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NOTE

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Echolocation depths and acoustic foraging behavior of Baird's beaked whales (*Berardius bairdii*) based on towed hydrophone recordings

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Little is known about the foraging depths of Baird's beaked whales (*Berardius bairdii*). One Baird's beaked whale was tagged with a time-depth recorder in slope waters east of central Honshu, Japan (Minamikawa et al., 2007). In that study, five deep dives were observed with mean durations of 45.8 min (SD = 11.4) and mean maximum depths of 1,566 m (SD = 208). One Baird's beaked whale was tagged with a multi-sensor DTAG off southern California (Stimpert et al., 2014). In that study, two deep foraging dives were observed with durations of 55.7 and 81.7 min and maximum depths of 945 and 1,410 m, respectively. The portions of those dives with actual foraging behavior (near-constant echolocation and inverted swimming orientation) lasted 31.6 and 52.6 min, respectively. The mean foraging depths were not reported, but foraging behavior began at ~400 m and ended coincident with the beginning of their steep ascent. Both foraging dives in the California study were thought to reach the seafloor. In both prior studies (Japan and California), deep dives were interspersed among shorter dives to shallow (<100 m) and intermediate depths (100–1,000 m).

Baird's beaked whales make a wide variety of sounds including frequency-modulated (FM) echolocation pulses, burst pulses, feeding buzzes, and whistles (Baumann-Pickering et al., 2013; Dawson & Ljungblad, 1998; Stimpert et al., 2014). Each of these studies have found multiple frequency peaks in the impulsive sounds (echolocation pulses), but peaks differed among studies. In general, frequency peaks tended to cluster in the ranges of 15–19 kHz, 22–26 kHz, and 30–45 kHz. Baird's beaked whales also produce low frequency whistles with fundamental frequencies of 4–8 kHz. FM pulses have been recorded only on deep foraging dives, but whistles and burst pulses occur on both intermediate and deep dives (Stimpert et al., 2014).

Aside from Stimpert et al. (2014), little is known about the timing of Baird's vocalizations or group foraging behavior. Baird's beaked whales have larger group sizes than their *Mesoplodon* and *Ziphius* cousins, with average group sizes of 5–20 animals (Thewissen, 2018). Diving behavior of Blainville's (*Mesoplodon densirostris*) and Cuvier's beaked whales (*Ziphius cavirostris*) exhibit strong coordination between individuals in a group, with an apparent lack of or minimal social calling, as determined through multiple acoustic tags placed on different animals in a group (Aguilar de Soto et al., 2020; Alcázar-Treviño et al., 2021). Individuals in a group overlapped in their vocal phases by 98% (the time between the first and last echolocation click) and dispersed primarily in the horizontal plane at the bottom of their dive, then ceased clicking and ascended together to the surface (Aguilar de Soto et al., 2020). Here, we describe the foraging behavior of multiple Baird's beaked whales in a single group, and examine the timing of social calls (whistles, burst pulses) within a single deep foraging dive.

Acoustic and visual data were collected from Oregon State University's R/V *Pacific Storm* as part of the Gyre Expedition (GyreX) which focused on visually and acoustically identifying and tracking beaked whales off the coast of Oregon beyond the shelf break into the abyssal plain. Two visual observers searched for beaked whales using high powered binoculars “big-eyes” (Fujinon 25 × 150) from the crow's nest 13 m above sea level. A passive acoustics team monitored a linear hydrophone array towed 150 m behind the vessel. The array was an oil filled tube containing three HTI-96-min hydrophones (sensitivity = −170 dB re 1μPa/V; High Tech, Inc., Long Beach, MS) each spaced 1 m apart. An external depth sensor (Sensus Ultra Data Recorder; Dive Gear Express, Pompano Beach, FL) attached to the tail end of the array was used to collect the array depth at 1 min intervals upon submergence. The depth sensor was calibrated by the manufacturer to 0.305 m accuracy and was rated to 152 m. The preamplified HTI-96-Min hydrophones had a 1 kHz high pass filter and an additional 38 dB of gain was applied with an external differential amplifier. Signals from the first two hydrophones within the array were digitized using a USB-6341 (National Instruments, Austin, TX) I/O device sampling at 400 kHz and were recorded onto hard drives using the acoustic software PAMGuard v. 2.01.05 (Gillespie et al., 2008). Signals were also decimated within PAMGuard to a sample rate of 200 kHz for ease of viewing the FM upsweeps that are characteristic of the beaked whale family. A simple click detector within PAMGuard was applied that included a digital 4th order 10 kHz high pass filter (to reduce low frequency noise), and a click trigger threshold of 8 dB.

