Geographic differences in Blainville's beaked whale (*Mesoplodon densirostris*) echolocation clicks

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Blainville's beaked whale, Photo by Adam Ü

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Blainville's beaked whales have a cosmopolitan distribution from temperate to tropical waters. They have been previously known to produce species-specific FM pulses with a steep energy onset at around 25 kHz, a small energy peak at 22 kHz, a peak frequency of 30 to 34 kHz, and an inter-click interval of 280 ms. We have identified several FM signals at recording sites across the North Pacific and North Atlantic which have spectral shapes and temporal characteristics resembling Blainville's beaked whale FM pulses, and are not attributable to other known beaked whale species or signal types. Quantification of the variability in spectral shapes and inter-click intervals measured within and between encounters was achieved through weighted network clustering. Spectral averages obtained from the primary clusters identified at each site exhibited frequency shifts of up to 6 kHz relative to previously described Blainville's FM pulses, and occurred instead of the "usual" Blainville's beaked whale FM pulse type at any given site. We identified a latitudinal cline, with higher peak frequencies occurring in lower latitudes.
The observed variability may have several possible origins. Body size has been shown to influence signal frequency, with lower frequencies being produced by larger animals. In turn, larger animals tend to be found in higher latitudes for some species, but this has not been investigated in beaked whales. Furthermore, prey size may shape the frequency content of echolocation signals and larger prey items may occur in higher latitudes, resulting in lower echolocation

frequencies of their predators. The observed differences in echolocation signal frequency may be a first indication of acoustic delineation between population-level boundaries of Blainville's beaked whales that have not been identified previously.

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Table of Contents

Executive Summary

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Introduction

Mass strandings of Blainville's beaked whales (*Mesoplodon densirostris*) have been linked to concurrent naval exercises and the use of mid-frequency active sonar (Cox *et al.*, 2006). Management and mitigation efforts to protect this species need foremost reliable population status information and substantial knowledge of its life history and behavior. Our project objectives were a) to improve our understanding of Blainville's beaked whale geographic distribution and b) to quantify acoustic differences in the echolocation signals emitted by this species as a potential tool for population-level discrimination of individuals within this species.

Blainville's beaked whales are identified as "Data Deficient" in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Taylor *et al.*, 2008). However, under the Endangered Species Act (1973), they are neither recorded as "threatened" nor "endangered" and they are not considered "depleted" under the Marine Mammal Protection Act. US stock assessments consider three stocks: the Hawaiian, northern Gulf of Mexico, and western North Atlantic stocks (Carretta *et al.*, 2018; Hayes *et al.*, 2018). These stock assessments have only limited information on animals in offshore regions or remote naval use areas such as the Northern Marianas Islands.

Blainville's beaked whales (Md) are generally distributed in deep waters >500 m of temperate to tropical oceans worldwide (Jefferson *et al.*, 2008). They undergo foraging dives into the meso- and bathypelagic (Arranz *et al.*, 2011) to prey on both fish and cephalopods (Santos *et al.*, 2007). During these foraging dives they produce frequency-modulated (FM) echolocation pulses while searching for prey and buzz clicks when capturing a target (Johnson *et al.*, 2006). The signal parameters for these Md FM pulses have been described as species-specific (Baumann-Pickering *et al.*, 2013), with a steep energy onset at around 25 kHz, a small energy peak at 22 kHz, a peak frequency of 30 to 34 kHz, and an inter-click interval (ICI) of 280 ms. Recordings collected at a seamount near the equator in the central Pacific, which was suitable habitat for Blainville's beaked whales, did not have any detections of the Md FM pulse type (Baumann-Pickering *et al.*, 2016). Instead, a similar looking signal type that was shifted by about 5 kHz to higher frequencies dominated and was hence termed BW38. Similarly, along the US Atlantic coast, a BW38 signal type was identified at a site termed Onslow Bay (Stanistreet *et al.*, 2017).

In this project, we hypothesize that Blainville's beaked whales produce both the Md FM pulse type as well as the BW38 pulse type, and that geographic and possible population-level differences are the underlying driver for these differences. We investigate this hypothesis through analysis of long-term passive acoustic monitoring data collected throughout the North Pacific, along the US Atlantic coast, and in the Gulf of Mexico, many of these sites located within areas of naval interest.

Material and methods

Site description and instrumentation

Passive acoustic recordings were obtained with High-frequency Acoustic Recording Packages (HARPs) at 68 sites in the North Pacific (Figure 1, Table S1). HARPs are autonomous instruments, developed to continuously record marine acoustics from 10 Hz to 100 kHz over extended periods of up to one year (Wiggins and Hildebrand, 2007). During some deployments, a recording duty cycle was set with five minutes of recordings every 7 to 45 minutes, depending on data storage and battery capacity. HARPs were configured in a variety of small to large moorings or sea-floor package configurations. At the majority of sites, where depths ranged from 250 to 1400 m (Table S1), the hydrophone was located within 30 m of the seafloor. At five deeper sites, the hydrophone was placed near 800 to 1200 m depth, with a seafloor depth between 3600 and 4400 m (Table S1). Each hydrophone's electronic circuit board was calibrated in the laboratory, and representative data loggers with complete hydrophones were full-system calibrated at the U.S. Navy's Transducer Evaluation Center in San Diego, CA to provide the full-band frequency response of the instrument.

