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RESEARCH ARTICLE

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

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Abstract

Aim: Understanding cetacean species' distributions and population structure over space and time is necessary for effective conservation and management. Geographic differences in acoustic signals may provide a line of evidence for population-level discrimination in some cetacean species. We use acoustic recordings collected over broad spatial and temporal scales to investigate whether global variability in echolocation click peak frequency could elucidate population structure in Blainville's beaked whale (*Mesoplodon densirostris*), a cryptic species well-studied acoustically.

Location: North Pacific, Western North Atlantic and Gulf of Mexico.

Time period: 2004–2021.

Major taxa studied: Blainville's beaked whale.

Methods: Passive acoustic data were collected at 76 sites and 150 cumulative years of data were analysed to extract beaked whale echolocation clicks. Using an automated detector and subsequent weighted network clustering on spectral content and inter-click interval of clicks, we determined the properties of a primary cluster of clicks with similar characteristics per site. These were compared within regions and across ocean basins and evaluated for suitability as population-level indicators.

Results: Spectral averages obtained from primary clusters of echolocation clicks identified at each site were similar in overall shape but varied in peak frequency by up to 8 kHz. We identified a latitudinal cline, with higher peak frequencies occurring in lower latitudes.

Main conclusions: It may be possible to acoustically delineate populations of Blainville's beaked whales. The documented negative correlation between signal peak frequency and latitude could relate to body size. Body size has been shown to influence signal frequency, with lower frequencies produced by larger animals, which are subsequently more common in higher latitudes for some species, although data are lacking to adequately investigate this for beaked whales. Prey size and depth may shape frequency content of echolocation signals, and larger prey items may occur in higher latitudes, resulting in lower signal frequencies of their predators.

KEYWORDS
biogeography, Blainville's beaked whale, latitudinal cline, passive acoustic monitoring, population differentiation, species management

1 | INTRODUCTION

Effective conservation requires knowledge of a species' abundance, population trends and ecology. Although beaked whales occur globally, there is not enough data available to determine status or population trends for most species, primarily due to their occupation of deep, offshore habitats. Blainville's beaked whale (*Mesoplodon densirostris*) is one of a few species of beaked whales recently identified as "Least Concern" in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species but abundance estimates are largely unavailable, and trends remain unknown (Pitman & Brownell Jr., 2020). Blainville's beaked whales have a cosmopolitan distribution from temperate to tropical waters. Due to a general lack of understanding of the ecology of elusive beaked whales, this species is currently not managed at a population level. US stock assessments consider three stocks: Hawaiian, northern Gulf of Mexico and western North Atlantic (Byrd et al., 2021; Carretta et al., 2021), but they offer only limited information on animals in offshore regions or remote naval use areas such as the Northern Marianas Islands. However, mass strandings of Blainville's and other beaked whales have occasionally been linked to concurrent naval exercises and the use of mid-frequency active sonar (Cox et al., 2006). Conservation and management efforts to protect this species need foremost reliable population status information and substantial knowledge of its life history and behaviour.

Blainville's beaked whales (Md) are generally distributed in waters >500 m depth in 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 between 30 and 34 kHz, and a median interclick interval (ICI) of 280 ms, allowing for acoustic monitoring of this species in remote habitats that would be otherwise difficult to survey. 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 highly similar looking signal type that was shifted by about 5 kHz to higher frequencies dominated and was hence termed BW38. Baumann-Pickering et al., 2016 hypothesized that this signal type could either originate from Blainville's beaked whales given their known geographic distribution or constitute a beaked whale-like signal of unknown origin.

We hypothesize that Blainville's beaked whales produce both the Md FM pulse type and the BW38 FM pulse type and that geographic and possible population-level differences are the underlying driver for the different peak frequencies of all Md signals as outlined below. Using these signal types documented in different regions as indicators of Blainville's beaked whale acoustic presence, our 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 worldwide population-level discrimination of individuals within this species. We achieve these objectives through analysis of passive acoustic data collected over 18 years throughout the North Pacific, along the US Atlantic coast, and in the Gulf of Mexico. Within cumulative 61 years of acoustic recordings at sites with Blainville's beaked whale presence, we detect Md FM pulses for 91,000 min, which is an indication of acoustic monitoring being highly suitable to document presence of this elusive beaked whale species. Evidence of geographic differences in the FM pulses of Blainville's beaked whales could facilitate species monitoring at the population level, an effort that is particularly warranted for the conservation of a species known to be vulnerable to anthropogenic noise.

2 | MATERIALS AND METHODS

2.1 | Site description and instrumentation

Passive acoustic recordings were obtained with High-frequency Acoustic Recording Packages (HARPs) at 61 sites in the North Pacific, 11 sites in the Western North Atlantic and four sites in the Gulf of Mexico (Figure 1, Table S1). High-frequency Acoustic Recording Packages are autonomous instruments, developed to continuously record marine acoustics from 10 Hz to 100 kHz over extended periods of up to 1 year (Wiggins & Hildebrand, 2007). During some deployments (Table S1), a recording duty cycle was set with 5 min of recording every 7 to 45 min, depending on data storage and battery capacity. High-frequency Acoustic Recording Packages were configured in a variety of small-to-large moorings or sea-floor package configurations. At most 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 with a seafloor depth between 3600 and 4400 m, the hydrophone was buoyed near 800 to 1200 m depth, (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.

Sites were grouped for regional analysis. We defined six broad geographic regions (Table 1) including (1) Eastern North Pacific (47 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 (three sites near the Main Hawaiian Islands and two sites near the Northwestern Hawaiian Islands); (3) Northern Line & Pacific Remote Islands (4 sites located at Kingman Reef, Palmyra Atoll, and a seamount near the equator, as well as two sites at Wake Atoll and Howland Island); (4) Northern Mariana Islands (three sites at Pagan, Saipan, and Tinian); (5) Western Atlantic (10 sites along the shelf break from Heezen Canyon to Jacksonville, and one site near Bermuda) and (6) Gulf of Mexico (four sites, ranging from Green Canyon to Dry Tortugas). The median (quartiles) recording effort across all sites was 431 (154–875) days, ranging from as little as 12 days up to 4083 days at a single site.

