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Acoustic and foraging behavior of a Baird's beaked whale, *Berardius bairdii*, exposed to simulated sonar

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Beaked whales are hypothesized to be particularly sensitive to anthropogenic noise, based on previous strandings and limited experimental and observational data. However, few species have been studied in detail. We describe the underwater behavior of a Baird's beaked whale (*Berardius bairdii*) from the first deployment of a multi-sensor acoustic tag on this species. The animal exhibited shallow (23 ± 15 m max depth), intermediate (324 ± 49 m), and deep (1138 ± 243 m) dives. Echolocation clicks were produced with a mean inter-click interval of approximately 300 ms and peak frequency of 25 kHz. Two deep dives included presumed foraging behavior, with echolocation pulsed sounds (presumed prey capture attempts) associated with increased maneuvering, and sustained inverted swimming during the bottom phase of the dive. A controlled exposure to simulated mid-frequency active sonar (3.5–4 kHz) was conducted 4 hours after tag deployment, and within 3 minutes of exposure onset, the tagged whale increased swim speed and body movement, and continued to show unusual dive behavior for each of its next three dives, one of each type. These are the first data on the acoustic foraging behavior in this largest beaked whale species, and the first experimental demonstration of a response to simulated sonar.

The susceptibility of beaked whales to sound¹, particularly mid-frequency active (MFA) military sonar, is not well understood, but it may relate to the physiological consequences of extreme diving^{2,3}. Largely because of their involvement in MFA-related strandings, recent research has focused on Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales. Major strides have been made in understanding these species using short-term multi-sensor tags (DTAGs⁴) as well as longer-term dive and movement satellite tags⁵. However, basic aspects of behavior and response to sound in most other beaked whale species remain almost completely unknown. This includes the largest of the beaked whales, Baird's beaked whale (*Berardius bairdii*).

Baird's beaked whales range throughout the North Pacific Ocean, but have been studied primarily off the coast of Japan in summer. Data on population distribution, lung anatomy, and diet have been gathered from sighting surveys and whaling records in this area^{6–8}, and stomach content analyses have indicated that the animals feed at depths greater than 1000 meters^{6,9}. These depths were validated by Minamikawa et al.¹⁰, who deployed a time-depth recording tag for 29 h on a Baird's beaked whale near Japan, resulting in the first record of diving behavior for the species. More limited data exist for populations of Baird's beaked whales in the eastern North Pacific, although the only published information on acoustic behavior of the species is from this area, and consists of a small number of short sequences of clicks and whistles from recordings during two encounters: one off the coast of Oregon, and the other in the Gulf of California¹¹.

Though the species has not been part of any documented MFA-related strandings¹, its taxonomic grouping and deep diving behavior¹⁰ suggest that Baird's beaked whales may respond to sonar in a manner similar to that of other beaked whales^{12,13}. We deployed a DTAG on a Baird's beaked whale and performed a controlled exposure experiment (CEE) using simulated mid-frequency active (MFA) sonar as the sound stimulus. Here we report the first descriptions of underwater foraging behavior from this species, and identify a change in behavior likely related to the sound exposure.



Results

We observed both unique foraging behavior and a change in behavior coincident with the simulated MFA sonar exposure in a tagged Baird's beaked whale, the first of its species to be tested.

Dive behavior. The tagged animal exhibited 18 shallow, 17 intermediate, and 3 deep dives (Table 1, Figure 1a). The first deep dive lacked acoustic indications of foraging (e.g. continuous clicking and buzzes), which were present in the second and third. Additionally, the tagged whale remained inverted for the entire bottom phase of these second two deep dives. Deviations from an upside-down orientation were small, and often coincided with a series of fast clicks, or acoustic “buzzes,” as well as spikes in the rate of change in tri-axial acceleration, or “jerk” (Figures 1b, 1c).

Acoustic behavior. Very little sound production was recorded during most shallow or intermediate dives, though some clicks, whistles, and pulsed sounds were recorded during the intermediate dive following exposure (Figure 1a). The first deep dive contained only intermittent clicking (longest continuous period of clicking by the group 73 seconds) not associated with pulsed sounds, but the second two deep dives both contained nearly continuous echolocation (longest continuous period of clicking by the group 1894 and 3157 seconds, respectively), associated with pulsed sounds interpreted to be foraging buzzes (51 and 30, respectively). The majority of click spectra (from an identified subset, see Methods) contained a peak frequency of approximately 25 kHz (Figures 2a, 2b, and Table 2). Whistles were uncommon. Inter-click intervals (ICIs) were 0.32 (± 0.09) seconds during 17 selected click trains taken from the first foraging dive.

CEE Response. Localized elevations in fluke rate, root-mean-square (RMS) flow noise (indicative of swim speed), and Overall Dynamic Body Acceleration (ODBA)¹⁴ were sustained through the exposure period (Figure 3a–3d), as well as at the end of the tag record. Though a slight shift in travel direction is evident in raw heading (Figure 3e) and the surface focal follow track (Figure 4) around the time of exposure, heading variability did not change appreciably during exposure. Changes in RMS flow noise levels during exposure suggested an increase in speed from approx. 1.4 m/s (before exposure) to 3.0 m/s (during), and returning to 1.5 m/s (after). Sonar transmission time of flight calculations similarly showed animal movement away from the sound source at 2.4 m/s during exposure.