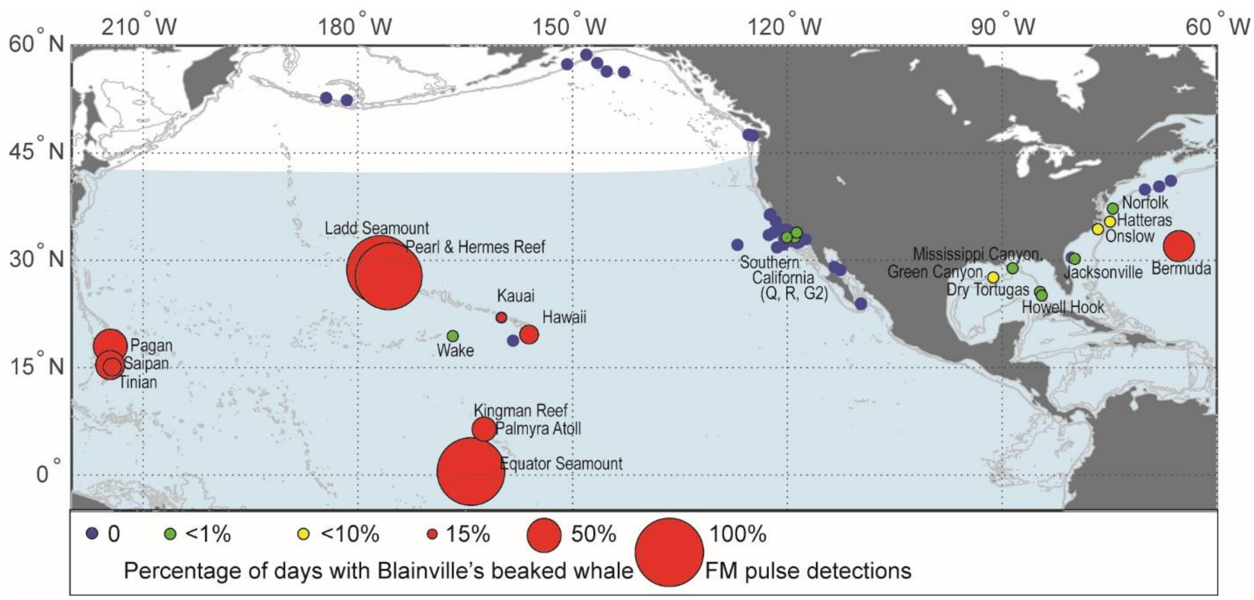

Figure 1. *Deployment location of HARPs (circles) in the Northern Hemisphere. Sites were marked in varying colors and sizes dependent on percentage of days with Blainville's beaked whale acoustic detections. Light blue background shading indicates known range of this species based on the IUCN Red List map (Taylor et al., 2008).*

Sites were grouped at multiple scales for regional analysis. We defined 6 broad geographic regions including (1) Eastern North Pacific (including 42 sites, ranging from the Aleutian Islands, along the west coast of North America, and into the Gulf of California, with most sites located in the Southern California Bight); (2) Hawaiian Islands (3 sites near the Main Hawaiian Island, 2 sites near the Northwestern Hawaiian Islands, and the Pacific Remote Island, Wake Atoll); (3) Northern Line Islands (4 sites located at Kingman Reef, Palmyra Atoll, and a seamount site near the equator); (4) Northern Mariana Islands (3 sites at Pagan, Saipan, and Tinian); (5) Western Atlantic (8 sites along the shelf break from Heezen Canyon to Jacksonville, and 1 site near Bermuda), and (6) Gulf of Mexico (4 sites, ranging from Green Canyon to Dry

Tortugas). The median (quartiles) recording effort across all sites was 413 (197 – 824) days, ranging from as little as 18 days up to 2713 days (over 7 cumulative years) at a single site.

Automated beaked whale detections and site comparisons

Signal processing was performed using the MATLAB (Mathworks, Natick, MA) based custom software program *Triton* (Wiggins and Hildebrand, 2007) and other MATLAB custom routines. A Teager-Kaiser energy click detector (Soldevilla *et al.*, 2008; Roch *et al.*, 2011) in Triton was run over all recorded data, and spectral and temporal signal parameters were computed for all detected clicks regardless of beam angle. A decision about presence or absence of beaked whale signals was based on detections within 75 second segments. Only segments with more than seven detections were used in further analysis. All echolocation signals with a peak and center frequency below 32 and 25 kHz, respectively, a duration less than 355 μs, and a sweep rate of less than 23 kHz/ms did not resemble beaked whale FM pulses and were therefore deleted. If more than 13% of all initially detected echolocation signals remained after applying these criteria, the segment was classified as containing beaked whale FM pulses. This threshold was chosen to obtain the best balance between missed and false detections. A third classification step, based on computer-assisted manual decisions by a trained analyst, labeled the automatically detected segments to beaked whale species or pulse type and rejected false detections (Baumann-Pickering *et al.*, 2013). The rate of missed segments was tested during detector development and was not verified for this analysis effort. It ranges approximately between 5 and 10%, depending on site conditions, mostly missing low amplitude and short duration acoustic encounters. The start and end of each segment containing beaked whale signals was logged.

For a comparison of beaked whale species presence across sites, we computed cumulative minutes with acoustic detections per site and the percentage that each species contributed towards these detections. We calculated the percentage of days with any beaked whale detection at each site and the percentage of days with detections for each species and site.

Blainville's beaked whale (Md) signal clustering

An unsupervised learning strategy (details in Frasier *et al.*, 2017) was applied to document within and across site variability of the Md FM pulse type and to eliminate false detections. Spectral shape (1 kHz bin width from 10 to 90 kHz) and inter-click interval (ICI) distribution were used for clustering. Broadly, a two-phase method grouped in *Phase 1* spectrally-similar signals within 5-minute bins and identified a mean spectrum and modal ICI for each cluster formed within successive 5-minute time windows (bins) (Figure 2, left). *Phase 2* grouped similar signal types based on the mean spectra and modal ICIs from Phase 1 within a deployment or site (Figure 2, right).

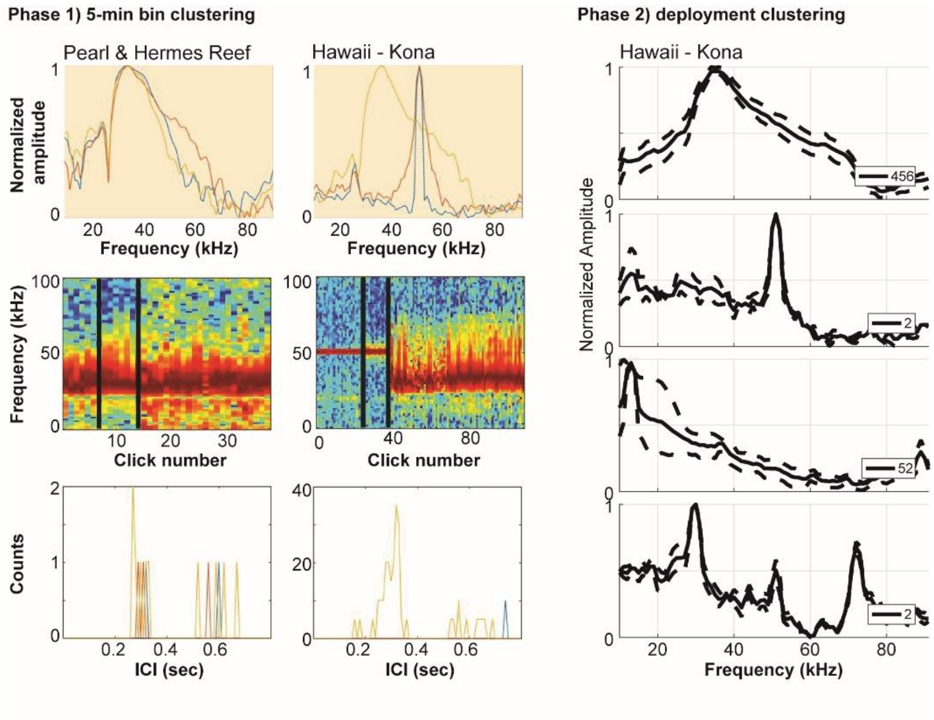

Figure 2. *Examples for clustering phases 1 (5-min bin, click-based, left) and 2 (spectral average- and ICI mode-based, right). Phase 1 at Pearl and Hermes Reef: 3 Blainville's beaked whale (Md) FM pulse spectral averages (top), concatenated spectra of all FM pulses in these averages (middle) and corresponding ICI distribution (bottom); Hawaii-Kona: 2 clusters of echosounders and one cluster of FM pulses. Phase 2 (Hawaii, 1 deployment): most 5-min bin spectral averages and ICI modes were clustered within the Md FM pulse type while several different echosounder categories occurred as well (additional not shown).*