2.2 | Automated beaked whale detections and site comparisons

Signal processing was performed using the MATLAB (Mathworks, Natick, MA)-based custom software program *Triton* (Wiggins & Hildebrand, 2007) and other MATLAB custom routines. A Teager–Kaiser energy click detector (Roch et al., 2011; Soldevilla et al., 2008) 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 the presence or absence of beaked whale signals within 75-second segments, the raw file length and subsequently referenced as "segments," was based on a heuristically optimized expert system (Baumann-Pickering et al., 2013). Only segments with more than seven individual click detections were used in further analyses. All echolocation signals with a peak and centre 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 and other thresholds were chosen heuristically to obtain the best balance between missed and false detections. A third classification step manually assigned species or signal type labels to beaked whale-positive segments, allowing for the following labels: Mb: Sowerby's beaked whale *Mesoplodon bidens*; Md: Blainville's beaked whale *M. densirostris*; Me/Mm: Gervais's beaked whale *M. europaeus* or True's beaked whale *M. mirus*; Mh: Deraniyagala's beaked whale *M. hotaula*; Ms: Stejneger's beaked whale *M. stejnegeri*; Zc: Cuvier's beaked whale *Ziphius cavirostris*; BW37V: possibly Hubbs' beaked whale *M. carlhubbsi*; BW38: possibly Blainville's beaked whale *M. densirostris*; BW43: possibly Perrin's beaked whale *M. perrini*; BW70: possibly pygmy beaked whale *M. peruvianus*; BWC: possibly ginkgo-toothed beaked whale *M. ginkgodens*; and BWG: unknown origin from the Gulf of Mexico (Baumann-Pickering et al., 2013, 2014; Cholewiak et al., 2013; DeAngelis et al., 2018; Griffiths et al., 2019). A trained analyst manually decided on labels to beaked whale species or FM pulse type-level and rejected false detections using a custom, Matlab-based process which displayed the average spectrum of all detected FM pulses within a segment, overlaying reference type spectra together with a histogram of interclick intervals (Baumann-Pickering et al., 2013). The rate of missed beaked whale-positive 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, that is with only one or few consecutive segments. The time of each segment containing beaked whale signals was logged.

For a relative comparison of the presence across sites of all beaked whale species specified above, we computed cumulative minutes with acoustic detections per site and the percentage that each species contributed towards these detections. We calculated

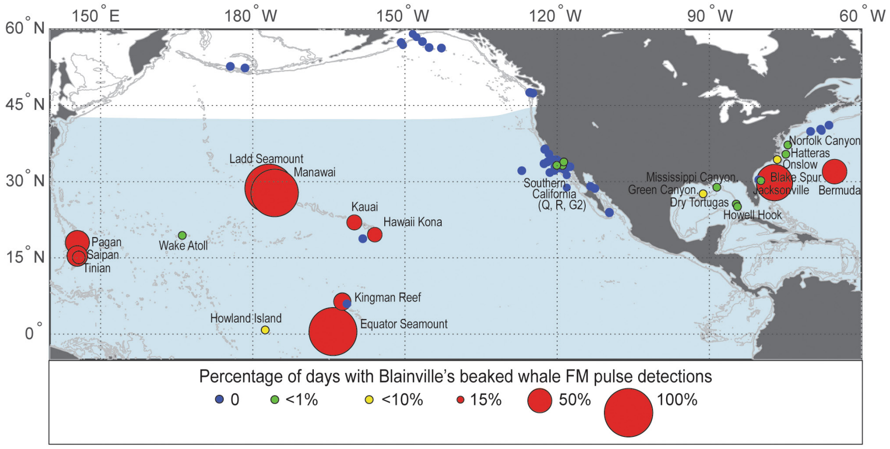


FIGURE 1 Deployment locations of HARPs (circles) in the Northern Hemisphere. Circle colour and size indicate the percentage of days with Blainville's beaked whale (Md) acoustic detections at that site. Light blue background shading indicates known range of this species based on the International Union for the Conservation of Nature (IUCN) Red List map (Pitman & Brownell Jr., 2020). Site names are only labelled for sites with Md detections; see Table S1 for more details on site locations.

TABLE 1 Regions and sites with acoustic detections of Blainville's beaked whales (Md: *Mesoplodon densirostris*) and BW38.

Region	Site	Recording days	Mb	Md/BW38	Me	Me/mm	Mh	Zc	BW37V	BW43	BW70	BWC	BWG
Eastern North Pacific	Southern California G2	269		<1				37	<1	1			
Eastern North Pacific	Southern California Q	268		<1							<1		
Eastern North Pacific	Southern California R	487		<1				82					
Northwestern Hawaiian Islands	Ladd Seamount D	90		98				67				13	
Northwestern Hawaiian Islands	Manawai	1368		97				57				10	
Main Hawaiian Islands	Kauai	718		31								13	
Main Hawaiian Islands	Hawaii Kona	2125		30				4				8	
Pacific Remote Islands	Wake Atoll	1377		<1				56				3	
Pacific Remote Islands	Howland Island	284		4			35	68				<1	
Northern Line Islands	Kingman Reef	123		35			100	33				15	
Northern Line Islands	Equator Seamount	104		97				81				9	
Northern Mariana Islands	Pagan	688		49				13				12	
Northern Mariana Islands	Saipan	2129		43				33				13	
Northern Mariana Islands	Tinian	1548		27				1				8	
Western Atlantic	Norfolk Canyon	1114	25	<1		19		18					
Western Atlantic	Hatteras	290		<1		49		99					
Western Atlantic	Onslow Bay	186		8		97		6					
Western Atlantic	Bermuda	693		50		<1		12					
Western Atlantic	Blake Spur	426		75		51		11					<1
Western Atlantic	Jacksonville D	1311	<1	<1		1		<1					
Gulf of Mexico	Mississippi Canyon	1855		<1	25			10					9
Gulf of Mexico	Green Canyon	2108		2	35			10					5
Gulf of Mexico	Dry Tortugas	1994		<1	68			85					2
Gulf of Mexico	Howell Hook	707		<1	68			87					2
	Total Recording Days	22,262											
	Total Recording Years	61											

Note: For easy comparison, values are in percentage of days with detections of each beaked whale species as well as signal types of unknown origin. Recording periods for each site are provided in the supplement (Table S1).