Mahalanobis distance change-point analysis was used to identify a response period that began 3.1 minutes after the start of the MFA exposure, and continued until 1.6 minutes after the end of the exposure (Figure 3h). Mahalanobis distance was not calculated for the end of the tag record because of a tag shift to a location with much more animal body movement (see Methods). Received levels (hereafter RLs, in dB re 1 μ Pa RMS) of sonar on the tag began at 100 dB at exposure onset (first transmission was detectable), and increased to a maximum of 138 dB, which occurred during the first exposure dive. Received levels then decreased (presumably as the animal moved away) to a mean level of 109 dB in the period from the first surface interval after onset through the end of the exposure (Figure 3a, right axis). The most recent sonar transmission before the identified response had an RL of 127 dB. Some sonar received levels could not be measured due to flow noise and surfacing noise on the tag.

The shape of the first two exposure dives was qualitatively different than other dives of the same type (Figure 5), with the exposure shallow dive being deeper and longer than others in its class. The dive-by-dive statistical analysis also showed that the dive behavior changed in response to the CEE, with response intensity (RI) dependent on exposure RL and decaying with time post-exposure. This exposure effect extended several dives beyond the exposure period (approximately 1.5 hours post-exposure), suggesting a

Table 1 | Dive statistics for tag deployment on a Baird's beaked whale. Dives were classified as shallow, intermediate, or deep based on maximum depth. Values for shallow and intermediate dives represent means for all dives in the class (standard deviations in parentheses); values for each deep dive are presented individually. *Tag fell off on the ascent of Deep dive 3, after 73 minutes. This dive's duration was estimated based on a continuous ascent at the current rate. Ascent pitch and rate were excluded because only a short portion of the ascent took place with tag attached

Dive type	Duration (min)	Max Depth (m)	Ascent pitch (degrees)	Ascent rate (m/s)	Descent pitch (degrees)	Descent rate (m/s)	Bottom time (min)	Following surface interval (min)	Mean absolute roll during bottom time (degrees)	Variability in heading	Percent time clicking (by the group)	Longest continuous period of clicking (s) (by the group)	Number of pulsed sounds (by the group)
Shallow (n = 18)	10.5 (4.4)	22.8 (15.2)	5.5 (11.1)	0.1 (0.2)	-7.2 (9.6)	0.2 (0.3)	4.5 (3.7)	3.2 (1.3)	8.6 (7.5)	0.07	1%	1	0 (0)
Intermediate (n = 17)	21.9 (3.7)	323.8 (49.6)	22.9 (8.9)	0.8 (0.2)	-25.1 (11.4)	0.8 (0.2)	9.4 (1.8)	4.1 (1.9)	8.5 (4.9)	0.02	4%	12	2 (7)
Deep 1 (no foraging)	51.4	1058.2	16.4	0.9	-32	1	19.9	4	10.7	0.06	23%	73	6
Deep 2 (foraging)	55.7	945	15	0.9	-60.8	1.8	34.1	3.1	138.1	0.02	59%	1894	51
Deep 3 (foraging)	81.7*	1410.5	n/a	n/a	-22.1	1.1	47.6	n/a	129.5	0.06	51%	3157	30