The initial detector output from Md acoustic encounters was not screened for false click detections. A first round of broad category clustering was applied to group and eliminate false detections. For *Phase 1* computation, spectra of all detections were truncated at 10 and 90 kHz and normalized [0, 1]. A similarity metric was computed (Frasier *et al.*, 2017) between pairs of spectra resulting in a matrix of [0, 1] edge weights. Values closer to 1 identified similar normalized spectra. A network was established for each 5-min bin that contained detections as nodes and edge weights as connections. Weak edges were pruned (edge pruning threshold, p_e = 0.5) to reduce computational time and to facilitate improved identification of distinct clusters. Clusters of similar nodes were defined through the CW clustering algorithm (Biemann, 2006), using a maximum of 15 assignment iterations for each 5-min bin. Mean spectra were computed for all resulting clusters. ICIs were calculated for sequential clicks (Au, 1993) within each cluster and sorted in 10 ms bins up to 800 ms. An ICI mode was associated with each cluster and stored as "summary nodes" together with the spectral information for input into *Phase 2*.

In *Phase 2*, recurrent mean spectra were identified as clusters across all 5-min bins of an instrument deployment period. Spectral similarities were again computed as in *Phase 1*. Euclidean distance between modal ICIs was calculated to determine ICI distance values and converted into a similarity metric (Frasier *et al.*, 2017). These two similarity scores were then combined and subsequently used in the CW clustering algorithm, allowing for 25 iterations with a pruning threshold of p_e = 0.5 and at least 5 nodes remaining in each resulting cluster. The normalized mutual information (NMI) criterion was used to assess which of the iterations had the best cluster consistency on a [0,1] scale (Fred and Jain, 2005). The highest average NMI value across all comparisons was chosen as the final output. Two trained analysists (SBP, JST) visually evaluated the clusters per instrument deployment. Detections in clusters containing non-beaked whale type signals were eliminated. This resulted in data from several instrument deployments to be removed due to a lack of sufficient numbers of beaked whale type clicks (Table S1 and S3: Palmyra NS 10, Hawaii 09, Howell Hook 05, Wake Atoll 03, 05, 06).

This process was repeated with the remaining signals, although with slight adjustments of the clustering parameters to allow for a finer differentiation of true beaked whale type signals. In the *Phase 1* process of grouping original detections based on their spectral similarities, a cluster within a 5-min bin needed to contain at least 5 signals. The pruning threshold was set to p_e = 0.95. Resulting 5-min bin mean spectra and ICI values per cluster were collected across all data within each site. During *Phase 2* per site network analysis in which clustering operated at the bin level, a cluster had to include at least 2 bins and the pruning threshold was set to p_e = 0.7. The resulting clusters were again manually screened and a few remaining clusters with noise were removed.

For final site comparison, the primary cluster containing most bins per site was selected. Median and 10th and 90th percentiles of peak frequency, center frequency, and ICI mode were extracted from all bins of each primary cluster to compare across sites. A linear regression of site latitude and median peak frequency was calculated.

Results

Blainville's beaked whale (Md) FM pulse type was found at 23 of 68 sites with recording effort (Tables 1, S1 and S2). In some regions it was present only very infrequently (e.g., Southern California or Gulf of Mexico), while in others it was detected nearly daily (e.g., Northwestern Hawaiian Islands) (Figures 1 and 3). Pelagic, island-associated sites had the highest percentage of days with detections. Occurrences were relatively infrequent along continental shelf breaks. Md signals dominated over other beaked whale type signals at all island sites except Wake Atoll, where Cuvier's beaked whale signals dominated, and Kingman Reef and Palmyra Atoll, which where Deraniyagala's beaked whale signals were more common (Figure 3, Tables 1 and S2).

Overall, there were close to 1,135 cumulative hours of recordings with Md signals across all sites. However, there was uneven effort and uneven acoustic density at these sites, resulting in Pearl and Hermes Reef, for example, having 32,845 minutes (~860,000 FM signals) and Howell Hook having only 9 minutes (29 FM signals) with reliable Md detections (Tables 2 and S3). Sites were grouped into those with regular presence of Md (Figure 1, >1% of recording days; 13 sites) and those with only transient occurrence (Figure 1, 10 sites, two of which had too few signals for further analysis).

***Table 1**. Regions and sites with acoustic detections of Blainville's beaked whales (Md: Mesplodon densirostris). For comparison, values are in percentage of days with detections of any beaked whale species (All bw) as well as each individual signal type. Mb: M. bidens; Me: M. europaeus; Mh: M. hotaula; Zc: Ziphius cavirostris; BW43: possibly M. perrini; BW70: possibly M. peruvianus; BWC: possibly M. ginkgodens; BWG: unknown origin (Baumann-Pickering et al., 2013; Baumann-Pickering et al., 2014).*

Region	**Site**	**Recording Days**	**All bw**	**Mb**	**Md**	**Me**	**Mh**	**Zc**	**BW43**	**BW70**	**BWC**	**BWG**
Eastern North Pacific	Southern California G2	211	38		**<1**			36	2			
Eastern North Pacific	Southern California Q	263	<1		**<1**					<1		
Eastern North Pacific	Southern California R	483	83		**<1**			83				
Northwest Hawaiian Islands	Ladd Seamount D	89	100		**99**			67			13	
Northwest Hawaiian Islands	Pearl and Hermes Reef	1363	98		**97**			55			9	
Main Hawaiian Islands	Kauai	319	24		**14**						13	
Main Hawaiian Islands	Hawaii Kona	2078	33		**27**			3			7	
Pacific Remote Islands	Wake Atoll	1371	55		**<1**			54			2	
Northern Line Islands	Kingman Reef	123	100		**35**		100	33			15	
Northern Line Islands	Palmyra NS	333	82		**<1**		82	<1			<1	
Northern Line Islands	Equator Seamount	103	98		**98**			82			9	
Northern Mariana Islands	Pagan	687	62		**49**			13			12	
Northern Mariana Islands	Saipan	1753	64		**42**			30			12	
Northern Mariana Islands	Tinian	1555	30		**26**			<1			5	
Western Atlantic	Norfolk Canyon	714	48	29	**<1**	16		16				
Western Atlantic	Hatteras	1275	98		**1**	44		95				
Western Atlantic	Onslow Bay	433	97		**6**	97		6				
Western Atlantic	Bermuda	690	49		**45**			10				
Western Atlantic	Jacksonville D	829	2		**<1**	<1		<1				
Gulf of Mexico	Mississippi Canyon	2080	39		**<1**	28		11				8
Gulf of Mexico	Green Canyon	2098	46		**2**	35		10				5
Gulf of Mexico	Dry Tortugas	1763	96		**<1**	72		88				2
Gulf of Mexico	Howell Hook	822	95		**<1**	70		88				1
	Total days	**21,435**										
	Total years	**59**										