Mb: *M. bidens*; Me: *M. europaeus*; Mm: *M. mirus*; Mh: *M. hotaula*; Zc: *Ziphius cavirostris*; BW37V: possibly *M. carlhubbsi* (Griffiths et al., 2019); BW43: possibly *M. perrini*; BW70: possibly *M. peruvianus*; BWC: possibly *M. ginkgodens*; BWG: unknown origin (Baumann-Pickering et al., 2013, 2014).

the percentage of days with any beaked whale detections at each site and the percentage of days with detections for each species and site. Sites were grouped into those with Blainville's beaked whale and BW38 acoustic presence and those without (Table S1), as all subsequent analysis focussed exclusively on the FM pulse characteristics of these two types.

2.3 | Blainville's beaked whale (Md) and BW38 signal clustering

An unsupervised learning strategy (further details in Frasier et al., 2017) was applied to initially eliminate false signal detections within segments classified as containing Md FM pulses (Step 1). Subsequently, within and across site variability of the Md FM pulse type was documented (Step 2). Spectral shape (1 kHz bin width from 10 to 90 kHz) and interclick interval (ICI) distribution were used for final clustering. For each step, 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 each 5-minute time bin (Figure 2, left). This time increment was chosen for clustering computational purposes to optimize processing time while providing enough variability within each time bin. *Phase 2* grouped similar signal types based on the 5-minute bin mean spectra and modal ICIs from *Phase 1* within a deployment (Figure 2, right) or within a site for Step 2. Details for each Step and *Phase* follow. Summary statistics of counts of 5-minute bins, signal detections and number of clusters were retained for each step (Table S2) and the primary cluster per site which also included peak and centre frequency, ICI, and signal duration median and percentiles (Table 2).

Step 1: The detector output of individual FM pulse detections within manually verified Md acoustic encounters, that is within one or more consecutive segments, was not further manually screened for false signal detections within these encounters. Instead, a first round of broad category clustering was applied to group and eliminate most false signal detections. For *Phase 1* computation, spectra of all detections were truncated at 10 and 90 kHz and normalized [0, 1]. A similarity metric using the Chinese Whispers (CW) algorithm (Biemann, 2006) with pairwise correlation distance was computed resulting in a matrix of [0, 1] edge weights (Frasier et al., 2017). 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, using a maximum of 15 assignment iterations and a maximum network size of 10,000 clicks for each 5-min bin. Clusters were formed with a minimum of two clicks. Individual isolated clicks were excluded. Mean spectra were computed for all resulting clusters per 5-min bin. Interclick intervals 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*, in this iteration on the binned mean spectra. Euclidean distances between modal ICIs were 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 five nodes remaining in each resulting cluster. The normalized mutual information criterion was used to assess which of the iterations had the best cluster consistency on a [0, 1] scale (Fred & Jain, 2005). The highest average normalized mutual information value across all comparisons was chosen as the final output. Trained analysts (SBP and JST) visually evaluated the clusters per instrument deployment. All clusters with their respective detections containing nonbeaked whale type signals were eliminated.

Step 2: This process was repeated with the remaining individual detections, now with most false signals removed, although with slight adjustments of the clustering parameters to allow for a finer differentiation of beaked whale signal types. In the *Phase 1* process of grouping individual detections based on their spectral similarities, parameters were kept as previously, except that a cluster within a 5-min bin needed to contain at least five signals and 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 two bins and the pruning threshold was set to $p_e = 0.7$. The resulting clusters per site were again manually screened, and a few remaining clusters with noise were removed at some sites (Table S2). These false clusters predominantly contained residual pings from fisheries echosounders (most prominent at site Hawaii Kona), but also small amounts of instrument noise, faint clicks, strongly distorted clicks, which were likely far off-axis, and possibly clicks from mixed species encounters. Per site, between 1 and 3, in one case, five clusters containing Md echolocation clicks remained. In all cases, a primary cluster containing most clicks per site (median 99%) was available and selected while secondary clusters were discarded (Table S2). Median, 10th and 90th percentiles of peak frequency, centre frequency and ICI mode were extracted from all 5-min bins of primary clusters to compare variability across sites.

Sites were grouped into those with regularly reoccurring acoustic presence of Md echolocation clicks (>25% of recording days, >35-h cumulative detection time), infrequent occurrence (>2% of recording days, 1.5–9.5-h cumulative detection time) and transient occurrence (<1% of recording days, <1-h cumulative detection time, Figure 1, Tables 1 and 2). A linear regression of site latitude and median peak frequency was calculated for sites with regular presence to document a latitudinal cline.