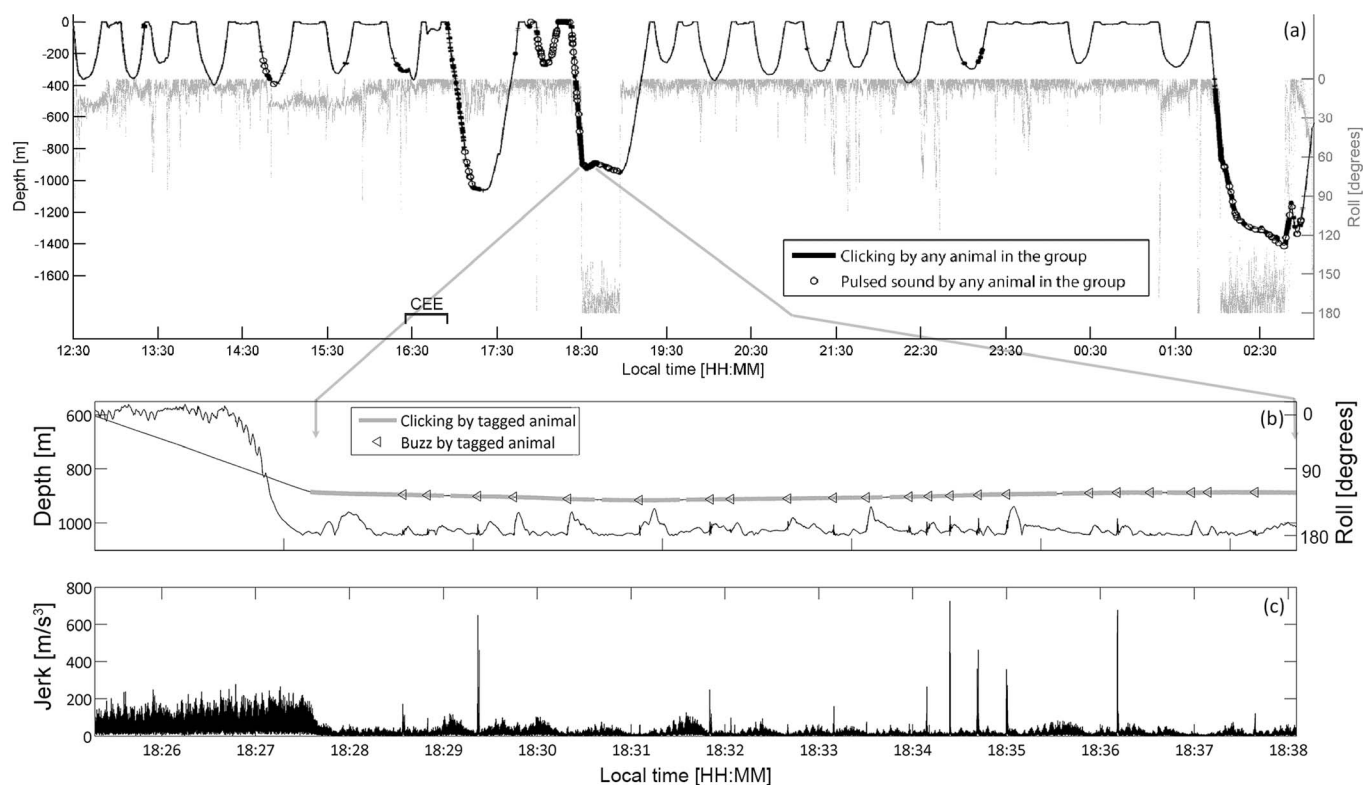


Figure 1 | Dive behavior of tagged Baird's beaked whale and sound production behavior of the group. (a) Left axis (black): Dive profile showing entire tag deployment (CEE = Controlled Exposure Experiment, see detail in Figure 3). Sound production of *any animal in the group* is overlaid on the dive profile. Pulsed sounds of all types were grouped together for the purposes of this display to avoid uncertainty in focal animal identification (see Methods). Note that high density of pulsed sounds are difficult to resolve at this scale – see detail below. Right axis (gray): Absolute value of roll of the tagged animal during entire tag deployment. This metric ignores left/right direction, and a value of 180 indicates the animal is completely upside down. (b) and (c) Detail of a portion of the second deep dive, as the animal initially reaches the bottom phase. (b) Depth on left axis (straight line descending from 600 to ~900 m). Clicking periods (thicker gray line) and buzzes (triangles) of the focal animal were identified manually using a spectrogram of the acoustic record. The marker indicates the end point of the buzz. Roll on right axis, depicted as in panel (a). Roll is the more jagged line descending to a value close to 180. (c) Jerk (rate of change in tri-axial acceleration), indicating quick changes in body movement (values are higher in the beginning due to fluking activity during descent).

slightly longer response period than that identified by the change-point analysis (Figure 6).

Discussion

This dataset provided the first synchronized dive, kinematic, and acoustic data for Baird's beaked whales, and also documented a change in behavior coincident to a simulated MFA sonar exposure.

The tagged animal in our study exhibited shallow, intermediate, and deep dives, consistent with the only previous Baird's beaked whale tag deployment¹⁰. However, the addition of acoustic and body orientation sensors allowed identification of inverted foraging, which is a unique and intriguing aspect of this dataset. Rolling maneuvers prior to and during feeding events have been documented in many cetaceans, including both baleen whales^{15–17} and odontocetes^{18,19}. Captive harbor porpoises may also roll during prey capture²⁰, but may not always turn completely upside down²¹. Sustained inverted foraging for durations as long as the complete bottom phase of a foraging dive has not been as widely documented. Frstrup and Harbison²² hypothesized that sperm whales may locate prey visually by swimming upside down so as to identify the silhouettes of prey against the light of the surface, but while tag studies have shown rolling maneuvers during prey capture in this species, these whales do not seem to spend the entire bottom phase of a dive upside down^{19,23}. Short bursts of upside-down maneuvering are reported in dolphins chasing prey near the surface, but these animals also generally right themselves after prey capture attempts^{24,25}.

Narwhals have been shown to spend a large portion of their time in a supine position, especially near the bottom²⁶. However, this orientation was not tightly paired with foraging behavior as was that of our tagged Baird's beaked whale, which spent the entire bottom phase of both foraging dives upside down. Slight changes in roll occurred during presumed prey capture attempts (as indicated by pulsed sounds associated with steady echolocation), but the whale returned to an inverted orientation rather than swimming upright until another prey item was found. The continuous upside-down orientation indicates that the search, as well as the fine-scale localization, may be more efficient in an inverted position. Rolling to an inverted orientation has been hypothesized to broaden the search area covered by a narrow, directional sonar beam²⁷, and also to decrease surface reflections when foraging near the surface given a slightly upward facing beam²⁵. We do not know for certain how close our tagged animal was to the seafloor, and were unable to determine this using acoustic echo techniques with the tag data. However, the seafloor depths associated with the surfacing positions immediately preceding and following the foraging dive shown in Figure 1b were 817 and 828 m, respectively (Bathymetric data from NOAA, National Geophysical Data Center at 3-arc second resolution, extracted using Mysticetus, Entiat River Technologies, V 1.8.0.124). The tag data indicate the animal foraged at ~900 m, so it is likely that the Baird's beaked whale was swimming close to the seafloor throughout the dive. This may imply a downward facing echolocation beam, since otherwise the inverted orientation would

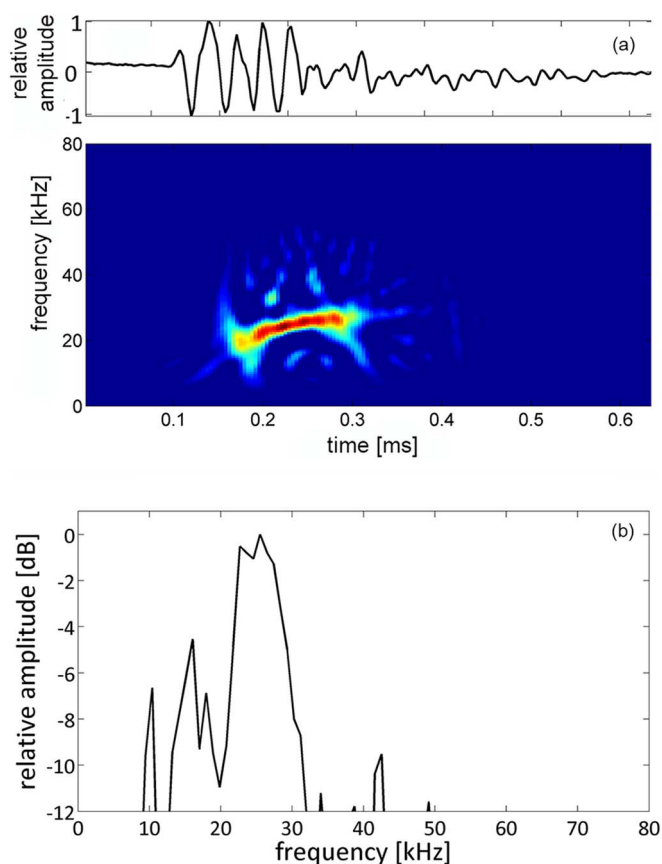


Figure 2 | Representative sample of Baird's beaked whale echolocation click. (a) Time waveform and time–frequency (Wigner-Ville) distribution of a typical click. (b) Spectrum of a typical click (high pass filtered above 1 kHz, FFT size 256).