On September 10, 2021, in Beaufort 2 sea conditions, a group of 12 Baird's beaked whale were sighted by the visual team at 43.919°N, 125.216°W, 102 km seaward of central Oregon in ~1,600 m water depth (Figure 1 inset). They were first seen from 17:40 to 17:43 UTC before they dove for 32 min (Table 1). During this time, no echolocation pulses or other vocalizations were detected from the array, thus it is assumed that they were not foraging. They were seen again from 18:15 to 18:17 UTC before conducting another short dive devoid of vocalizations which lasted 20 min. The third and last sighting was from 18:37 to 18:42 UTC. At the end of this surfacing, all animals in the group exhibited a high arch as they dove, indicative of commencing a deep foraging dive. Within 8 min, the first FM pulses were detected. These pulses were recorded continuously for 30 min. In addition, 29 burst pulses and 16 whistles were recorded towards the end of the vocalizing period (Figure 1). The group was not seen again after the vocal phase of the foraging dive; thus, a full dive time is not known but was at least 38 min long (silent descent + vocal phase). Less than an hour later, more FM pulse trains of Baird's beaked whales were detected for 10 min, 7.4 km from the original sighting. Based on the short period between detection times and the distance between the two detection events, we assume there was a second group of Baird's beaked whales in the area. The pulse trains from the second group are not included in this analysis.

We analyzed the echolocation data from the encounter with PAMGuard Viewer software. PAMGuard software automatically estimates the conical bearing angles to detected “clicks” (any impulsive sound which includes beaked whale FM pulses) using the time-difference-of-arrival of the same signal received on two hydrophones in the towed array. To identify clicks from the Baird's beaked whales, impulsive sounds were viewed using a 2 min page window and the combination of the bearing-time, waveform, click spectrum, and Wigner-Ville and concatenated spectrogram plots (Figure 2). A total of 6,127 impulsive signals (FM pulses and clicks within burst pulses) were attributed to the

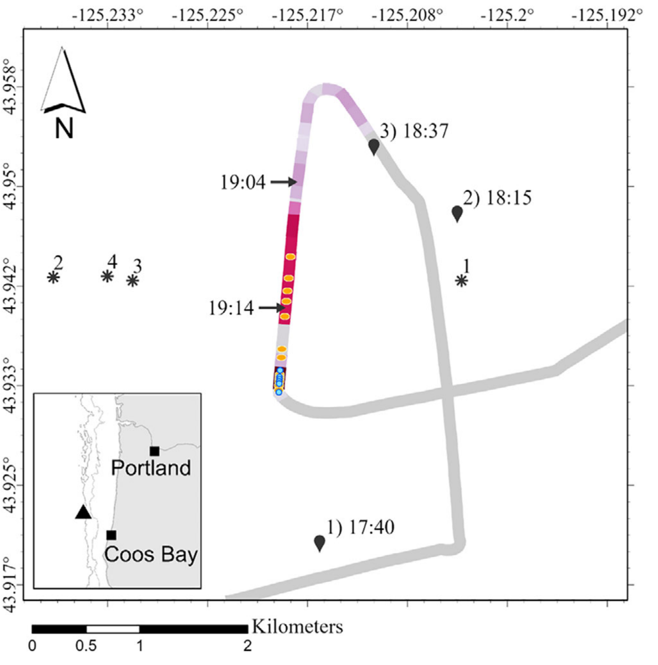

FIGURE 1 Maps of the encounter with a group of Baird's beaked whales. Inset map shows the encounter location (triangle) off the coast of Oregon with the 500 m and 1,500 m bathymetric lines in gray. Details of the encounter are shown in the larger map; the lines indicate the ship's track; number of pulses per minute received are indicated by the color gradient from gray (no signals) to purple (11 pulses/min) to red (654 pulses/min). Yellow ellipses indicate burst pulses, blue circles indicate whistles. Locations of the sightings (numbered pins) indicate: (1) first sighting, (2) next sighting, and (3) last sighting. The time of the sighting is also displayed next to the sighting number. Numbered asterisks indicate the acoustic 2D localizations of the four individuals for which echolocation depths could be estimated. The times noted by the arrows indicate the section of trackline in which echolocation depths were estimated. All times are reported in UTC.