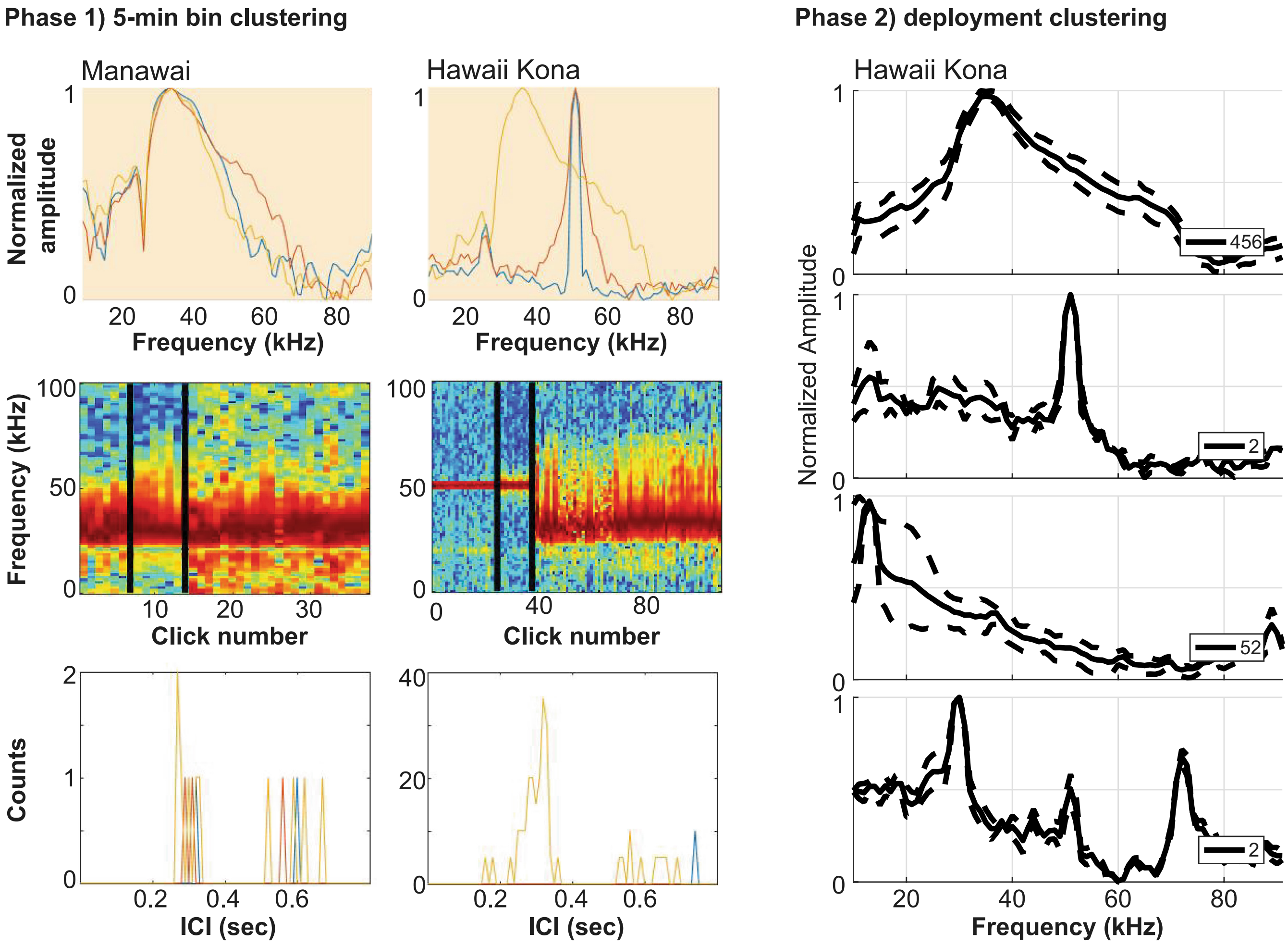


FIGURE 2 Examples for Step 1 clustering phase 1 (5-min bin, click-based, left) and phase 2 (spectral average- and ICI mode-based, right). Phase 1 at Manawai: 3 Blainville's beaked whale (Md) FM pulse spectral averages (top), concatenated spectra of all FM pulses in these averages (middle) and corresponding ICI distribution (bottom); Hawaii Kona: 2 clusters of echosounders and one cluster of Md FM pulses. Phase 2 (Hawaii Kona, 1 deployment): cluster result of 5-min bin spectral averages and ICI distribution resulted in ten signal type clusters, four shown here. Most were associated with the Md FM pulse type (top, *n* = 456) while several echosounder categories occurred (bottom; *n* = 2; 52; 2) (additional echosounder and other delphinid clusters not shown).

3 | RESULTS

Blainville's beaked whale (Md) FM pulse type or the highly similar BW38 FM pulse type was found at 24 of 76 sites with recording effort (Tables 1 and S1, Figure 1). Additionally, one to four other beaked whale species were encountered at these sites (Figure 3). The BW38-type was noted at all sites with lowest latitudes in the Pacific, at Kingman Reef (123 days of recording), Equator Seamount (104 days) and Howland Island (284 days). When comparing spectral averages across sites, a range of peak frequencies from 32 to 40 kHz was noted, with a corresponding signal energy onset ranging from 21 to 31 kHz (Figure 4, Table 2). Md and BW38 FM pulse characteristics were otherwise largely the same in centre frequency, ICI and duration (Table 2); the shape of the spectrum was highly similar yet varied regionally in its frequency onset which also shifted the peak frequency (Figure 4). A smaller spectral peak was characteristic at about 2–3 kHz below the main energy onset. This smaller peak was more prominent in the Pacific and less in the Atlantic (Figure 4).

Sites with BW38-type occurrence were in known Blainville's beaked whale geographic distribution (Figure 1); however, no typical Md FM pulse type was acoustically documented at any of these sites despite substantial effort (Table S1). Species occurrence and similarities in Md and BW38 FM pulse types led us to the conclusion that BW38 most likely is representative of Blainville's beaked whale at these low-latitude sites and will in subsequent analyses be treated as an Md FM pulse type.

In some regions, Md FM pulse type 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, subtropical and tropical sites had the highest percentage of days with Md detections. Occurrences were relatively infrequent along continental shelf breaks. Md signals dominated over other beaked

TABLE 2 Final dominant clustering results for Blainville's beaked whales (Md).