arguably produce more interference from seafloor reflections. While this may be an unusual pattern by a single individual, the behavior merits further study.

The majority of sound production recorded during our tag deployment was during the latter two deep dives, and consisted mostly of echolocation clicks and pulsed sounds interpreted to be foraging buzzes. Click parameters were consistent with previous passive acoustic data from Baird's beaked whales. Individual clicks previously measured averaged 463 μ s in duration, with the largest spectral peak between 22 and 25 kHz¹¹, as compared to 479 μ s and 24.6 kHz in this study. These frequencies are lower and durations longer than those recorded from some of the best studied beaked whale species, including Blainville's beaked whale (*Mesoplodon densirostris*) and Cuvier's beaked whale (*Ziphius cavirostris*) (both show a flat spectrum between 30–48 kHz, and durations of 250 and 175 μ s, respectively)²⁸ and Northern Bottlenose whales (*Hyperoodon ampullatus*, 43 kHz center frequency and 207–377 μ s duration)²⁹. The clicks we recorded are similar in frequency to biosonar pulses of another large beaked whale species, Longman's beaked whale (*Indopacetus pacificus*, 24.7 kHz peak frequency and 288 μ s duration)³⁰, but longer in duration. A combination of parameter comparisons may therefore indicate size, if not species, of

beaked whale in acoustic recordings of unknown origin. Also of note is that the \sim 300 ms ICI here was similar to ICIs reported for tagged Blainville's (200–500 ms)¹⁸ and Cuvier's beaked whales (400 ms)²⁸. This may indicate stereotypy in beaked whale clicking behavior that could help distinguish this class of marine mammals from other groups when encountering unknown species in passive acoustic data.

These data are based on a small dataset of clicks that were the strongest clicks within high-dynamic range (non-focal) click trains, but we recognize that if none of the conspecifics in the group echolocated on the tag, it is possible that no truly on-axis clicks were recorded. Also, if larger beaked whales, like Baird's and Arnoux's (*Berardius arnuxii*), click with substantially lower frequency energy³¹, the low-frequency diagnostic to identify tagged animal clicks (see Methods) may not be as effective for these species. However the concordance of our results with previously published descriptions based on passive acoustics¹¹ is indicative that our selected click set is representative of non-focal clicks in this case.

A change in behavior coincident with the CEE is apparent in several of the recorded data streams. All three dives that occurred during the exposure period were notably different from others in their respective categories. The exposure shallow dive was deeper than any of the other shallow dives, and while the exposure intermediate dive was not the deepest in its class, there was an abrupt change in vertical direction (where the whale appeared to temporarily abort its ascent) that was coincident with the onset of exposure, a pattern not seen in any other intermediate dives. A similar abrupt reversal of direction was also recorded near the end of the last deep dive, just before tag detachment and in the absence of sonar exposure, so it is possible that such vertical displacement occurs within normal dive behavior. Elevated ODBA and RMS flow noise also occurred during this latter portion of the tag record. It is likely that the tag attachment was weak at this point, as evidenced by sliding noises in the acoustic record and the tag's imminent detachment. If the tag became loose and/or slid to a point further back on the body, this might have caused a response from the whale, indicated by these measured parameters. But even if the animal was not reacting to detachment, a tag sliding to a location further back on the peduncle, for example, would be subject to artificially high movement (ODBA) and flow noise levels. This explanation would not explain the dramatic change in depth readings on the tag, but as the animal was probably foraging near the sea floor and in an area with more varied bathymetry, the change in vertical direction may have been associated with changes in habitat or prey characteristics, neither of which should have affected a mid-water intermediate dive. These differences plus the coincident timing of the intermediate dive's direction reversal with the onset of the controlled exposure (confirmed by acoustic sensors in the tag) support the conclusion that this vertical direction change in the exposure intermediate dive is part of a response to the simulated sonar.

The deep dive that began near the end of the exposure period was also unusual in that it had no indication of foraging behavior; only intermittent clicks and some unclassified pulsed sounds were recorded during the dive, and the animal remained upright throughout it. This was unlike the other two deep dives, where nearly continuous echolocation was recorded and the animal remained inverted throughout the bottom phase. It is possible that non-foraging deep dives could be one type of response to disturbance for beaked whales^{10,32}.