Table 2. *Final dominant cluster results for Blainville's beaked whales (Md: Mesoplodon densirostris) at each site, showing varying data size per site in the analysis and the resulting peak and center frequencies as well as inter-click interval (ICI) – median and 10th to 90th percentile – of FM pulses within each site-specific dominant cluster.*

Region	Site	Md acoustic encounters (min)	Count of 5-min bins	Count of FM pulses	Peak frequency (kHz)	Center frequency (kHz)	ICI (ms)
Eastern North Pacific	Southern California G2	1	--	--	--	--	--
Eastern North Pacific	Southern California Q	9	4	116	34.5 (32-38)	50.1 (50.0-50.3)	365(303-601)
Eastern North Pacific	Southern California R	9	3	17	40 (37-40)	50.2 (49.9-50.4)	345 (310-370)
Northwest Hawaiian Islands	Ladd Seamount D	5,294	1,867	161,484	34 (32-36)	49.6 (49.4-49.9)	320 (270-570)
Northwest Hawaiian Islands	Pearl and Hermes Reef	32,845	11,560	863,256	35 (33-37)	49.7 (49.1-49.9)	320 (260-600)
Main Hawaiian Islands	Kauai	184	52	2,706	35 (34-37.3)	49.7 (49.4-50.0)	320 (280-616)
Main Hawaiian Islands	Hawaii Kona	8,117	1,981	186,377	36 (34-38)	49.9 (49.6-50.2)	310 (240-590)
Pacific Remote Islands	Wake Atoll	21	5	816	34 (34-37)	49.6 (49.5-49.8)	315 (231-574)
Northern Line Islands	Kingman Reef	333	122	3,664	39 (35-41)	49.8 (49.6-50.1)	320 (240-630)
Northern Line Islands	Palmyra NS	5	--	--	--	--	--
Northern Line Islands	Equator Seamount	5,371	1,499	96,628	39 (37-41)	50.2 (50.0-50.6)	340 (310-630)
Northern Mariana Islands	Pagan	2,119	723	29,029	35 (33-37)	49.7 (49.5-49.9)	310 (210-564)
Northern Mariana Islands	Saipan	4,660	1,998	80,067	36 (34-38)	49.7 (49.5-50.0)	300 (200-570)
Northern Mariana Islands	Tinian	5,553	2,328	268,669	36 (34-38)	49.7 (49.5-50.0)	310 (270-570)
Western Atlantic	Norfolk Canyon	13	4	157	33 (32-36)	50.0 (50.0-50.1)	310 (230-480)
Western Atlantic	Hatteras	115	43	2,400	32 (23-36.2)	49.4 (49.1-49.8)	300 (128-615)
Western Atlantic	Onslow Bay	230	62	8,009	33 (31-36)	49.5 (49.4-49.7)	330 (230-515)
Western Atlantic	Bermuda	2,552	1,015	26,643	33 (29-38)	49.8 (49.6-50.0)	360 (180-620)
Western Atlantic	Jacksonville D	39	207	25,369	35.5 (33-37.5)	49.7 (49.7-49.9)	330 (244-694)
Gulf of Mexico	Mississippi Canyon	31	12	416	33 (30.7-33)	49.4 (49.5-49.8)	350 (317-689)
Gulf of Mexico	Green Canyon	571	157	17,319	34 (31-35)	49.6 (49.4-49.9)	330 (290-630)
Gulf of Mexico	Dry Tortugas	13	4	78	37 (30-38)	50.1 (50.0-50.4)	390 (314-770)
Gulf of Mexico	Howell Hook	9	3	29	37 (36-37)	49.5 (49.5-49.8)	320 (293-612)

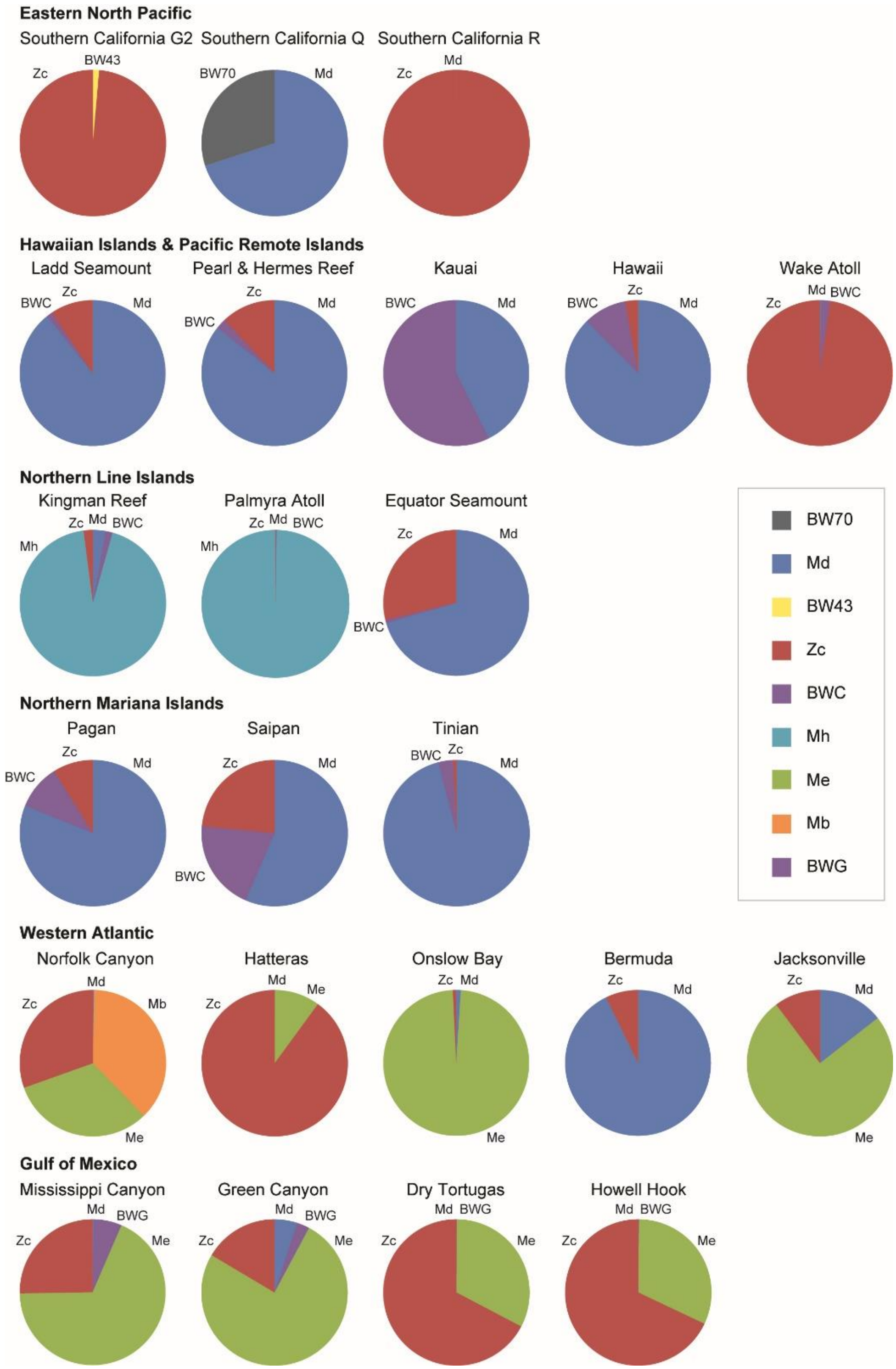

Figure 3. *Relative presence of all beaked whale species at sites with Md pulse type detections based on cumulative minutes of acoustic encounters.*

