27.0)	20.4 (14.7, 31.3)	8.6 (4.7, 19.1)	504 (275, 875)	204 (80, 369)	yes
Longman's beaked whale	22.0 (14.2, 29.8)	22.7 (16.9, 28.1)	20.8 (11.1, 39.1)	182 (101, 375)	–	yes
Blainville's beaked whale	34.4 (31.3, 44.1)	37.3 (32.3, 44.0)	11.7 (5.5, 23.0)	581 (299, 950)	280 (111, 427)	no
Cuvier's beaked whale	40.2 (20.3, 49.2)	35.9 (28.7, 42.5)	10.9 (5.1, 21.9)	585 (306, 976)	337 (94, 491)	no
BW40	42.6 (33.6, 52.3)	40.1 (33.1, 46.5)	10.5 (4.7, 20.7)	575 (250, 1031)	435 (314, 538)	yes
Northern bottlenose whale	–	43 ± 7	–	276 ± 58 [a]	306 ± 118	no
Gervais' beaked whale	43.8 (35.9, 55.9)	45.2 (37.5, 55.0)	18.8 (7.8, 34.8)	450 (260, 765)	275 (114, 353)	no
BW43	43.4 (37.7, 55.1)	45.2 (37.5, 53.8)	19.9 (7.8, 38.7)	395 (270, 621)	217 (132, 441)	no
Deraniyagala's beaked whale	47.3 (28.9, 69.1)	46.8 (33.5, 57.1)	19.5 (9.0, 36.7)	475 (305, 720)	194 (70, 429)	no
BWG	46.9 (33.6, 56.1)	43.0 (33.8, 52.6)	30.9 (16.8, 43.8)	535 (155, 1023)	133 (72, 355)	no
BWC	46.9 (28.9, 73.8)	47.4 (30.3, 65.4)	26.2 (5.9, 48.4)	779 (270, 1210)	127 (66, 338)	yes
Stejneger's beaked whale	50.4 (45.7, 73.8)	56.1 (46.1, 67.8)	21.1 (8.6, 39.1)	420 (245, 746)	90 (65, 224)	no
BW70	66.4 (60.9, 78.9)	66.9 (60.9, 75.1)	23.4 (12.4, 31.6)	435 (291, 655)	119 (92, 217)	no

[a]Durations derived from 95% energy, in comparison to Teager-energy as used in this manuscript, may be slightly shorter and not fully comparable.