Region	Site	Md acoustic encounters (min)	Count of 5-min bins	Count of FM pulses	Peak frequency (kHz)	Centre frequency (kHz)	ICI (ms)	Dur (µs)
Eastern North Pacific	Southern California Q	8.75	3	150	32 (31–34)	50.0 (50.0–50.2)	310 (310–320)	440 (352.5–505)
Eastern North Pacific	Southern California R	8.75	3	17	40 (37–40)	50.2 (49.9–50.4)	345 (310–370)	385 (371–461)
Northwestern Hawaiian Islands	Ladd Seamount	5929	1882	154,158	34 (32–36)	49.6 (49.4–49.9)	320 (270–575)	465 (380–540)
Northwest Hawaiian Islands	Manawai	33,980	9955	606,394	35 (33–37)	49.6 (49.4–49.9)	320 (260–600)	410 (305–510)
Main Hawaiian Islands	Kauai	2387	441	49,926	36 (26–46)	50.1 (49.2–50.5)	310 (110–608)	390 (170–515)
Main Hawaiian Islands	Hawaii Kona	12,018	4034	454,822	36 (34–38)	50.0 (49.6–50.5)	310 (130–590)	385 (175–510)
Pacific Remote Islands	Wake Atoll	36.25	4	123	34 (34–36)	49.7 (49.5–49.8)	320 (224–576)	395 (319–465)
Pacific Remote Islands	Howland Island	80	15	151	39 (37–40)	50.0 (49.8–50.4)	340 (308–690)	390 (313–477)
Northern Line Islands	Kingman Reef	332.5	105	3568	39 (35–41)	49.8 (49.6–50.1)	320 (250–622)	395 (305–495)
Northern Line Islands	Equator Seamount	5371	1514	94,343	39 (37–41)	50.2 (49.9–50.6)	340 (310–630)	445 (355–550)
Northern Mariana Islands	Pagan	2119	747	29,898	35 (33–37)	49.7 (49.5–49.9)	310 (220–590)	415 (325–515)
Northern Mariana Islands	Saipan	6144	1726	69,210	36 (34–37)	49.8 (49.6–50.1)	300 (210–570)	415 (295–515)
Northern Mariana Islands	Tinian	6200	1342	190,689	36 (34–38)	50.0 (49.7–50.3)	310 (250–570)	445 (300–535)
Western Atlantic	Norfolk Canyon	17.5	5	186	33 (32–33)	49.7 (49.6–49.8)	310 (300–320)	480 (410–520)
Western Atlantic	Hatteras	26.25	32	2316	33 (27.7–37)	49.6 (49.2–49.8)	300 (144–648)	430 (200–530)
Western Atlantic	Onslow Bay	171.25	58	9529	33 (27.6–36)	49.5 (48.9–49.8)	290 (128–532)	400 (190–545)
Western Atlantic	Bermuda	2947	642	14,740	35 (29–39)	49.7 (49.4–49.9)	370 (200–700)	425 (310–525)
Western Atlantic	Blake Spur	12,683	4184	436,788	32 (30–33)	50.1 (49.9–50.3)	340 (240–610)	450 (325–535)
Western Atlantic	Jacksonville D	58.75	21	761	35 (30.6–37)	49.8 (49.4–49.8)	330 (280–650)	425 (346–510)
Gulf of Mexico	Mississippi Canyon	31.25	12	408	33 (30.7–33)	49.6 (49.5–49.8)	340 (320–686)	475 (389–590)
Gulf of Mexico	Green Canyon	571.25	166	17,642	34 (31–35)	49.6 (49.4–49.9)	330 (290–630)	460 (335–530)
Gulf of Mexico	Dry Tortugas	12.5	3	70	37 (30–38)	50.2 (50.0–50.4)	390 (352–736)	540 (497–565)
Gulf of Mexico	Howell Hook	8.75	3	29	37 (36–37)	49.6 (49.5–49.8)	320 (293–612)	440 (392–501)

Note: Varying overall presence across site documented with total encounter minutes, 5-minute bin counts and counts of individual FM pulses in each site-specific dominant cluster, not effort adjusted (sum over all Md acoustic encounters across all sites: 91,142 min or 1519 h). FM pulse characteristics within each dominant cluster showing median (10th to 90th percentile) peak and centre frequencies (kHz) as well as interclick interval (ICI; ms) and duration (dur; µs). The Southern California G2 site had too few Md signals for clustering.

whale signal types at most island sites except Wake Atoll, where Cuvier's beaked whale (*Ziphius cavirostris*) signals dominated, and Kingman Reef and Howland Island, where Deraniyagala's beaked whale (*Mesoplodon hotaula*) signals were more common (Table 1 and Figure 3). Md signals were absent from Palmyra Atoll, where Deraniyagala's beaked whale signals dominated, and were also absent from Cross Seamount, where only BWC signals were detected.

Overall, there were 1519 cumulative hours of recordings with Md signals across all sites (Table 2). However, there was uneven effort and uneven acoustic density at these sites; for example, Manawai (also known as Holoikauaua or Pearl and Hermes Reef) had reliable Md detections of 33,980 min (606,394 FM pulses) over 1368 recording days and Howell Hook had only 9 min (29 FM pulses) over 707 recording days (Tables 2 and S1). There were 11 sites with regularly reoccurring acoustic presence of Md (>25% of recording days, >35-h cumulative detection time), three sites (Howland Island, Onslow Bay, Green Canyon) with infrequent occurrence (>2% of recording days, 1.5–9.5-h cumulative detection time) and 10 sites with only very transient occurrence (<1% of recording days, <1-h cumulative detection time, Tables 1 and 2, Figure 1).

At sites with reoccurring presence of Md (>1% of recording days, >1-h cumulative detection time; includes sites with regular and infrequent Md encounters) the variation in median peak frequency had a negative linear relationship with geographic latitude (Figure 5), with higher peak frequencies occurring at lower latitudes.

When comparing ICI across sites, the median ICI of dominant clusters ranged from 270 to 390 ms (Table 2). However, across regions, there were no clear differences in median ICI values, meaning ICI did not show the same latitudinal cline noted for peak frequency. The greatest variability within a region occurred in the Atlantic (70 ms), whereas in the Pacific, median ICI values were within 35 ms for all regions (Table 2, Figure 6).