Table 2 | Acoustic parameters (and standard deviations) of non-focal clicks. Clicks selected ($n = 23$) are those within 3 dB RMS received level of the strongest click in each click train that registered greater than 15 dB dynamic range (see Methods)

Duration (μ s)	Peak frequency (kHz)	Center frequency (kHz)	3 dB Bandwidth (kHz)	RMS Bandwidth (kHz)	Inter-click interval (sec)
479 (51)	24.6 (7.3)	28.2 (3.0)	4.4 (5.5)	12.1 (1.1)	0.32 (0.09)

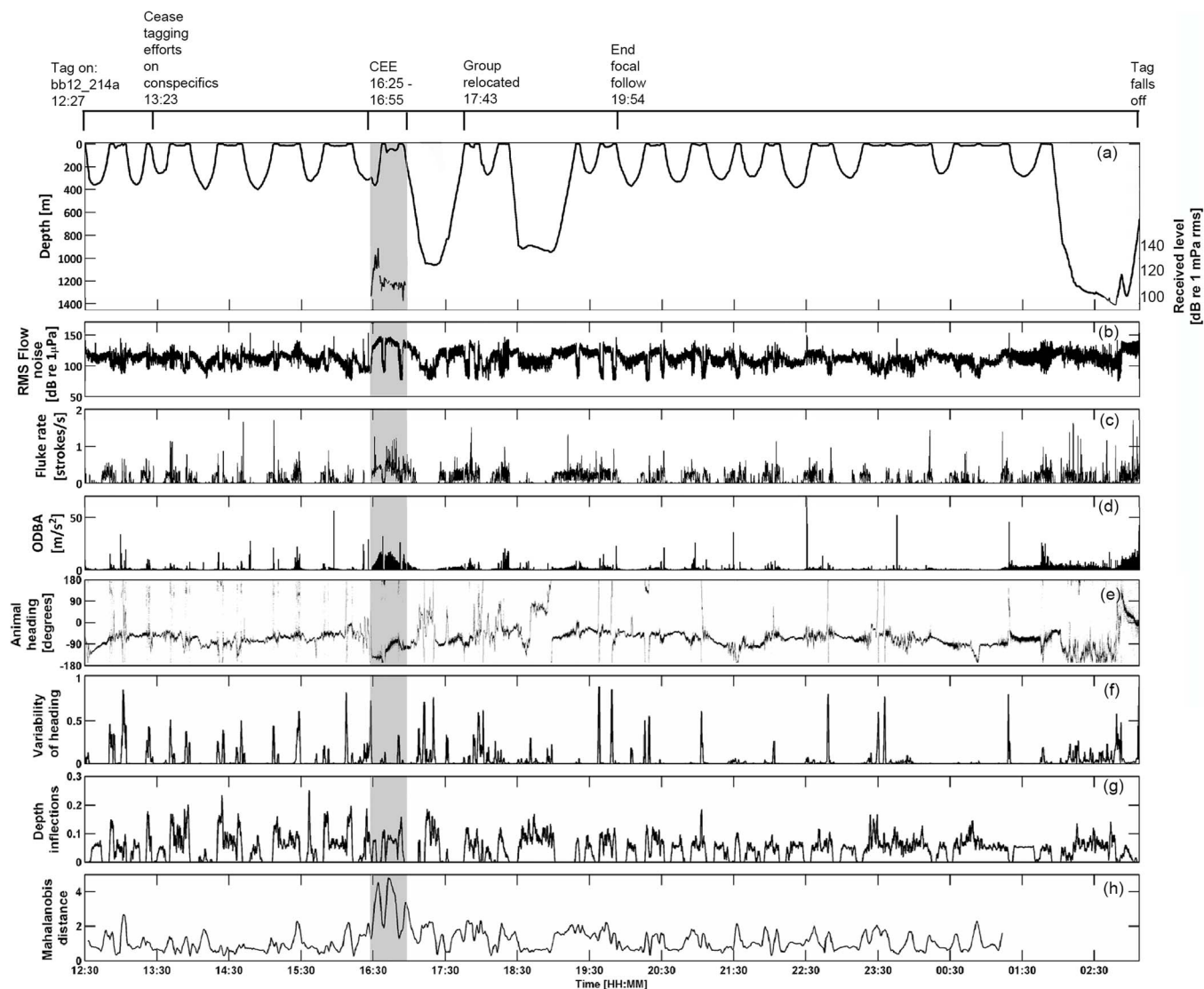


Figure 3 | Baird's beaked whale DTAG deployment and controlled exposure overview. (a) The dive profile, including a timeline of events (above) and exposure received level (right). Below are related parameters during tag deployment in the following order: (b) RMS flow noise (66–94 Hz pass band), a proxy for relative speed; (c) Fluke rate (strokes/second); (d) ODBA (Overall Dynamic Body Acceleration) averaged over 5 seconds; (e) Raw heading (degrees); (f) Variability of heading (varies from 0 to 1); (g) Depth inflections (a measure of the “wiggleness” of the dive profile, varies from 0 to 1); (h) Mahalanobis distance metric estimating response intensity. The exposure period is shaded gray for all panels.

Localized elevations in flow noise, fluke stroke rate, and ODBA are apparent during the CEE, and the change-point analysis identified a response period for the tagged animal that began 3.1 minutes after the start of the MFA exposure, and continued until 1.6 minutes after its cessation, supporting the hypothesis that an overall change in behavior was evident during the controlled exposure. The dive-by-dive analysis indicated an even longer response period. There may also have been some effect on feeding, due to the lack of acoustic foraging behavior in the first deep dive. RMS flow noise indicated an increase in speed during exposure, and sonar transmission time of flight calculations showed animal movement away from the sound source during exposure. These variables all suggest that the tagged animal in this study demonstrated an avoidance response for the duration of the exposure³³. In contrast, variability of heading did not decrease (indicating directed movement in one direction) appreciably during exposure, and raw heading showed only a slight shift in direction during exposure, but not a dramatic or prolonged heading change (Figure 3), which is less indicative of avoidance³³. Heading related data in general were more variable from dive to dive overall,

and the pattern of this variability was not related to the exposure phase. Thus, a qualitative severity response scale^{34,35} interpretation of the response might classify several aspects; moderate to prolonged changes in locomotion and dive profile (5); modification of vocal behavior and possible effect on foraging behavior (5), and possible moderate avoidance of the sound source (6).