When comparing spectral averages across sites, a range of peak frequencies from 32 to 39 kHz was noted, with a corresponding signal energy onset ranging from 21 to 31 kHz (Figure 4, Table 2). A smaller spectral peak was characteristic at about 2-3 kHz below the main energy onset. This variation in peak frequency had a negative linear relationship with geographic latitude (Figure 5, top), with higher peak frequencies occurring at lower latitudes, when calculating with median values from sites with regular presence of Md.

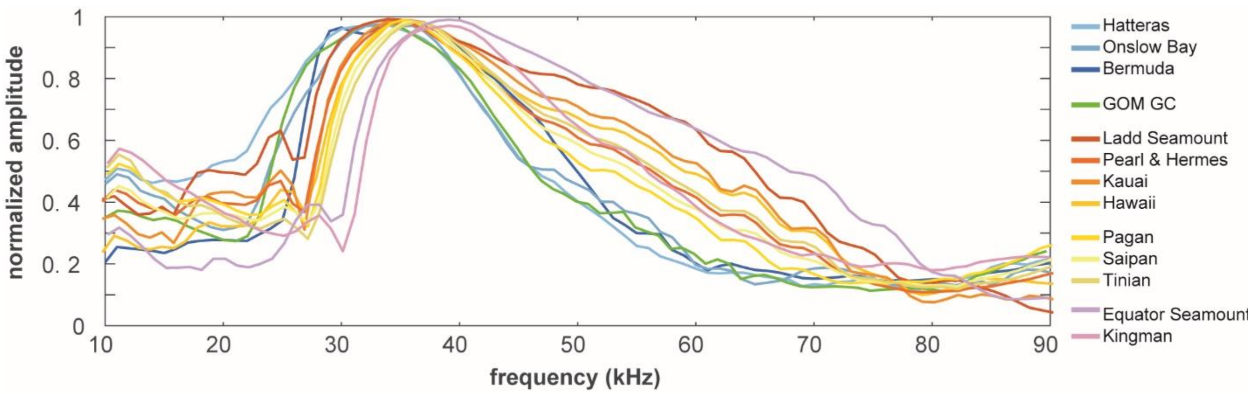

Figure 4. *Spectral averages of primary cluster at sites with regularly occurring Md pulse type detections.*

Discussion

Blainville's beaked whale was one of the first beaked whale species to receive an echolocation FM pulse description (Johnson *et al.*, 2004), and their acoustic behavior has since been reported on in a number of subsequent publications (e.g., Johnson *et al.*, 2006; Arranz *et al.*, 2011; Madsen *et al.*, 2013; Dunn *et al.*, 2017). However, the potential for variation in the echolocation click spectra of Blainville's beaked whale was first documented at an equatorial Pacific seamount site (Baumann-Pickering *et al.*, 2016). The dominant beaked whale signal type recorded during this deployment was labeled BW38, as it resembled Blainville's beaked whale FM pulses but the peak frequency was shifted upward to 38 kHz from an expected 34 kHz. Building on this initial observation, the present study documents for the first time the intra-specific variation in Blainville's beaked whale echolocation signals across geographic regions, including ocean basin differences.

The use of passive acoustic monitoring to examine odontocete ecology relies on the assumption that some animals produce echolocation clicks with consistent features that are identifiable to species. For beaked whales in particular, the spectral and temporal characteristics of their echolocation signals have been thought to be not only species-specific but also stable across wide-ranging spatial scales (Baumann-Pickering *et al.*, 2014). However, Risso's dolphin has recently been found to exhibit geographic variation in its echolocation click spectra (Soldevilla *et al.*, 2017), and a latitudinal cline in frequencies was also noted. Likewise, the geographic differences in Blainville's beaked whale echolocation parameters described here suggest that global populations of this species are also acoustically distinct. Building on this assumption, one might be able to infer spatial connectivity within an ocean basin. Sites with irregular occurrence of Md FM pulses, such as those documented in southern California, Wake Atoll in the central Pacific, or Howell Hook in the Gulf of Mexico, might be a model for this concept. Southern California site R had detections with a median peak frequency that would place the origin of the individuals in an equatorial region, while values recorded at southern California site Q were more similar to those from the Hawaiian Islands. Wake Atoll, directly south of the Hawaiian Islands, had signals most closely resembling those from the Northwestern Hawaiian Islands. FM pulses recorded at Howell Hook had signatures that would potentially place the whales' origin to the southern Caribbean region. In fact, Stanistreet *et al.* (2017) reported detections of both the Md and BW38 signal types at Onslow Bay. A future study may want to inspect sites with large variability (e.g., most of the Western Atlantic) to determine whether some of the more extreme values should possibly be treated as being produced by transiting individuals or groups, rather than members of a resident population within that region.