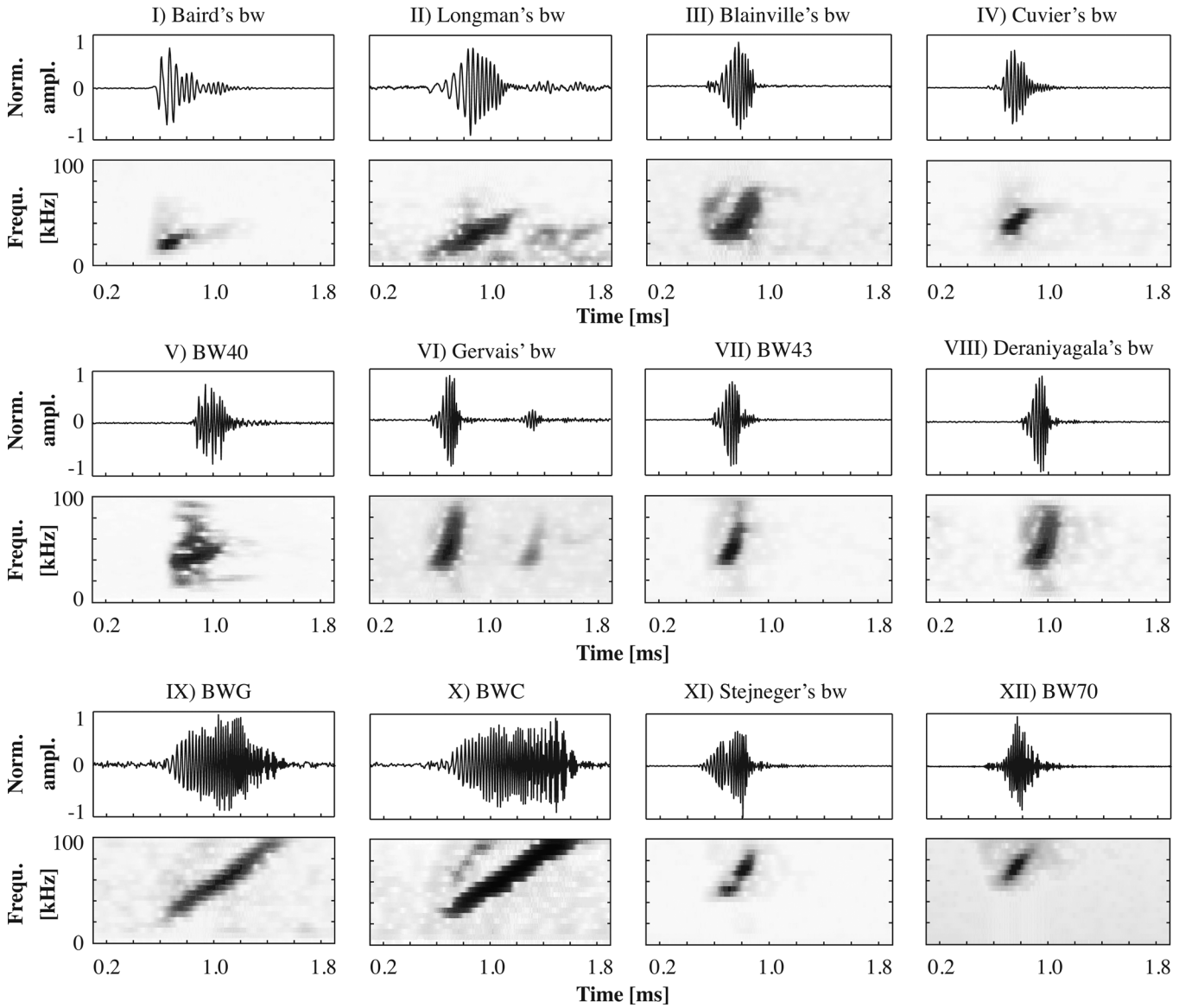

FIG. 4. Examples of species-specific frequency modulated (FM) pulses of known (I–IV, VI, VIII, XI) and unknown origin (V, VII, IX, X, XII). Time series with normalized (top) amplitude and (bottom) spectrogram (60-points DFT, Hann window, 98% overlap). bw = beaked whale.