TABLE 1 Focal follow dive times of Baird's beaked whale.

Behavior	Start time (UTC)	End time (UTC)	Duration (min)	Vocalizations present
Surface 1	17:40	17:43	3	N
Short dive 1	17:43	18:15	32	N
Surface 2	18:15	18:17	2	N
Short dive 2	18:17	18:37	20	N
Surface 3	18:37	18:42	5	N
Foraging dive 1	18:42	NA	>38	
Silent descent	18:42	18:50	8	N
Vocal phase	18:50	19:20	30	FM, BP, W

Note. FM = echolocation FM pulses, BP = burst pulses, W = whistles, N = no vocalizations detected.

group of Baird's beaked whales. The peak frequency of these signals was 15.6 kHz, with additional peaks at 10.9 and 24.2 kHz (Figure 2D); the median interpulse interval (IPI) was 0.20 s (Figure 2B).

Impulsive sounds appearing along consistent bearings with a steady IPI were grouped together into events. These events were separated at the individual level when possible, and echoes from the clicks were manually

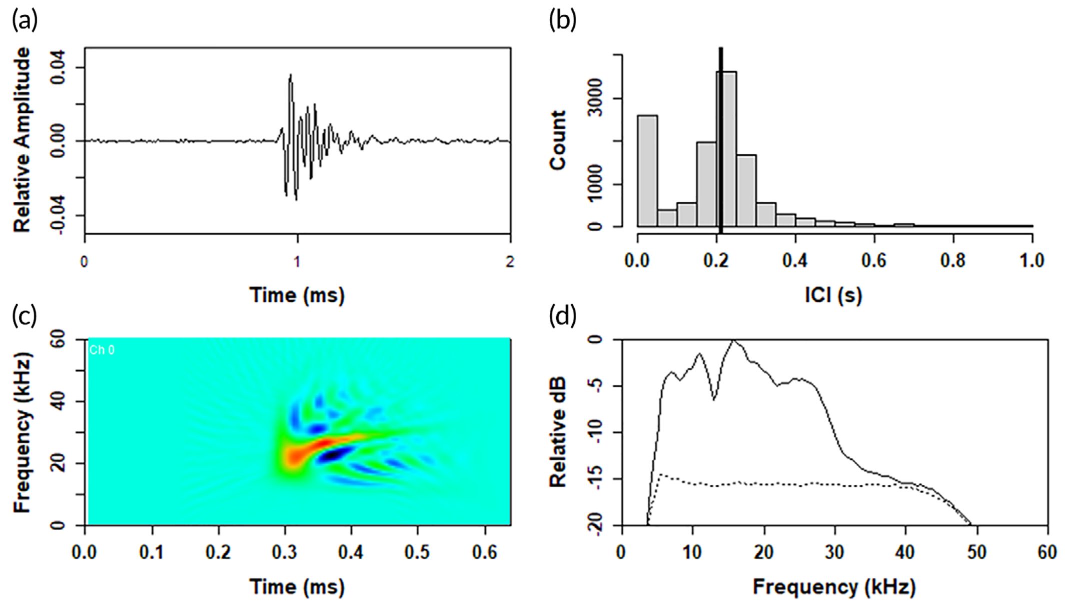

FIGURE 2 Pulse characteristics from the Baird's beaked whale encounter: (a) waveform from an exemplar FM pulse, (b) histogram of the IPIs recorded from both FM and burst pulses (bold line indicates the median value), (c) Wigner-Ville spectrogram of the exemplar FM pulse, and (d) average spectra from all pulses in the encounter (dotted line indicates the average noise spectra in the 1.3 ms (512 samples) preceding each pulse).