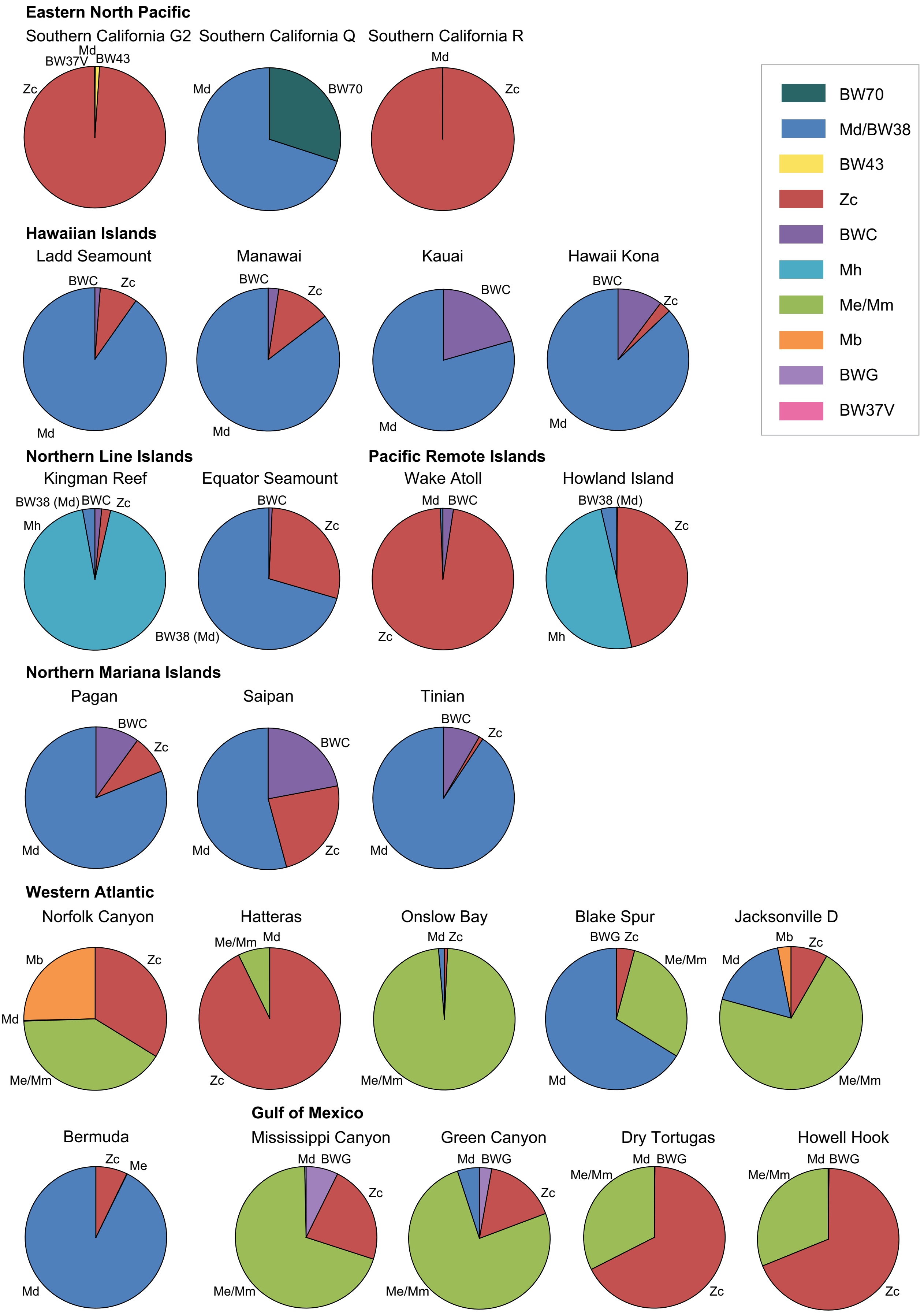
4 | DISCUSSION

Echolocation signals of Blainville's beaked whale were one of the first FM pulse descriptions of any beaked whale species (Johnson et al., 2004), and its acoustic behaviour has since been reported in several subsequent publications (e.g. Arranz et al., 2011; Dunn et al., 2017; Johnson et al., 2006; Madsen et al., 2013). The potential for variation in the echolocation FM pulse 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 at that site was labelled BW38, as it resembled Blainville's beaked whale FM pulses, but the observed peak frequency was at 38 kHz rather than the expected 34 kHz. Within this study, we present an additional two low-latitude, central Pacific sites at which this shift to higher frequencies occurred. The most parsimonious explanation seemed to be that these BW38 signals represent Md in the broader, low-latitude region as already postulated by Baumann-Pickering et al. (2016) when the signal type was first introduced. In all three cases, there was a complete lack of "typical" Md FM pulse detections within established Blainville's beaked whale geographic range, as represented on the IUCN Red List map (Pitman & Brownell Jr., 2020; Figure 1), which has primarily been inferred from stranding records. The inclusion of the BW38 signal type detected at these low-latitude sites in determining Blainville's beaked whale acoustic presence was based on its very similar spectral shape, only shifted in frequency, and its highly comparable ICI distributions. Alternatively, yet less likely, BW38 is produced by a to-be-determined species of beaked whale with only tropical distribution or, even further unlikely, as an alternative signal of a different species within tropical environments. Including BW38 within the broader Md FM pulse class allowed for a more accurate representation of the geographic distribution based on the acoustic record of this infrequently observed species than was reported previously (Baumann-Pickering et al., 2014). Baumann-Pickering et al. (2014) included 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 further included in this study.

The present study documents for the first time the intraspecific 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 signals with consistent features that are identifiable to species. For beaked whales, 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, geographic differences in acoustic signals have been documented in some cetacean species. The biogeographic characterization of blue (*Balaenoptera musculus*) and fin (*B. physalus*) whale song has provided insight into population structure in these species (e.g. Archer et al., 2020; Delarue et al., 2009; Helble et al., 2020; McDonald et al., 2006; Širović et al., 2017). The population-level acoustic differentiation appears to be more stable in blue than fin whales (Helble et al., 2020; Širović et al., 2017). Risso's dolphins have also recently been found to exhibit geographic variation in their echolocation click spectra (Soldevilla et al., 2017), with a noted latitudinal cline

FIGURE 3 Relative presence of all beaked whale species at sites with Blainville's beaked whale (Md) FM pulse type and BW38 detections based on cumulative minutes of acoustic encounters. Mb: *M. bidens* (Cholewiak et al., 2013); Me: *M. europaeus*; Mm: *M. mirus* (DeAngelis et al., 2018); Mh: *M. hotaula*; Zc: Ziphius cavirostris; BW37V: possibly *M. carlhubbsi* (Griffiths et al., 2019); BW43: possibly *M. perrini*; BW70: possibly *M. peruvianus*; BWC: possibly *M. ginkgodens*; BWG: unknown origin (Baumann-Pickering et al., 2013, 2014).