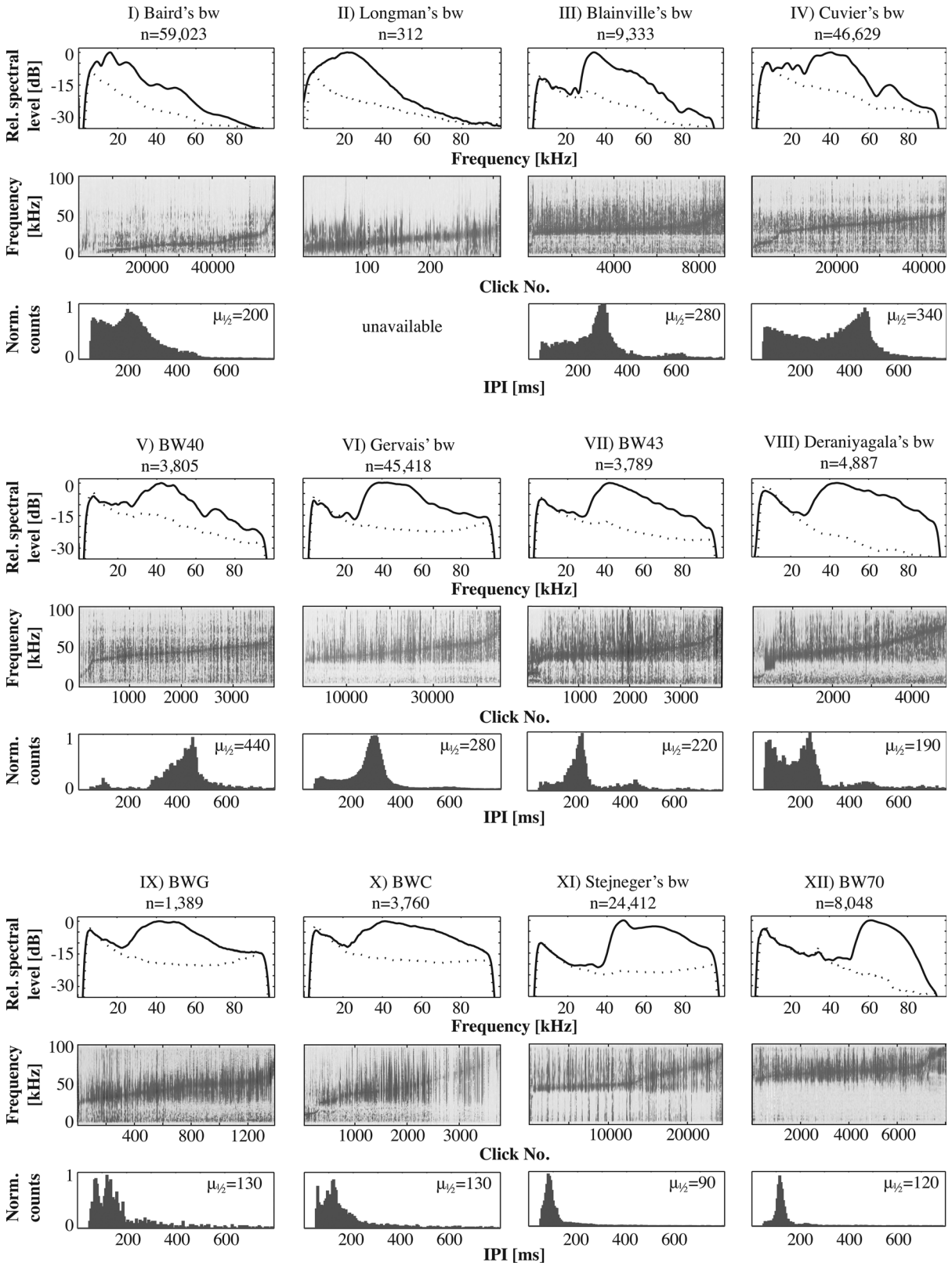

FIG. 5. Description of echolocations signals in all acoustic encounters per FM signal type of known (I–IV, VI, VIII, XI) and unknown origin (V, VII, IX, X, XII). Peak frequency has determined the order in which they are displayed. (top) Mean spectra (solid line) and mean noise preceding each signal (dashed line), (middle) concatenated spectrograms of all signals sorted by increasing peak frequency, and (bottom) histograms of inter-pulse interval (512-points DFT, Hann window, no overlap). bw = beaked whale. IPI = inter-pulse interval. n = number of signals. $\mu_{[1/2]}$ = median IPI.

best fit: $\mathrm{cf} = -3.9\mathrm{bl} + 62.8$, $R^2 = 0.6$; Pearson's linear correlation $\rho = -0.8$, $p = 0.03$; Fig. 7) with larger species producing lower frequency signals. However, this relationship was strongly driven by Baird's beaked whales, which have the largest body length and lowest center frequency. When removing this species from the analysis, the correlation was no longer significant ($\rho = -0.5$; $p = 0.2$).

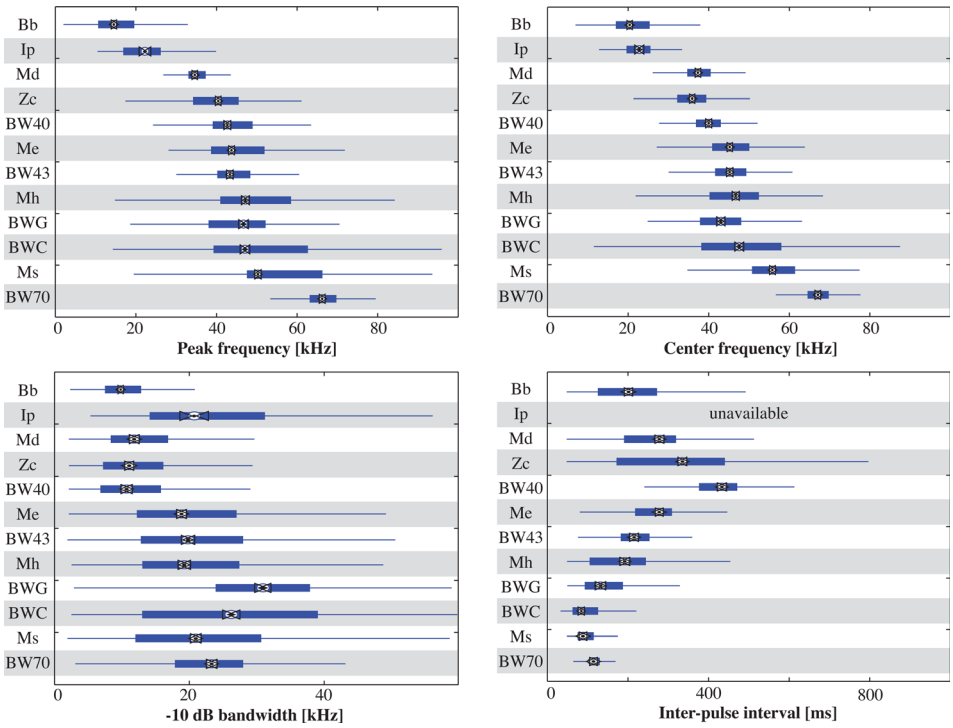

FIG. 6. (Color online) Comparative box plot showing parameter variability of peak and center frequency, −10 dB bandwidth, and inter-pulse interval for all FM pulse types. Baird's (Bb), Longman's (Ip), Blainville's (Md), Cuvier's (Zc), Gervais' (Me), Deraniyagala's (Mh), Stejneger's beaked whale (Ms), and unknown signal types BW40, BW43, BW70, BWG and BWC.