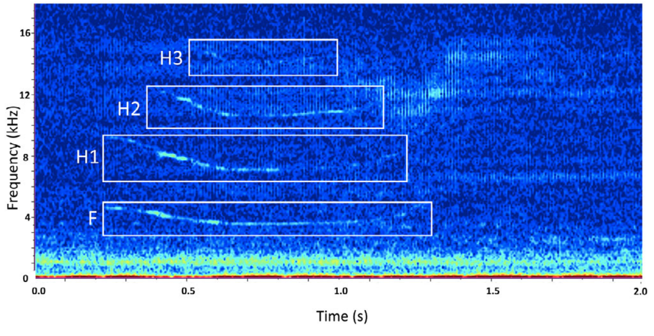

FIGURE 3 Example of a Baird's whistle where the fundamental (F) and each harmonic (H1, H2, H3) are encapsulated in individual boxes.

removed. Individuals were primarily identified based on received bearing angles, where click trains received on bearings >5° apart indicated more than one individual and click trains <5° were assigned to multiple individuals by differences in their pulse patterns (IPI; DeAngelis et al., 2017). Over the course of the encounter, we identified a total of seven echolocating individuals.

Whistles recorded during the encounter were characterized using Raven Pro 2.0 software (K. Lisa Yang Center for Conservation Bioacoustics, Ithaca, NY). Spectrograms were viewed from 0 to 20 kHz with a 4,096-point FFT window and a 50% overlap (frequency bin size = 97 Hz, time bin size = 5 ms). Each whistle was given a unique ID and measurements were taken of the overall signal as well as individual harmonics, where present (Figure 3). For each whistle, time and frequency measurements of 90% duration, peak frequency, and the 5% and 95% frequency bounds were used to minimize the influence of the selection box size. In one case where two signals overlapped and one could not be measured clearly using the built-in tools, point measurements were taken of high and low frequencies, durations were visually estimated, and peak frequency was not calculated.

All 16 distinct whistles were detected during a single 1.75 min period towards the end of the vocal phase (Figure 1). Whistles ranged in duration from 0.61 s to 1.40 s, with a mean of 0.89 s (Table 2). The lowest fundamental frequency of the whistles (Freq 5%) ranged from 2.7 kHz to 8.9 kHz, with a mean of 4.6 kHz; the highest frequency of the fundamental (Freq 95%) ranged from 3.8 kHz to 10.7 kHz with a mean of 6.5 kHz. The peak frequency ranged from 3.5 kHz to 9.5 kHz with a mean of 5.4 kHz. Most of the peak frequencies came from the fundamental, with only one whistle having a harmonic stronger than the fundamental (Whistle 5). All whistles had a minimum of one harmonic in addition to the fundamental, with 38% reaching up to three clearly discernible harmonics. Of the 16 whistles detected, 8 were detected as part of four pairs of whistles, indicating the presence of more than one source of vocalization (at least two individuals). These were Whistles 2 & 3, Whistles 5 & 6, Whistles 10 & 11, and Whistles 14 & 15 (Table 2).

The whales were localized in three dimensions using a two-step process (DeAngelis et al., 2017). In the first step, we used PAMGuard's Target Motion Analysis (TMA), which requires the array to be towed relatively straight behind the vessel. TMA estimates the radial distance from the ship at the location where bearing angles (measured over a period of time) converge and provides the perpendicular slant radial distance (as beaked whales are echolocating at some unknown depth). Because the bearing angles from a linear array are actually conical angles, the convergence defines a circle with a radius equal to that perpendicular slant radial distance. We used the 90° arc of this circle that

TABLE 2 Characteristics of whistles emitted during the Baird's encounter on September 10, 2021.

Whistle ID	Begin time	Overlap with whistle ID	Harmonics	Dur 90% (s)	Freq 5% (kHz)	Freq 95% (kHz)	Peak Freq (kHz)	Peak Freq location
1	19:19:00.00	None	2	1.17	3.7	7.6	3.8	F
2	19:19:26.26	3	1	0.78	4.7	6.8	5.2	F
3	19:19:27.27	2	3	0.84	4.7	7.5	4.7	F
4	19:19:28.28	None	1	0.69	3.8	4.2	3.9	F
5	19:19:31.31	6	3	0.83	4.6	8.1	9.6	H1
6	19:19:31.31	5	2	0.80	4.0	4.7	—	—
7	19:19:41.41	None	1	0.61	8.9	10.3	9.0	F
8	19:19:43.43	None	3	1.12	3.4	3.8	3.5	F
9	19:19:45.45	None	3	0.94	3.5	4.8	4.2	F
10	19:19:48.48	11	3	0.62	4.6	6.6	4.7	F
11	19:19:49.49	10	3	0.74	4.2	4.8	4.3	F
12	19:19:51.51	None	2	0.99	6.0	7.0	6.6	F
13	19:19:56.56	None	2	0.93	5.5	6.6	6.6	F
14	19:19:57.57	15	1	0.91	2.7	5.6	3.9	F
15	19:19:57.57	14	1	1.40	6.6	10.7	8.0	F
16	19:20:45.45	None	2	0.84	2.9	4.2	3.6	F
			Minimum	0.61	2.7	3.8	3.5	
			Maximum	1.40	8.9	10.7	9.6	
			Average	0.89	4.6	6.5	5.4	

