Received: 3 June 2022 | Accepted: 14 October 2022

DOI: 10.1111/mms.12987

NOTE

Marine Mammal Science

Beaked whale dive cycle estimation based on acoustic data from drifting recording systems

Jay Barlow[1] | Jennifer L. K. McCullough[2]

[1]National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center, California (retired)

[2]National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, Honolulu, Hawaii

Correspondence
Jay Barlow, 5072 Gasconade Avenue, San Diego, CA 92110.
Email: jaybarlow33@yahoo.com

Funding information
Bureau of Ocean Energy Management, Grant/Award Number: M17PG00024; NOAA Pacific Islands Fisheries Science Center; NOAA Southwest Fisheries Science Center; U.S. Navy, Chief of Naval Operations, Grant/Award Number: N0002518GTC032-06; U.S. Navy, Pacific Fleet, Grant/Award Number: N0007018MP4C587-01

Most beaked whales have a stereotypical diving behavior that consists of a long, deep dive separated by one or more shallower dives (Baird et al., 2008; Tyack et al., 2006). Acoustic recording tags show that echolocation pulses are commonly produced only during a portion of the long, deep dives (Johnson et al., 2004; Warren et al. 2017), which has led to the characterization of those dives as deep foraging dives. This echolocation period is highly synchronous within a group with an estimated 99% overlap among individuals (Aguilar de Soto et al., 2020). The period between the start of one deep foraging dive and the start of the next is referred to as a dive cycle (Tyack et al., 2006). Although two deep foraging dives can occur consecutively after a single surfacing series (a short series of surfacings to breathe; Schorr et al., 2014), foraging dives are more typically separated by several surfacing series and shorter dives to intermediate depths (Tyack et al., 2006). The dive cycle duration of beaked whales has been estimated as the sum of the deep dive duration and the inter-deep-dive interval (IDDI; Tyack et al., 2006) or as the inverse of the mean dive rate (the mean number of deep dives divided by the hours of observation; Schorr et al., 2014). The dive cycle duration is an important parameter in estimating acoustic availability for acoustic-based abundance estimation methods (Barlow et al., 2021).

Beaked whale diving is best known from tagging studies of two species: Cuvier's beaked whales (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*). The dive cycle components of these two species are characterized in Table 1 from several studies in different areas. Overall, mean dive cycles appear to be slightly longer for Cuvier's than for Blainville's beaked whales; however, dive cycle durations vary among study sites. Compared to these two species, dive cycle durations are poorly known for all of the 22 other beaked whale species. In large part, this dearth of information is due to the difficulty of tagging species that are found far out to sea and are relatively rare.

In examining our acoustic data from drifting recording systems, we found what appears to be consecutive dive cycles for beaked whales recorded on a single drifting recorder. If these signals are from the same group, the time between the starts of echolocation on two successive dives can be used as a proxy for dive cycle duration. This

 |

TABLE 1 Duration of dive cycles and their components from tagging studies of Cuvier's and Blainville's beaked whales. Dive cycle duration is estimated as the sum of the mean deep foraging dive duration (DFDD) and the inter-deep-dive interval (IDDI) or as the inverse of the dive rate (number of observed foraging dives divided by observation period). The DFDD includes a vocal phase as well as a silent ascent and descent. Values of some parameters are not available (na) from some studies.

Species	Study area	DFDD (hr)	Vocal phase (min)	IDDI (hr)	Dive cycle (hr) (DFDD+IDDI)	Dive cycle (hr) (1/Dive rate)	Source
Cuvier's beaked whale	Southern California	1.09	39.2	1.72	2.81	3.19	1
Cuvier's beaked whale	Hawaii	1.13	na	na	na	2.50	2
Cuvier's beaked whale	Ligurian Sea	0.97	32.8	1.06	2.03		3
Blainville's beaked whale	Hawaii	0.88	na	na	na	2.38	2
Blainville's beaked whale	Canary Islands	0.78	26.4	1.54	2.32	na	3
Blainville's beaked whale	Canary Islands	na	25.0	na	na	na	4