IV. DISCUSSION

The 12 FM pulse types characterized here all have upsweeps and are consistent in both the overall spectral composition of each signal type as well as the use of a preferred, stable IPI. These characteristics allow the pulses to be discriminated to a species or type. Each species of beaked whale known to produce FM pulses seems to be restricted to one species-specific FM pulse type [*Bb* (Dawson *et al.*, 1998), *Ip* (Rankin *et al.*, 2011), *Md* (Johnson *et al.*, 2004; Madsen *et al.*, 2005; Johnson *et al.*, 2006), *Zc* (Zimmer *et al.*, 2005), *Ha* (Wahlberg *et al.*, 2011), *Me* (Gillespie *et al.*, 2009), *Mh* (Baumann-Pickering *et al.*, 2010), *Ms* (Baumann-Pickering *et al.*, 2013a)], while some species additionally produce dolphin-like clicks in regular click trains [*Bb* (Dawson *et al.*, 1998) (Table II), *Ip* (Rankin *et al.*, 2011), BW40 and BWC (Table II)] or during the final approach phase in a prey capture attempt, called a buzz [e.g., *Md* (Johnson *et al.*, 2006), *Zc* (authors' unpublished data), *Mh* (Baumann-Pickering *et al.*, 2010), *Ha* (Wahlberg *et al.*, 2011), *Ip* (Rankin *et al.*, 2011)]. To date, there has not been any indication that a single species might produce multiple types of FM pulses. While this cannot be ruled out, current evidence would suggest that the FM pulse types with unknown origin (BW40, BW43, BW70, BWG, and BWC) are also species-specific and are each produced by a separate species.

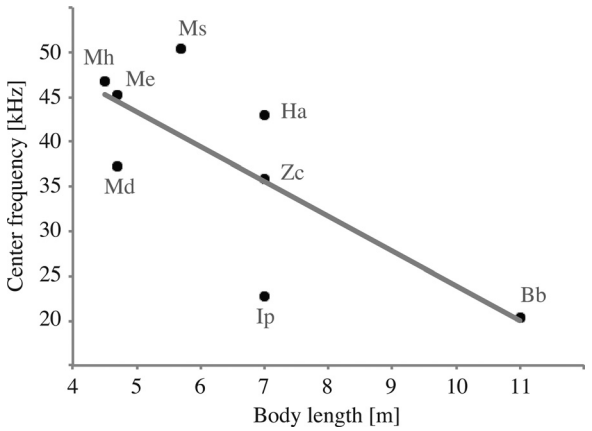

FIG. 7. Relationship of median center frequency (cf) and maximum body length (bl) of all beaked whale species with known signal type: Baird's (Bb), Longman's (Ip), Blainville's (Md), Cuvier's (Zc), Gervais' (Me), Deraniyagala's (Mh), Stejneger's beaked whale (Ms), and Northern bottlenose whale (Ha). Line of best fit (gray; cf = −3.9bl + 62.8, R^2 = 0.6; Pearson's linear correlation $\rho = -0.8$, $p = 0.03$).

Acoustic recordings in the presence of identified animals in the field are missing for Perrin's, Hubbs', pygmy, and ginkgo-toothed beaked whales in the Pacific as well as True's beaked whale in the Atlantic. The four unknown FM pulse types in the Pacific (BW40, BW43, BW70, and BWC) could correspond with the four Pacific beaked whale species with unknown acoustic signal properties. An analysis of the geographic distribution of these unknown signals with a comparison to the expected geographic range of known species based on sightings and strandings should provide further insight into which species produce which of the FM pulse types.

The BWG type is currently the only unknown FM pulse near the Atlantic, recorded on a regular basis at various locations in the Gulf of Mexico but without recording effort in the Atlantic. Despite a single stranding of Sowerby's beaked whale from Florida in the Gulf of Mexico, interpreted as an extralimital record, repeated acoustic encounters of this species in the Gulf of Mexico seem highly unlikely as it is well beyond their more northerly geographic range (Jefferson *et al.*, 2008). This would leave True's beaked whale as the only known candidate to produce the BWG signal in the Gulf of Mexico, near the Atlantic. However, True's beaked whales have never been sighted or stranded in the Gulf of

Mexico. Given that new species of beaked whale were found over the past decades this signal type might also be produced by a yet undescribed species or a known species may produce multiple signal types.