The biological significance of these changes is difficult to assess given the paucity of data from this species. However, while other Baird's beaked whale datasets are unavailable for comparison, the fine-scale picture obtained from the suite of sensors on these tags allows us to identify changes in behavior of this animal relative to its own patterns and to the timing of a known potential disturbance. These results are the first indication that this species of beaked whale may have some level of sensitivity to simulated military sonar sounds from a nearby source.

This type of response also exhibits similarities to those documented from other beaked whales. *Mesoplodon* in the Bahamas stopped beaked clicking and showed an avoidance response to real and simulated sonar at RLs of approximately 140 dB, and in some cases animals did

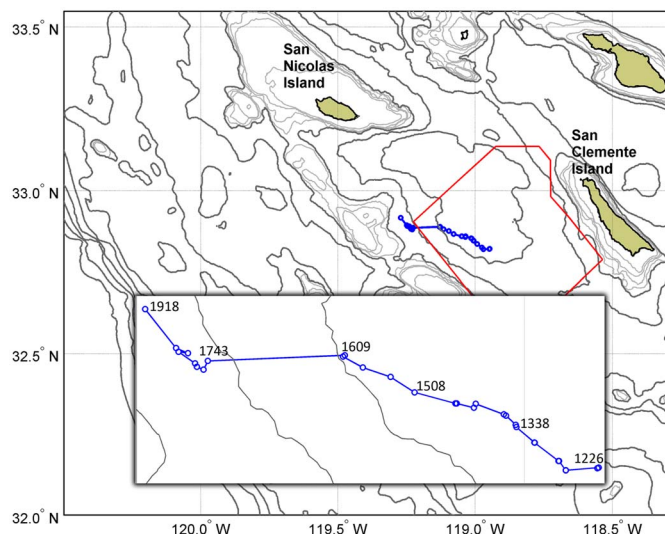


Figure 4 | Surface track derived from the focal follow of the group of Baird's beaked whales during the first 5.5 hours of tag attachment. Controlled exposure experiment began at 16:25 and ended at 16:55. The positions represent surfacings; travel under water was not necessarily in a straight line. Red box outlines the Southern California Anti-submarine warfare Range (SOAR). Map was created in MATLAB R2013b using a Mercator projection.

not return to the area until 2–3 days later¹². Two tagged *Ziphius* off southern California also showed energetic fluking and elevated ODBA; delayed foraging; and swam away from the simulated sonar sound source at relatively high average speeds (2.6 m/s and 3.1 m/s for the two whales studied)¹³. These reactions began at 98 and 127 dB, respectively, and statistically identified response periods continued until 2.7 and 3.8 hours after exposure. The response of this tagged Baird's beaked whale based on the change-point analysis was shorter in duration than those of the other two species, and the intensity of the response based on the dive-by-dive analysis was less, but the 1.5 hour time decay for the dive-by-dive response was more similar to the *Ziphius* response¹³. Thus all beaked whale experimental

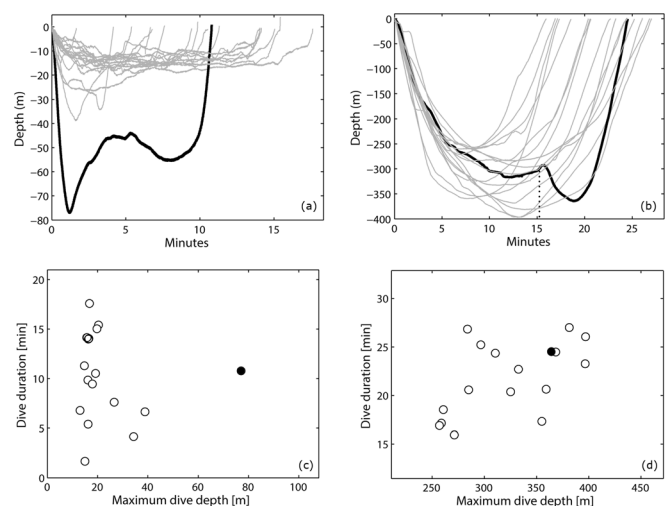


Figure 5 | Comparison of “shallow” and “intermediate” dives. (a) Shallow and (b) Intermediate dive depth profiles, with the exposure dives in black. The thicker black dotted line in panel (b) indicates the start time of the exposure, relating only to the black exposure dive trace. (c) Shallow and (d) Intermediate dives: Maximum dive depth vs. Dive duration in minutes. Exposure dives are filled black circles in each panel.

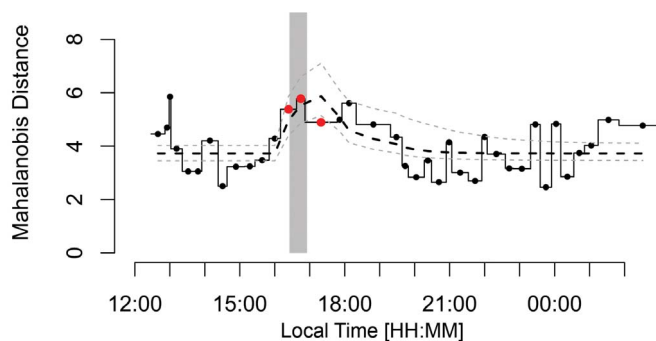


Figure 6 | Mahalanobis distance model with effect of exposure (RL-dependent) and time decay. Solid black line is data, with circles at the midpoint-time of each dive, colored red on exposure dives; dashed black line is expected distance based on the fitted model, and dashed grey lines span a 95 percent confidence interval for that expected distance (from a parametric bootstrap). The exposure period is shaded grey.

studies so far show evidence of avoidance responses at relatively low received levels compared to those for many other species³⁴, including many blue whales exposed during MFA CEEs in the same experiment³⁶. We hope that these results form a foundation for future research that will give a complete picture of the range of behavior exhibited by Baird's beaked whales, to further resolve the severity of behavioral change in response to anthropogenic disturbance.