Note. The Dur 90% measurement is of the total whistle (fundamental + harmonics), the 5% and 95% frequencies are of the fundamental, and the Peak Freq location indicates where the peak frequency measurement came from (F = fundamental, H# = harmonic number).

is underwater, and the perpendicular slant radial distance on the side of the vessel that gives the best convergence as measured by PAMGuard's chi-square goodness of fit metric. In the second step, we used surface reflections of the detected pulses to identify the slant angle at which the pulses occurred along the 90° arc and then subsequently estimated the depth (DeAngelis et al., 2017). For all of this we assumed that the whale's horizontal location is fixed throughout the detection period.

In our encounter, the ship maintained a consistent heading for the latter 10 min of the foraging dive, thus this time period was selected to estimate echolocation depths. Additionally, to obtain reliable localization estimates, events had to be longer than 5 min in duration to ensure enough change in received bearing angles. This constraint limited our dive depth estimates to four of the seven individuals. All FM pulses ($n = 2{,}448$) attributed to those individuals were extracted from PAMGuard binary files using the R package *PAMPal*.[1] *PAMPal* also extracted the metadata contained within the PAMGuard database that are required to estimate the depth of each FM pulse. The metadata included: the depth of the array at the closest time to the pulse, array depth error (a function of the height of a wave in a Beaufort 2 sea state (0.5 m), accuracy of the depth sensor (0.305 m), and array depth), PAMGuard's values for slant range and associated 2D error for the event that contained the pulse, and the radial distance between the event's 2D localization and the ship's latitude and longitude at the time closest to the pulse (DeAngelis et al., 2017). Lastly, *PAMPal* was used to automatically extract audio clips of each annotated pulse, with a time window long enough to encompass both the direct and surface reflected pulse (total clip length = 0.04 s). These FM pulses were then analyzed with custom built Matlab scripts (DeAngelis et al., 2017) to autocorrelate the direct pulses with their surface reflections and to estimate the depth at the time of each FM pulse from each foraging individual. Before the autocorrelation was calculated, the waveform of each FM pulse was filtered by an 8th order Butterworth band-pass filter (from 8 to 32 kHz) to reduce noise in the autocorrelation. Erroneous FM pulse depth estimates can result from an incorrect association between a direct and reflected arrivals, such as the second surface reflection or signals from other whales. Initially, potentially erroneous depth estimates were removed if the difference between successive depth estimates for an individual was greater than plausible given their typical swim speeds (1.5 m/s; Stimpert et al., 2014; Tyack et al., 2006). This is equivalent to accepting depth estimates that were within 30 s and 50 m of one another. The click depths over time were reviewed in Matlab, and, using a custom written script, additional outliers were manually identified as inconsistent depth values and were discarded from further depth calculations (Figure 4).

Of 2,448 FM total pulses, 2,352 contained a surface reflected arrival. From these pulses, 1,745 (76%) were selected to estimate echolocation depths of the four individuals (Figure 4). Mean depths using these selected pulses ranged from 480 m to 704 m (Table 3). The absolute difference between using mean depths from the 2,352 pulses versus the 1,745 pulses was small, (13–63 m); however, the precision of the average time delay error increased by ~25% and reduced the range of average depths per individual (as false depth estimates were removed). A steady ascent towards the surface was clear for all four whales' depths of the individual FM pulses through the time when the array was straight (14–24 min into the vocal phase, Figure 4).