Eastern North Pacific
Southern California G2
BW37V
Md
BW43
Zc
Southern California Q
Md
BW70
Southern California R
Md
Zc
Hawaiian Islands
Ladd Seamount
BWC
Zc
Md
Manawai
BWC
Zc
Md
Kauai
BWC
Md
Hawaii Kona
BWC
Zc
Md
Northern Line Islands
Kingman Reef
BW38 (Md)
BWC
Zc
Mh
BW38 (Md)
Equator Seamount
BWC
Zc
Pacific Remote Islands
Wake Atoll
Md
BWC
Zc
Howland Island
BW38 (Md)
Zc
Mh
Northern Mariana Islands
Pagan
BWC
Zc
Md
Saipan
BWC
Md
Zc
Tinian
BWC
Zc
Md
Western Atlantic
Norfolk Canyon
Mb
Zc
Md
Me/Mm
Hatteras
Me/Mm
Md
Zc
Onslow Bay
Md
Zc
Me/Mm
Blake Spur
BWG
Zc
Me/Mm
Md
Jacksonville D
Mb
Zc
Md
Me/Mm
Bermuda
Zc
Me
Md
Gulf of Mexico
Mississippi Canyon
Md
BWG
Zc
Me/Mm
Green Canyon
Md
BWG
Zc
Me/Mm
Dry Tortugas
Md
BWG
Me/Mm
Zc
Howell Hook
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BW37V

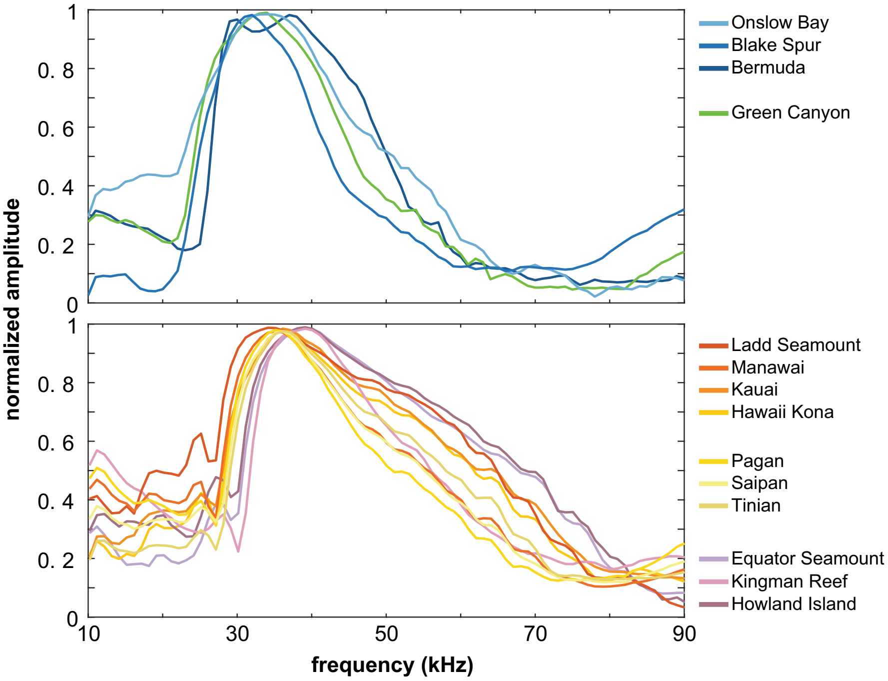

FIGURE 4 Spectral averages of primary cluster at sites with reoccurring Blainville's beaked whale FM pulse type detections (>1% of recording days, >1 h cumulative recording time) in the Atlantic and Gulf of Mexico (top) and Pacific (bottom). Sites are grouped according to region.

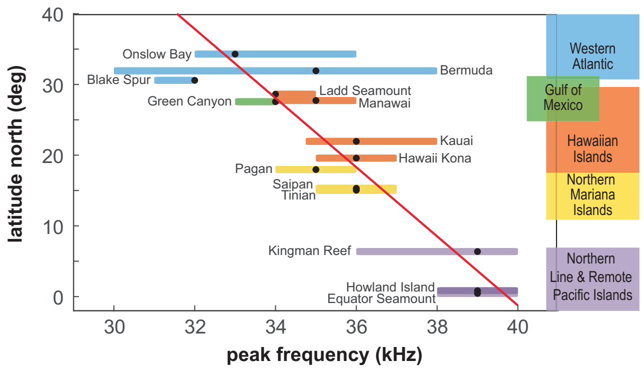

FIGURE 5 Increasing median peak frequency (with 25th and 75th percentiles) with lower latitudes (red regression line fit to medians; $y = -4.8x + 191.7$, $R^2 = 0.93$) at sites with regular Blainville's beaked whale presence (>1% of recording days).

in frequencies, and it has been suggested that population-specific click types may occur in Pacific white-sided dolphins (Soldevilla et al., 2010). Likewise, the geographic differences in Blainville's beaked whale echolocation parameters described here suggest that global populations of this species may also be acoustically distinct. Building on this assumption, one might be able to infer spatial connectivity within an ocean basin. Hypothetically, sites with transient occurrence of Md FM pulses (<1% of recording days), such as those documented in the Southern California Bight, Wake Atoll in the central Pacific, or Howell Hook in the Gulf of Mexico, might be a model for this concept. In Southern California, where our group has screened > 60 years of cumulative acoustic recordings for beaked whales (Table S1), there were only three instances with Blainville's beaked whale acoustic detections. At Site R, the single encounter showed a median peak frequency that would place the origin of the individuals in a low-latitude region (Table 2), whereas at Site Q, peak frequencies would lend to the assumption that these animals may originate from a more temperate region. 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 a latitude such as the southern Caribbean region. 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. By contrast, site-specific observed differences in inter-click intervals did not support population-level differentiation but may instead be more closely aligned with short-term behavioural changes during foraging. They are relevant, however, in the context of understanding animal abundance acoustically at these sites when counting of clicks as cues is being used for density estimation (e.g. Hildebrand et al., 2015; Marques et al., 2009, 2019).

The acoustic recordings analysed in this study were collected over 18 years, did not always overlap in time across regions and it may be possible that the Md FM pulse type could have changed over time. However, the temporal coverage of each region is broad such that temporal differences in recording effort would not adequately explain the differences in signal frequency reported here.