Methods

These data were collected as part of the Southern California Behavioral Response Study (SOCAL-BRS), the methodology of which is described in detail elsewhere³⁷.

Fieldwork. On 1 August, 2012, a Baird's beaked whale (*Berardius bairdii*) in a group of seven conspecifics was tagged using a version 3 DTAG (acoustic sampling rate 240 kHz; pressure and tri-axial accelerometers and magnetometers sampling rate 200 Hz, down-sampled for some analyses). A focal follow to confirm direction of travel was conducted on the animal from a 6.5 m rigid-hulled inflatable boat (RHIB) from about a 300 m distance, while the primary research platform, the *R/V Truth*, remained within 3 km throughout.

A controlled exposure experiment (CEE) was conducted beginning at 16:25 PDT, during which a stereotypic, simulated mid-frequency active (MFA) military sonar signal was transmitted (*R/V Truth* approximately 2.7 km from whale group at last surfacing). A custom vertical line array sound source was deployed to a depth of 30 m and transmitted the 1.6 s MFA sonar signal every 25 s. The initial source level of 160 dB re: 1 μ Pa was increased by 3 dB per transmission for the first 8 minutes to a maximum of 210 dB for 22 additional minutes (72 transmissions total over 30 minutes). After filtering with a 1/3 octave band Finite Impulse Response (FIR) filter centered at 3.7 kHz, received levels (RLs) on the tag for each sonar transmission were calculated over 200 ms windows. The levels reported for each transmission are the highest in any window over the full duration of that transmission¹², and are reported in dB re 1 μ Pa root-mean-square (RMS).

After the start of exposure, focal follow sightings became less frequent due to changes in whale behavior and declining observation conditions. The MFA CEE ended at 16:55, and the *R/V Truth* continued to track the Baird's beaked whale group from a distance. At 17:45, a RHIB resumed the focal follow until 19:54, when operations were suspended for the day due to nightfall and worsening weather conditions.

Animal movement analysis. Tag sensor data were calibrated for temperature offset (pressure) and orientation offset from tag placement on the whale (accelerometers and magnetometers) before analyses were begun. We defined a dive as any excursion to a depth below 10 m in order to capture “shallow” dives as previously described for this species¹⁰. The animal was considered to have reached the surface at 1 m depth. The “bottom depth” of each dive (used in determining bottom time and points of ascent/descent, but different than “Max depth” in Table 1) was defined as 85% of the maximum depth for that dive³⁸. Maximum depth was used to separate the three dive categories, “shallow” (<100 m), “intermediate” (>100 m and <900 m), and “deep” (>900 m).

Overall dynamic body acceleration (ODBA) was calculated as described by Qasem et al¹⁴, using 200 Hz accelerometer data with a 5 second running mean. Rate of change in triaxial acceleration, or “jerk”³⁹, was also calculated at a 200 Hz sampling rate as a proxy for quick body movements or potential prey capture events. Sensor data were decimated to 10 Hz for all other calculations except fluke rate, which was calculated at 1 Hz. Fluke strokes were identified as cyclic variation in the pitch record with magnitude greater than 3 degrees and with a period between 0.3 and 4 seconds, as used to



calculate fluke rate in other beaked whale species³. Dive profile inflections were defined as the proportion of zero-crossings in the first difference of the dive profile, calculated in sliding one minute windows and then averaged over the entire dive. When included in quantitative analyses, absolute heading was decomposed into its sine and cosine components, and heading variability was calculated as the circular variance in heading over a one minute window. Speed estimation was based on vertical velocity divided by the sine of body pitch angle to calculate speed during steep descents and ascents⁴⁰, which was then correlated to RMS flow noise (64–94 Hz band) during those times for an overall conversion factor applied to the rest of the tag record^{41,42}.

Acoustic analysis. The acoustic recording was first audited manually through detailed listening and visual examination of the spectrogram. All biological sounds were marked, including whistles and biosonar pulses (here termed “clicks”) potentially produced by other whales in the group. All series of fast-repetition clicks were conservatively marked as “pulsed sounds”, but when associated with continuous echolocation clicks, were further interpreted as foraging buzzes (prey capture attempts).

Following the audit, a supervised click detector as in Arranz et al.⁴³ identified clicks containing a low frequency energy component (between 1 and 5 kHz), which is considered diagnostic of tagged, or “focal”, animal click production in odontocetes¹⁸. These hypothesized focal animal clicks were then highlighted in a click display showing angle of arrival (based on time difference of arrival using cross-correlation of the waveform data from the two tag hydrophones). Click trains from non-focal individuals were identified manually based on a rapidly changing angle of arrival (as the animal swam past the tag) or a substantially different angle of arrival from that of the focal clicks, as well as a higher received level and a less distorted waveform than the focal clicks.

This method was only successful during the first portion of the first deep foraging dive, because fewer animals in the group were producing clicks in close proximity to the tag and there was less overlap between click trains. Also, the tag shifted further back on the animal prior to the second deep foraging dive, to a position with less resolution on the angle of arrival calculation, and less difference in amplitude between focal and non-focal clicks. We therefore used only non-focal clicks identified during the first portion of the first foraging dive to characterize general click parameters and inter-click intervals (ICIs), and only focal clicks during the same period to characterize correlated acoustic-movement behavior.