Similar to other beaked whale species (Aguilar de Soto et al., 2020), the Baird's beaked whales that we tracked appeared to exhibit tight coordination in depth, remaining within an estimated 200 m of each other's depths during the latter part of the dive (Figure 4). We cannot report the maximum dive depths of this foraging dive nor a complete dive profile due to this method's limitations. First, we could only use this method when the ship was traveling in a straight line, which only occurred during the last 10 min of the acoustic encounter once we finished maneuvering to track the group. Second, the method does not incorporate animal movement in the horizontal plane over time which could bias estimates of depth changes during a dive. Accounting for animal movement in target motion analysis is difficult (Barkley et al., 2021), and indeed, the trends depicted in Figure 4 may overestimate or underestimate depth for animals also traveling horizontally while foraging. Future studies could reduce this bias by incorporating a three-dimensional animal movement model that is constrained by what is known from animal borne tags. A less subjective method of removing outliers is also needed.

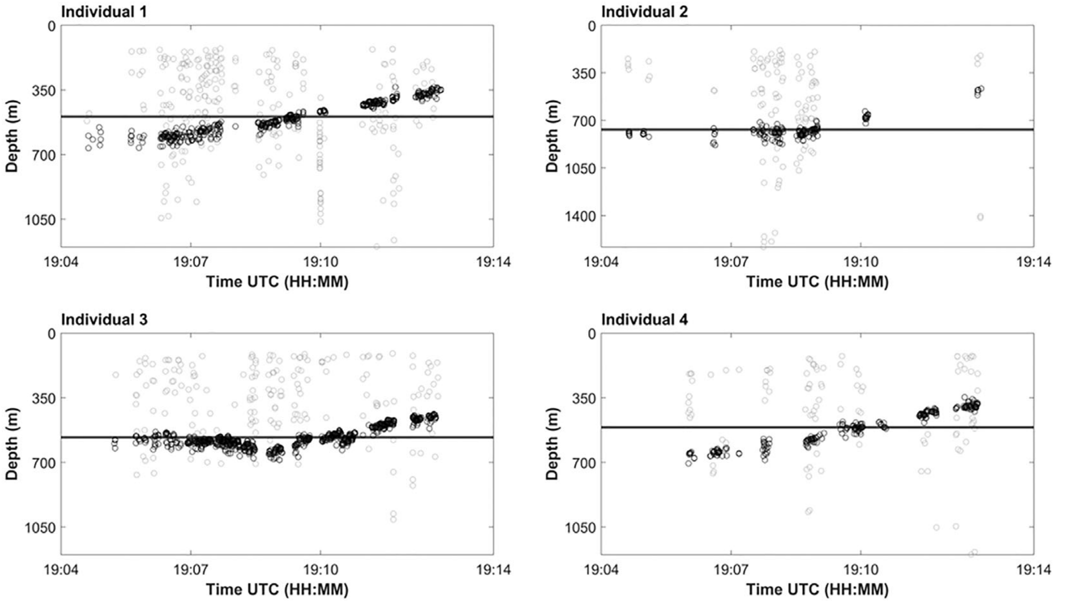

FIGURE 4 Estimated depths (open circles) of each detected FM pulse for the four individuals tracked in three dimensions. Manually identified outliers are shown in gray, accepted click depths are shown in black. The average depth per individual is shown as a solid black line.

TABLE 3 Sample sizes, slant ranges at the closest point-of-approach, and average echolocation depth estimates of four Baird's beaked whales. Errors in estimating the time delay, array depth, and slant range all contribute as fractional uncertainties towards estimating an echolocation depth.

Individual	# Clicks with a multipath	# Clicks used to estimate depth	Slant range (m)	Average depth (m) (range)	Standard deviation depth (m)	Average time delay error	Average array depth error	Average slant range error
1	755	515	1,153	493 (334–665)	11	25%	<2%	22%
2	277	181	1,566	767 (465–882)	29	33%	<2%	27%
3	969	796	1,036	564 (437–687)	7	13%	<2%	21%
4	351	253	1,207	510 (347–706)	15	19%	<2%	31%