Blainville's beaked whale is a cosmopolitan species, found in all oceans except the Arctic and Southern Ocean, 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, many aspects of its natural history continue to be poorly understood which remains a concern for conservation efforts. Knowledge of population-level differences is scarce. Relatively

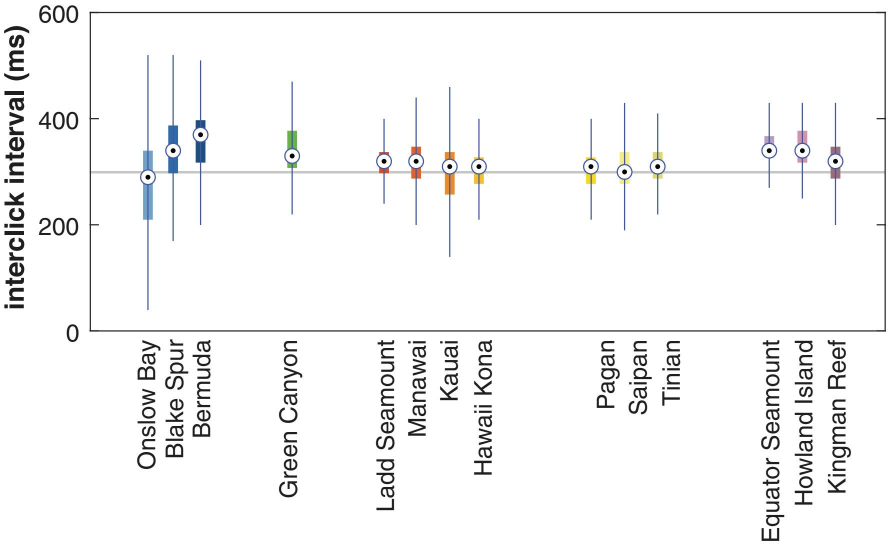

FIGURE 6 Interclick interval (ICI) of echolocation clicks in primary cluster at all sites with regularly occurring Blainville's beaked whale FM pulse type detections (>1% of recording days). Circle indicates median, bars show 25th and 75th percentile, lines represent most extreme data points, while outliers are excluded. Sites are grouped according to region. Grey line indicates 300 ms ICI for visual orientation.

few samples are available, precluding 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, 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 signals with lower frequency content (e.g. Bowling et al., 2017). However, there appears to be tighter relationship with minimum frequencies than maximum frequencies in mammalian and particular cetacean signals with phylogenetics playing an additional role (Martin et al., 2017; May-Collado et al., 2007). Moreover, body size might be influenced by latitude, with larger animals found in higher latitudes. This was first formulated as the ecogeographical “Bergmann's Rule” and based on a study of birds (Bergmann, 1847). It largely relates to intraspecific size comparisons of larger homeotherms over their biogeographic range, mechanistically possibly related to increased heat retention capability by lowering the volume-area ratio through increased body size in higher latitudes (e.g. discussed in review paper by Salewski & Watt, 2017). There is debate over whether the ecological rule and mechanistic hypothesis hold true for most homeotherms and whether it is also applicable to poikilotherm vertebrates and invertebrates; there appears to be strong evidence for homeotherms (e.g. reviews in Meiri & Dayan, 2003; Meiri, 2011) and indication for poikilotherm species, particularly under colder conditions (e.g. Rypel, 2014). Bergmann's rule has not been tested in beaked whales. Due to the relatively low number of Blainville's beaked whale strandings worldwide, and a lack of sufficient numbers of body size measurements obtained, for example from drone photogrammetry, it is currently not 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 higher latitudes could potentially be traced to larger prey items occurring there; again, possibly based on Bergmann's rule. However, little is known about the diet of Blainville's beaked whales, especially in temperate waters and much of the current knowledge on their prey preferences has been derived from stomach content analyses of stranded individuals in tropical waters (MacLeod et al., 2003; Santos et al., 2007).

Knowledge of beaked whale ecology is still very limited but has been substantially improved by the application of acoustic monitoring in pelagic and remote regions (e.g. Barlow, Cheeseman, & Trickey, 2021; Barlow, Fregosi, et al., 2021; Baumann-Pickering et al., 2014; McCullough et al., 2021; Simonis et al., 2020). The ability to use echolocation FM pulse spectral structure to determine population association for individual and groups of Blainville's beaked whales would represent a significant step in detailing the ecology of this cryptic species.

Consideration of geographic differences in other beaked whale or cetacean species' acoustic signals or possibly even more broadly in acoustically active species both marine and terrestrially would likewise improve monitoring capabilities, particularly for species in which population structure is poorly understood. From a management and conservation perspective, currently identified strong-to-moderate lines of evidence for population delineation are genetics, morphology, movements, low-density areas and contaminants (Martien et al., 2019). Acoustics can currently only be used in few species-specific cases but is an active area of interest from a conservation standpoint to support the available lines of evidence. It could possibly even serve as a first line of evidence as populations form before genetic differentiation may occur. In the case of cryptic species, such as beaked whales, where the more traditional lines of evidence are particularly difficult to obtain, acoustics may serve as a viable option to delineate populations, particularly for species as broadly distributed as Blainville's beaked whales to define conservation and management initiatives. Population-level acoustic discrimination would also allow for the consideration of regionally specific threats, such as anthropogenic noise, when developing effective strategies and goals for conservation.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

Acoustic metadata and detection output are available through Dryad under the title "Blainville's beaked whale (*Mesoplodon densirostris*) echolocation clicks from autonomous passive acoustic recordings" with DOI https://doi.org/10.6076/D12G6N. Original acoustic data can be requested from the authors directly.

PEER REVIEW

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BIOSKETCH

The research team investigates phenological patterns and spatial ecology of cetaceans, population abundance, foraging ecology and adaptations of animals to changes in their environment. We are largely using acoustic methodologies for our research and hence are invested in developing acoustic instrumentation and analytical approaches. Our goal is to contribute to the management and conservation of cetaceans and their ecosystem. https://mbarc.ucsd.edu, https://sael.ucsd.edu, https://sioml.ucsd.edu, https://cetus.ucsd.edu, https://www.fisheries.noaa.gov/contact/erin-oleson-phd

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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