Because Baird’s beaked whale echolocation clicks, like those of other odontocetes, are likely to be highly directional, off-axis clicks may show great variation in amplitude, duration, and spectral characteristics⁴⁴. For example, Madsen et al.⁴⁵ showed close to 20 dB (re 1 μ Pa peak-peak) and 28 kHz difference in center frequency between an on-axis click and the same click recorded from 10 degrees off-axis. This variability resulting from beam pattern, compounded with rapid heading changes or body movements by free-ranging animals, complicates identification of on-axis clicks. Therefore, we further refined our subset of 707 non-focal clicks by selecting click trains with high dynamic range (greater than 15 dB difference in RMS received level between the strongest and weakest clicks). Within those high dynamic range click trains, clicks with RMS received levels within 3 dB of the strongest click were selected for analysis ($n = 23$), in an attempt to describe clicks that were as close to on-axis as possible⁴⁶. Unfortunately our dataset did not allow more stringent criteria to be applied, as has been done in previous studies. Given the large number of clicks on the tag acoustic record, our non-focal click set was small, but there were few clicks with clean waveforms that were likely to be on-axis.

Before analysis, all clicks were mean-subtracted to remove DC offset and a 4th-order Butterworth high-pass filter at 1000 Hz was applied to remove low frequency flow noise. Click duration was calculated using a 97% energy criterion, where the start and end points of the analysis window were defined as the times when the sound exposure level (SEL) of the click reached 1.5% or 98.5% of its total value, respectively⁴⁵. Peak frequency (maximum of the click spectrum, 256-point FFT, bandwidth resolution = 937.5 Hz), center frequency (energy midpoint of the spectrum), 3 dB bandwidth (frequency band between the lower and upper half power points in the frequency spectrum), and RMS bandwidth (frequency band encompassing the standard deviation of the spectrum about the center frequency) were calculated as in Au et al.⁴⁴.

CEE response. We attempted to statistically identify significant changes in whale behavior over the entire tag record (change-point analysis) using a metric based on Mahalanobis distance⁴⁷, similar to that applied to the analysis of behavioral responses in Cuvier’s beaked whales¹³. The goal of this part of the analysis was to pinpoint the time (if any) at which behavior changed, rather than to assess whether specific exposure and post-exposure dives were unusual. Input variables for the change-point analysis included fluke rate, ODBA, RMS flow noise, raw animal heading (decomposed into sine and cosine components), variability of heading, and depth inflections, as in Figure 3. Depth data were excluded to focus on animal movements without respect to dive type. We used data from the pre-exposure period as baseline data. We then calculated the Mahalanobis distance between 1) the average data values for the baseline period and 2) the average data values within a 5-minute “comparison” window, which slid forward over the dataset with 90 percent overlap.

Mahalanobis distance calculation requires a variance/covariance matrix for all input variables. Because of the lack of baseline data for both our tagged individual and the species in general, we used a variance/covariance matrix calculated for the entire dive dataset in all calculations. Including the exposure period is conservative in that it

will reduce the apparent distance between truly unusual behavior and the “average”. In addition, the variability structure changed after the tag position on the animal shifted approximately 12 hours in to the tag deployment (well after the controlled exposure). To clarify analyses, data were truncated at the point of this shift for the purposes of change-point analysis only.

Change-points in the resulting Mahalanobis distance time series were identified using a simple resampling method, sampling 10,000 random contiguous blocks of the same duration as the exposure from the baseline period (with replacement) to find the expected maximum distance under the null hypothesis (no change in Mahalanobis distance during exposure). The response period was defined as the period when distance values exceeded the 95th percentile of these expected distances.

In addition to the change-point analysis, we evaluated the whale’s behavior on a dive-by-dive basis. Following DeRuiter et al.¹³, we calculated a Mahalanobis-distance-based metric for response intensity (RI) for each full dive. This metric quantified how much each dive differed from the average dive of the same type. Input variables into this calculation included those from the change-point analysis, as well as those listed in Table 1 (maximum depth, dive duration, bottom time, descent and ascent pitch and rate, following surface interval duration, roll during the bottom phase of the dive, total number of pulsed sounds (buzzes or burst pulses) from any animal in the group, percent of time clicking (by any animal in the group) over the course of each dive, and longest continuous period of clicking on the acoustic record for that dive), averaged for each dive. “Continuous” was defined as a time period in the acoustic record during which clicking by the tagged whale or other group members was present without a break of longer than twice the previous inter-click interval.

We then modelled this RI as a function of (a) maximum RL and (b) time since sonar exposure¹³. RI was modelled with a Gamma distribution, according to

$$RI = \beta_0 + \sum_{i=1}^n x_i(t), \quad x_i(t) = \begin{cases} \beta_1 RL \tau_i e^{\beta_2(\tau_i - t)} & \text{if } t \geq \tau_i, \\ 0 & \text{otherwise} \end{cases}$$

is the number of exposure dives, $RL\tau_i$ is maximum received level during dive number τ_i (the i th exposure dive), and $[\beta_0, \beta_1, \beta_2]$ are parameters estimated by maximum likelihood in R software⁴⁸; the best model had parameters (standard errors) $[\beta_0, \beta_1, \beta_2] = [1.32 (0.04), -4.72 (0.28), 0.46 (0.19)]$. We compared the full model with a nested set of models with fewer covariates using Akaike’s information criterion (AIC), finding that the full model was best ($\Delta AIC \geq 10.4$).

Acoustically-based estimates of relative source-whale range were determined by calculating the difference between inter-transmission intervals from signals recorded on a monitor hydrophone (at the source location) and tag hydrophone during exposure. The difference in seconds was converted to a relative range in meters, and then to a whale swim speed relative to the source. These methods are further described in DeRuiter et al.¹³.

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Author contributions

A.K.S., S.D.R., E.A.F., J.A.G. and G.S.S. contributed to data analysis. B.L.S., D.M., A.S.F. and J.C. contributed to experimental design. All authors contributed to fieldwork and writing the manuscript.

Additional information

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