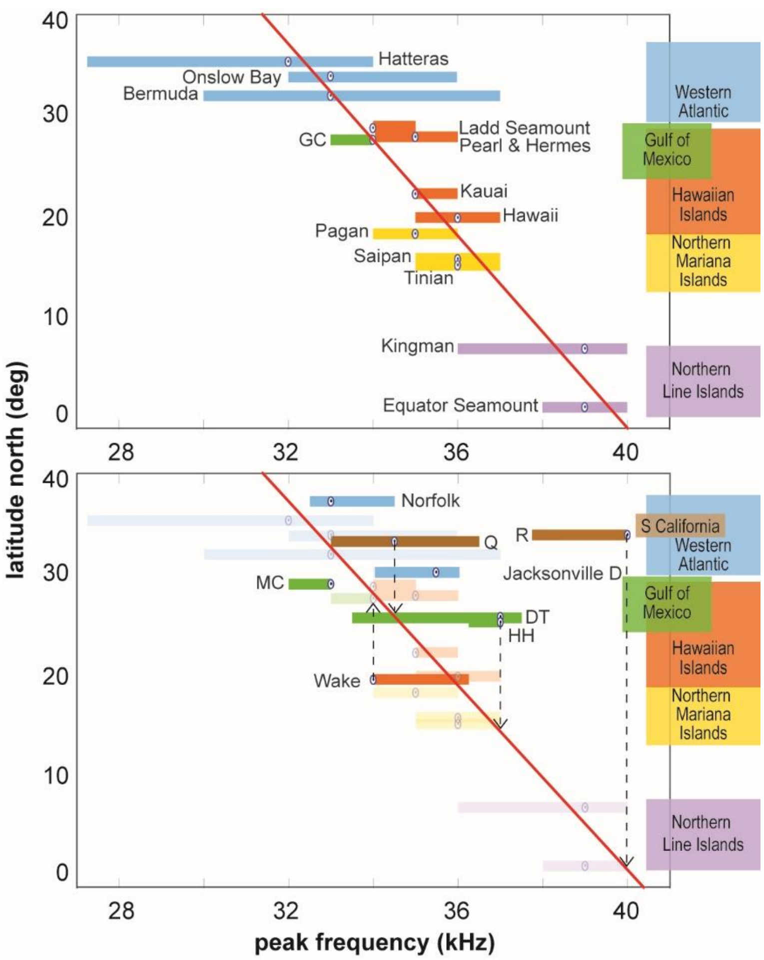

Figure 5. *Increasing peak frequency (median with 25th and 75th percentiles) with lower latitudes (red regression line; $y = -4.8x + 191.7$, $R^2 = 0.93$) at sites with regular Blainville's beaked whale presence (top). Sites with low numbers of detections (<1% of recorded days) may indicate transient whales from other regions (arrows, bottom).*

Blainville's beaked whale is a cosmopolitan species, found in all oceans except the Arctic, and it has the broadest and most diverse distribution of any species in the genus *Mesoplodon* (Jefferson et al. 2008). However, as is the case for all mesoplodonts this species is classified as "Data Deficient" under the IUCN Red List (Taylor *et al.*, 2008), and thus many aspects of its natural history remain poorly understood. Knowledge of population-level differences within this relatively rare cetacean is scarce. Relatively few samples are available for an extensive investigation of genetic diversity and population structure on a molecular level for any of the beaked whales, but there is evidence of limited gene flow within ocean basins for the few species in which this has been studied (Dalebout *et al.*, 2005; Dalebout *et al.*, 2007; Morin *et al.*, 2017). Due to the lack of global phylogeographic information on Blainville's beaked whales, it remains unknown whether the observed acoustic variability has a genetic basis.

It is possible that the spectral characteristics of an acoustic signal are correlated with body size, in that larger animals may produce clicks with lower frequency content (Baumann-Pickering et al. 2013). Moreover, body size might be influenced by latitude, with larger animals found in the higher latitudes (Bergmann, 1847). However, this has not been tested in beaked whales. Due to the relatively low number of Blainville's beaked whale strandings worldwide, it might not be possible to determine whether a latitudinal relationship exists between morphology and acoustic signal parameters.

Alternatively, this acoustic variability may be related to geographic differences in prey size. If prey size shapes the frequency content of the echolocation signals of these predators, then the tendency towards lower peak frequencies in the higher latitudes could potentially be traced to larger prey items occurring there. However, little is known of the diet of Blainville's beaked whales, and much of the current knowledge on their foraging habits has been derived from stomach content analyses of stranded individuals (MacLeod *et al.*, 2003; Santos *et al.*, 2007).

All Md acoustic detections in this study occur within the known range of this species based on the IUCN Red List map (Taylor *et al.*, 2008), which has primarily been inferred from stranding records. Baumann-Pickering *et al.* (2014) reported the acoustic presence of Blainville's beaked whale off the coast of Washington but this single detection was later determined to be a misclassification of a Cuvier's beaked whale encounter and hence is not included in our study. Overall, these findings provide insight into the geographic distribution of a rarely observed species, and also suggest that the characterization of spectral structure in Blainville's beaked whale echolocation signals can potentially be used to investigate population structure.

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Appendix

Table S1*. Overview of data in analysis; number of instrument deployments at each site (Count Depl.), location and depth, recording duty cycle (varying at some sites), start and end of effort, cumulative recording days in that time period and whether any beaked whale (bw) or Blainville's beaked whale specifically (MD) was acoustically detected at that site.*

Region	Site	Count Depl.	Latitude	Longitude	Depth (m)	Cycle Interval (min)	Recording Duration (min)	Start Date	End Date	Recording Days	Bw Presence
Eastern North Pacific	Aleutian Islands Kiska	1	52-19.007 N	178-31.240E	1100	0	0	6/3/10	7/20/10	47	bw
Eastern North Pacific	Aleutian Islands Buldir	1	52-38.000 N	175-37.990E	800	0	0	11/7/10	5/26/11	200	bw
Eastern North Pacific	Gulf of Alaska AB	1	57-30.820 N	146-30.050W	4400 (1200)	0	0	4/29/17	9/14/17	138	bw
Eastern North Pacific	Gulf of Alaska CB	8	58-40.28 N	148-01.25 W	900	12	10	7/13/11	9/12/17	1500	bw
Eastern North Pacific	Gulf of Alaska KO	1	57-20.179 N	150-41.749W	250	0	0	6/9/13	6/27/13	18	--
Eastern North Pacific	Gulf of Alaska PT	4	56-14.607 N	142-45.439W	1000	0	0	9/9/12	9/10/14	676	bw
Eastern North Pacific	Gulf of Alaska QN	5	56-20.341 N	145-11.183W	900	0	0	6/10/13	9/14/17	789	bw
Eastern North Pacific	Olympic Coast CE	1	47-21.141 N	124-43.275W	150	0	0	12/7/11	1/17/12	41	--
Eastern North Pacific	Olympic Coast QC A	2	47-27.960 N	125-09.195W	650	35	5	7/3/07	10/3/11	597	bw
Eastern North Pacific	Olympic Coast QC B	3	47-30.026 N	125-21.212W	1400	0	0	12/7/11	4/3/14	766	bw
Eastern North Pacific	CA Diablo Canyon C	1	35-24.000 N	121-33.750W	1000	0	0	11/7/12	3/19/13	132	bw
Eastern North Pacific	California Point Sur A	1	36-23.472 N	122-18.419W	850	10	5	6/21/11	4/7/12	291	bw
Eastern North Pacific	California Point Sur B	1	36-17.945 N	122-23.633W	1400	5	5	11/30/11	6/24/12	207	bw
Eastern North Pacific	Southern California A	5	33-15.127 N	118-15.044W	350	0	0	8/13/05	12/15/07	254	--
Eastern North Pacific	Southern California A2	9	33-13.812 N	118-16.442W	1150	0	0	2/9/08	7/5/08	416	bw
Eastern North Pacific	Southern California B	11	34-16.584 N	120-01.512W	600	7	5	4/17/08	7/9/11	841	--
Eastern North Pacific	Southern California C	9	34-18.477 N	120-47.796W	800	0	0	7/12/07	3/2/11	707	--
Eastern North Pacific	Southern California CB	2	33-13.000 N	118-36.000W	1200	0	0	7/20/16	8/2/16	26	bw
Eastern North Pacific	Southern CA CCE1	3	33-28.600 N	122-32.000W	4000 (800)	35	5	11/3/08	11/8/17	626	bw
Eastern North Pacific	Southern CA CORC1	2	32-08.700 N	120-30.110W	3850 (950)	45/10	5	12/19/09	4/7/13	663	bw
Eastern North Pacific	Southern CA CORC4	2	31-44.82 N	121-22.68 W	3900 (950)	30	15	5/1/14	12/4/15	582	bw
Eastern North Pacific	Southern California D	18	33-50.253 N	121-51.269W	3650 (1000)	15	5	7/24/07	10/15/07	83	bw
Eastern North Pacific	Southern California E	10	32-39.409 N	119-28.419W	1300	20/0	5/0	9/3/06	7/10/17	802	bw
Eastern North Pacific	Southern California G	4	31-55.609 N	32-55.619 W	450	15	5	7/23/07	7/28/08	277	--
Eastern North Pacific	Southern California G2	4	33-08.407 N	118-52.815W	1100	0	0	1/13/09	11/16/09	211	MD
Eastern North Pacific	Southern California H	29	32.50-8.13 N	119-10.6 W	1000	0	0	7/24/07	6/6/17	2713	bw
Eastern North Pacific	Southern CA Hoke	1	32-06.370 N	126-54.580W	800	35	5	9/15/08	6/6/09	264	bw
Eastern North Pacific	Southern California J	6	34-08.405 N	119-59.316W	250	7	5	6/6/08	10/23/09	317	--
Eastern North Pacific	Southern California K	3	33-50.207 N	120-07.270W	300	7	5	7/24/08	2/24/09	207	--
Eastern North Pacific	Southern California K3	2	33-54.776 N	119-33.810W	1000	0	0	8/1/09	11/11/09	79	bw
Eastern North Pacific	Southern California M	20	33-30.582 N	119-15.282W	900	0	0	1/13/09	2/5/15	1857	bw
Eastern North Pacific	Southern California N	27	32-22.204 N	118-33.908W	1350	0	0	1/14/09	6/7/17	2496	bw