The diving behavior of this group of 12 Baird's beaked whales aligns with what is known about this species and beaked whales in general. No vocalizations were detected during short dives, and only the longer dive contained FM pulses representing foraging behavior and burst pulses and whistles representing social communication. No buzzes were detected, probably due to the limitation of recording with a shallow array and because buzzes typically have lower source levels and higher directivity than FM pulses (Johnson et al., 2006; Madsen et al., 2005). FM pulse characteristics matched those reported by Baumann-Pickering et al. (2013), Dawson and Ljungblad (1998), and Stimpert et al. (2014). More whistles were detected during our encounter than in previous studies, and the fundamental frequency range (~2–10 kHz) was slightly larger than the 4–8 kHz range previously reported. In our encounter, social calls of burst pulses and whistles occurred toward the end of the vocal phase of the foraging dive. This differs from a study of Blainville's beaked whales, which showed burst pulses occurring throughout the vocal phase (Aguilar de Soto et al., 2011; Stimpert et al., 2014). Aguilar de Soto et al. (2011) also found that Blainville's emitted whistles in close proximity to rasps, which is consistent with our results. We could not determine the depth at which the whistles and burst pulses were emitted, but based on their timing, these social call types may be used to signal the end of a foraging dive and to coordinate their ascent.

Of the 12 individuals in our group, only seven were acoustically distinguishable during the vocal phase. Visual observations of all 12 individuals exhibiting a high arch before the foraging dive led us to believe that all would be foraging. It is possible that five individuals dove further away from the other seven, which, coupled with the inherent directivity of beaked whale FM pulses, and short detection range, meant that they were present but not detected. Both Aguilar de Soto et al. (2020) and Alcázar-Treviño et al. (2021) found that Cuvier's and Blainville's beaked whales forage separately along different headings, but maintained tight cohesion, remaining tens to hundreds of meters separated from others, with 98% vocal overlap between individuals in the group. It is also possible that due to this tight cohesion, individuals diving in close proximity to each other could have pulse trains occurring on similar bearing angles and we could have unintentionally merged two or three individuals together when assigning pulse trains to individuals. Currently, the only way to separate pulse trains into individuals using a linear towed hydrophone array are by differences in received bearing angles and the presence of overlapping pulse trains. If there are no overlapping pulse trains, and pulses occur on the same bearing, then they could be mistaken for one individual. A tetrahedral array or study on individual variation in IPIs could help to resolve this issue.

Average depth estimates calculated in this study of Baird's beaked whales (493–767 m) are shallower than those found by Stimpert et al. (2014) off southern California (means were not reported, but most foraging was deeper than 800 m). Although, in our sample, all four whales appeared to be ascending and were likely to have been foraging at deeper depths, foraging at such shallow depths during ascent was not seen in that previous study. These whales continued emitting FM pulses to a depth of ~350 m. It appears that, at least in some locations, Baird's beaked whales feed at shallower depths than other beaked whale species. Emitting pulses close to the surface would increase the chances of killer whales finding the group after a deep foraging dive. Killer whales are known to predate upon beaked whales (Aguilar de Soto et al., 2020; Wellard et al., 2016) and one individual in the group we encountered had unique scarring on its body that we presumed was left by killer whales. We were unable to re-sight the group after their foraging dive; and it could be that after cessation of all vocalizations the group traveled horizontally for a large distance to offset the shallow end of foraging clicks. The oceanographic conditions in our study area (slope waters ~26 km SW of Heceta Bank) may be unique and a contributor to this behavior. More observations from this area and others are clearly needed to better quantify the feeding behavior of this species.

Using a towed hydrophone array allows researchers to remotely study beaked whale group foraging behavior at a coarse level, providing information such as call types and their timing, a minimum group size of vocalizing individuals, and foraging depth. They are relatively easy to deploy, cost effective, and minimize disturbance to the study species. Multisensor acoustic recording tags can provide much higher resolution, but, to date, have only been applied to a few of the 24 beaked whale species due to the level of effort involved in tagging beaked whales. Combining these two approaches in the future can help to shed more light on the diving behavior of many beaked whale species.

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AUTHOR CONTRIBUTIONS

Annamaria Izzi DeAngelis: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Jay Barlow:** Conceptualization; data curation; investigation; project administration; resources; supervision; validation; writing – review and editing. **Daniel Gillies:** Formal analysis; visualization; writing – original draft; writing – review and editing. **Lisa T. Ballance:** Conceptualization; funding acquisition; investigation; project administration; resources; supervision; writing – review and editing.

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ENDNOTE

[1] https://github.com/TaikiSan21/PamBinaries

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