The species-specific differences that have been observed in FM echolocation pulses leads to a number of questions about the evolution of frequency-modulated echolocation calls in beaked whales.

There appears to be a weak relationship between center frequency and body length (Fig. 7) with larger animals producing lower frequency signals. A correlation exists between body size and sound producing organs for some invertebrate and many vertebrate species (e.g., insects, amphibians, deer, dogs, primates, bats, cetaceans, and to a lesser extent humans) (Davies and Halliday, 1978; Fitch and Hauser, 1995; Fitch, 1997; Riede and Fitch, 1999; Feng *et al*., 2002; Fitch and Hauser, 2002; Reby and McComb, 2003; González, 2004; Cocroft and Luca, 2006; Harris *et al*., 2006; May-Collado *et al*., 2007), which also relates to the frequency content of their acoustic signals. For bats it is presumed that larger prey are being caught by bigger species using echolocation signals with longer wavelengths (Feng *et al*., 2002). Aside from anatomical constraints on signal frequency, this argument is likely also true for beaked whale species, but quantitative data on prey preference exists only for a few species (MacLeod *et al*., 2003) and is insufficient to draw conclusions. Baird's beaked whales, the largest species, dominated the size-frequency relationship. Its sister species Arnoux's beaked whales in the southern hemisphere seem to have similar frequency characteristics (Rogers and Brown, 1999), however, with the current band-limited recordings and without having investigated the signals more closely, this cannot be determined without a doubt. There appeared to be no further significance when eliminating Baird's beaked whales from the analysis. There was large variation within species of similar size. Particularly Longman's beaked whale showed a much lower center frequency than other similarly sized beaked whales. This might be attributable to the use of maximum values for body length, which do not reflect variations in individuals, sex-specific difference in average body length, or the size of the monkey lips/dorsal bursae complexes (i.e., odontocete sound producing structures). This analysis also included species from five genera, which might have evolved differently. Furthermore, both acoustic and anatomical data are only available for a small number of species, so this relationship may still prove to be valid when considering all of these factors.

Additional sources of variability also might be explained by phylogeny or habitat and prey preference. Systematics and phylogeny of cetaceans is under continuous revision and identification of specific species call types is largely incomplete. Therefore, a judgment cannot be made yet on whether phylogenetic relationships have shaped echolocation signals.

BWC and BWG signal types are strikingly similar and could possibly be attributable to the occurrence of a single species spanning both oceans. However, the only species known to have a pantropical distribution are Cuvier's and Blainville's beaked whale. It is unlikely that either Cuvier's or Blainville's beaked whale produce this signal type in tropical waters given what is known of signal characteristics of these species. Alternatively, we may not be aware of the wide geographic range of another species. Another possibility is that two species of beaked whales in two separate oceans may produce a highly similar signal that has convergently evolved.

Evolutionary processes of niche separation for sympatric species may have driven some of the variability in species-specific beaked whale echolocation signals used for spatial orientation and foraging analogous to what is described for bats (Schnitzler *et al*., 2003), where bats inhabiting similar habitat use similar signal types. Bats use longer duration signals, longer IPIs, and less frequency modulation when flying in open space versus cluttered space along the edge or within vegetation. While little is known about the differences in habitat preference and foraging behavior for all of the beaked whale species, it would be enlightening to explore how habitat and prey may influence beaked whale signals. A few indicators for this influence might be given within the FM pulse parameters. Maximum prey size is likely driven by predator body size (MacLeod *et al*., 2003). Smaller species may tend to produce higher frequency signals, which are more suited to detect smaller prey items. Additionally, beaked whale species that echolocate with the highest frequency signals or a very broad bandwidth and likely low source levels (Urick, 1983), tend to use a higher repetition rate (Table II). The disadvantage of high frequency, low level, and broad bandwidth FM pulses is a shorter detection range. A higher repetition rate might compensate for this by providing more frequent updates on the immediate environment and nearby prey. Alternatively, higher repetition rates may indicate navigation and foraging closer to the seafloor, necessitating frequent updates.

Analysis of spatio-temporal distribution of all FM pulse types correlated with habitat and oceanographic variables should provide a better depiction of the habitat use for each species and the conditions that may drive prey abundance and beaked whale distribution.

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