Eastern North Pacific	Southern California P	12	32-53.598 N	117-22.714W	500	0	0	9/24/09	5/24/17	899	bw
Eastern North Pacific	Southern California Q	4	33-49.222 N	118-37.775W	700	0	0	9/24/09	7/21/10	263	MD
Eastern North Pacific	Southern California R	6	33-09.596 N	120-00.580W	1200	0	0	9/25/09	4/10/11	483	MD
Eastern North Pacific	Southern California S	6	32-29.095 N	118-16.407W	1400	0	0	9/26/09	5/1/11	410	bw
Eastern North Pacific	Southern California SN	5	32-54.913 N	120-22.544W	1100	35/0	5/0	5/19/09	1/7/17	905	bw
Eastern North Pacific	Southern California T	2	32-53.21 N	117-33.37 W	850	0	0	8/18/16	12/15/16	160	bw
Eastern North Pacific	Gulf of California PP A	2	23-49.830 N	109-37.870W	650	40/25	5	3/10/04	9/30/05	384	--
Eastern North Pacific	Gulf of California PP B	3	23-55.410 N	109-39.970W	800	30/0	5/0	11/27/05	2/7/06	162	bw
Eastern North Pacific	Gulf of California BLA	1	29-01.619 N	113-22.557W	700	20	5	8/8/08	12/25/08	139	bw
Eastern North Pacific	Gulf of California T	1	28-36.440 N	112-30.309W	400	20	5	6/21/07	12/7/07	169	bw
NW. Hawaiian Islands	Ladd Seamount D	1	28-37.647 N	176-43.678W	1100	10	5	5/18/09	8/15/09	89	MD
NW. Hawaiian Islands	Pearl and Hermes Reef	7	27-43.517 N	175-38.287W	750	30/20/8/7/0	5/0	10/20/09	3/14/17	1363	MD
Main Hawaiian Islands	Kauai	2	21-57.164 N	159-53.238W	700	20/0	5/0	10/8/09	9/14/10	319	MD
Main Hawaiian Islands	Hawaii Kona	22	19-34.890 N	156-00.912W	650	25/15/12/10/8/0	5/0	8/11/07	10/25/17	2078	MD
Pacific Remote Islands	Wake Atoll	6	19-21.667 N	166-41.0 W	800	30/10/6	5	1/31/10	12/16/16	1371	MD
Main Hawaiian Islands	Cross Seamount	2	18-43.325 N	158-15.230W	400	25	5	4/26/05	5/11/06	357	bw
Northern Line Islands	Kingman Reef	1	06-21.908 N	162-17.539W	850	0	0	11/10/11	3/11/12	123	MD
Northern Line Islands	Palmyra NS	4	05-54.252 N	162-02.219W	1100	20/0	5/0	6/2/09	12/9/10	333	MD
Northern Line Islands	Palmyra WT	4	05-51.846 N	162-09.907W	600	20	5	10/19/06	4/2/09	594	bw
Northern Line Islands	Equator Seamount	1	00-26.607 N	164-08.079W	1250	0	0	3/6/12	6/17/12	103	MD
N. Mariana Islands	Pagan	1	17-57.785 N	145-28.867E	850	15	5	5/25/15	4/11/17	687	MD
N. Mariana Islands	Saipan	7	15-18.998 N	145-27.542E	700	40/20/7/6	5	3/5/10	5/17/17	1753	MD
N. Mariana Islands	Tinian	6	15-02.344 N	145-45.130E	1000	20/7/6	5	4/13/11	11/5/16	1555	MD
Western Atlantic	Heezen Canyon	1	41-03.715 N	66-21.092 W	850	0	0	6/27/15	3/25/16	272	bw
Western Atlantic	Oceanographer Canyon	1	40-15.798 N	67-59.174 W	1100	0	0	4/26/15	2/9/16	289	bw
Western Atlantic	Nantucket Canyon	1	39-49.9486N	69-58.9284W	1000	0	0	4/27/15	9/18/15	144	bw
Western Atlantic	Norfolk Canyon	2	37-09.974 N	74-28.015 W	1000	0	0	6/19/14	6/28/17	714	MD
Western Atlantic	Hatteras	5	35-20.259 N	74-51.274 W	950	0	0	10/9/12	1/21/17	1275	MD
Western Atlantic	Onslow Bay	3	33-77.794 N	75-92.641 W	950	10	5	8/19/11	6/30/13	433	MD
Western Atlantic	Bermuda	3	31-55.575 N	65-12.900 W	700	0	0	6/10/13	10/2/15	690	MD
Western Atlantic	Jacksonville C	1	30-19.585 N	80-12.296 W	300	0	0	2/17/14	8/23/14	187	--
Western Atlantic	Jacksonville D	3	30-09.036 N	79-46.203 W	800	0	0	8/23/14	6/25/17	829	MD
Gulf of Mexico	Mississippi Canyon	11	28-50.746 N	88-27.927 W	1000	0	0	5/16/10	5/16/17	2080	MD
Gulf of Mexico	Green Canyon	10	27-33.470 N	91-10.010 W	1100	0	0	7/15/10	5/17/17	2098	MD
Gulf of Mexico	Dry Tortugas	10	25-31.911 N	84-38.251 W	1300	0	0	8/9/10	12/8/17	1763	MD
Gulf of Mexico	Howell Hook	4	25-01.702 N	84-23.769 W	1050	0	0	5/27/12	3/11/16	822	MD
									total days	**45,118**	
									total years	**124**	

Table S2*. Acoustic encounter durations (minutes) at sites with Blainville's beaked whale (Md: Mesoplodon densirostris) detections. Comparison of total acoustic encounters summing all beaked whale detections at a site and split up into minutes with encounters per species. Mb: M. bidens; Me: M. europaeus; Mh: M. hotaula; Zc: Ziphius cavirostris; BW43: possibly M. perrini; BW70: possibly M. peruvianus; BWC: possibly M. ginkgodens; BWG: unknown origin (Baumann-Pickering et al., 2013; Baumann-Pickering et al., 2014).*

Region	**Site**	**Total acoustic encounters (min)**	**Mb**	**Md**	**Me**	**Mh**	**Zc**	**BW43**	**BW70**	**BWC**	**BWG**
Eastern North Pacific	Southern California G2	1,271		**1**			1,254	16			
Eastern North Pacific	Southern California Q	13		**9**					4		
Eastern North Pacific	Southern California R	12,906		**9**			12,897				
NW Hawaiian Islands	Ladd Seamount	5,934		**5,294**			561			79	
NW Hawaiian Islands	Pearl and Hermes Reef	38,318		**32,845**			4,605			868	
Main Hawaiian Islands	Kauai	432		**184**						248	
Main Hawaiian Islands	Kona	9,270		**8,117**			260			893	
Pacific Remote Islands	Wake Atoll	5,689		**21**			5,559			109	
Northern Line Islands	Kingman Reef	11,773		**333**		11,019	241			180	
Northern Line Islands	Palmyra Atoll NS	3,671		**5**		3,658	3			5	
Northern Line Islands	Equator Seamount	7,619		**5,371**			2,193			55	
N. Mariana Islands	Pagan	2,612		**2,119**			233			260	
N. Mariana Islands	Saipan	8,244		**4,660**			1,935			1,649	
N. Mariana Islands	Tinian	5,785		**5,553**			44			188	
Western Atlantic	Norfolk Canyon	5,189	1,947	**13**	1,649		1,580				
Western Atlantic	Hatteras	206,032		**115**	20,606		185,311				
Western Atlantic	Onslow Bay	22,798		**230**	22,398		170				
Western Atlantic	Bermuda	2,751		**2,552**			199				
Western Atlantic	Jacksonville	270		**39**	203		28				
Gulf of Mexico	Mississippi Canyon	11,323		**31**	7,729		2,860				703
Gulf of Mexico	Green Canyon	11,374		**571**	8,611		1,873				319
Gulf of Mexico	Dry Tortugas	82,051		**13**	26,725		55,228				85
Gulf of Mexico	Howell Hook	44,668		**9**	14,238		30,357				64
	Cumulative minutes	499,993	1,947	**68,094**	102,159	14,677	307,391	16	4	4,534	1,171
	Cumulative hours	8,333	32	**1,135**	1,703	245	5,123			76	20
	Cumulative days	347	1	**47**	71	10	213			3	1

Table S3*. Count of clusters, FM pulses, and false or true detections at the A) initial step when using all detections before noise removal and the resulting counts of "clean" FM pulses after noise removal; B) once only clusters with FM pulse structure remain; and C) after identification of the primary cluster per site.*

		A) detections in clustering					B) FM pulse clusters				C) primary cluster only		
Region	**Site**	**count of detections before noise removal**	**count of clusters**	**count of 5-min bins**	**count of FM pulses**	**% false detec-tions**	**count of clusters**	**count of 5-min bins**	**count of FM pulses**	**% false detec tions**	**# 5-min bins**	**# Clicks**	**% of true FM pulses**
Eastern North Pacific	Southern California Q	275	2	6	184	33	2	6	184	0	4	116	63
Eastern North Pacific	Southern California R	88	2	6	32	64	2	6	32	0	3	17	53
NW Hawaiian Islands	Ladd Seamount	335,597	17	2,246	261,914	22	4	2,187	261,001	0	1,867	161,484	62
NW Hawaiian Islands	Pearl and Hermes Reef	2,223,084	20	11,753	866,677	61	1	11,560	863,256	0	11,560	863,256	100
Main Hawaiian Islands	Kauai	4,786	3	57	2,738	43	3	57	2,738	0	52	2,706	99
Main Hawaiian Islands	Kona	468,906	19	2,168	197,428	58	1	1,981	186,377	6	1,981	186,377	100
Pacific Remote Islands	Wake Atoll	960	1	5	816	15	1	5	816	0	5	816	100
Northern Line Islands	Kingman Reef	8,389	3	142	5,008	40	3	142	5,008	0	122	3,664	73
Northern Line Islands	Equator Seamount	173,987	10	1,772	108,630	38	4	1,729	105,173	3	1,499	96,628	92
N. Mariana Islands	Pagan	46,043	7	873	30,569	34	3	842	30,116	1	723	29,029	96
N. Mariana Islands	Saipan	131,689	6	2,050	80,803	39	1	1,998	80,067	1	1,998	80,067	100
N. Mariana Islands	Tinian	419,028	12	2,701	281,315	33	1	2,328	268,669	4	2,328	268,669	100
Western Atlantic	Norfolk Canyon	275	1	4	157	43	1	4	157	0	4	157	100
Western Atlantic	Hatteras	4,643	4	57	3,243	30	1	43	2,400	26	43	2,400	100
Western Atlantic	Onslow Bay	11,933	4	69	8,148	32	2	64	8,024	2	62	8,009	100
Western Atlantic	Bermuda	66,441	10	1,253	30,063	55	2	1,057	26,966	10	1,015	26,643	99
Western Atlantic	Jacksonville	658	1	8	329	50	1	8	329	0	8	329	100
Gulf of Mexico	Mississippi Canyon	842	1	12	416	51	1	12	416	0	12	416	100
Gulf of Mexico	Green Canyon	132,327	5	191	21,621	84	5	191	21,621	0	157	17,319	80
Gulf of Mexico	Dry Tortugas	231	2	8	107	54	2	8	107	0	4	78	73
Gulf of Mexico	Howell Hook	49	1	3	29	41	1	3	29	0	3	29	100

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