Note: (1) Barlow et al. (2020) and Barlow et al. (2021), (2) Baird et al. (2008), (3) Tyack et al. (2006), and (4) Aguilar de Soto et al. (2020).

might allow for acoustic-only estimates of dive cycle duration for the many beaked whale species that have never been tagged. There are, however, many reasons why these acoustic estimates of dive cycle might be less precise than estimates from tagging studies or be biased. Drifting recorders typically do not record a full record of echolocation from a foraging dive, even if the animals are relatively nearby. Barlow et al. (2021) estimate that the acoustic availability time for Cuvier's beaked whale (17.2 min) is less than half of the expected echolocation period for this species in their study area (39.2 min). Echolocation signals from beaked whales are highly directional (Zimmer et al., 2005) and signals are typically lost when animals are not oriented towards the hydrophone. The maximum detection range for on-axis signals is estimated to be ~4 km (Zimmer et al., 2008). Missed acoustic detections at the beginning of two consecutive foraging dives will add error to estimates of dive cycle durations but should not bias estimates. If an entire foraging dive is missed and the next foraging dive is detected, dive cycles will be overestimated by a factor of 2. If other groups of the same species are in the area, detection of the start of their foraging dives is likely to result in an underestimate of dive cycle duration. Estimation of dive cycle duration from acoustic-only data needs to be robust to the higher variance of estimates and to these potential sources of bias.

Here we estimate dive cycle durations from beaked whale echolocation pulses recorded on Drifting Acoustic Spar Buoy Recorders (DASBRs) from multiple studies in 2016–2021 (Barlow & Schorr 2018; Barlow et al., 2022; Keating et al., 2018; McCullough, Olsen, et al., 2021; McCullough, Wren, et al., 2021; Simonis et al., 2020; Yano et al., 2020). Study sites included the California Current (off the U.S. West Coast and west of northern Baja California, Mexico) and pelagic waters around islands of the central and western Pacific (main Hawaiian Islands and Mariana Archipelago). The DASBRs used a submerged digital recorder (SoundTrap ST4300 or Wildlife Acoustics SM3M) to record signals from two hydrophones (typically one HTI-92-WB and one HTI-96-min) configured as a vertical hydrophone array with a hydrophone spacing of either 5 or 10 m. Sample rates were 192, 256, 288, or 384 kHz and varied among studies. Recording durations were 2 min and were often duty cycled (e.g., 2 min every 5 or 10 min) to extend the recording times.

Beaked whale echolocation pulses were identified by analysts using PAMGuard software (Gillespie et al., 2009). The WAV recordings were preprocessed in PAMGuard to identify potential echolocation signals and to measure the vertical bearing angles to those signals using time-differences-of-arrival on the two hydrophones. The PAMGuard click detector module also color-coded the potential echolocation signals by peak frequency. Analysts then used PAMGuard Viewer to mark "events" consisting of beaked whale echolocation pulses received within a 2 min recording. Contextual cues (such as peak frequency and a bearing angle) were used to identify potential beaked whale echolocation pulses. Potential pulses were confirmed or rejected based on the waveform, frequency spectrum, and Wigner representations. Fuller descriptions of the data processing chain are given in Simonis et al. (2020), McCullough, Olsen, et al., (2021), and McCullough, Wren, et al., 2021.

Beaked whale echolocation pulses appear to be species-specific (Baumann-Pickering et al., 2013). Analysts classified "events" to species based on the closest match to a described echolocation pulse type. If a close match was not found, the event was excluded from our analyses. We included five beaked whale species groups in our analyses. Our identification of Cuvier's beaked whales, Blainville's beaked whale, Stejneger's beaked whale (*Mesoplodon stejnegeri*) and an unidentified beaked whale (designated BW43, possibly Perrin's beaked whale, *Mesoplodon perrini*) was based on pulse type characterizations given by Baumann-Pickering et al. (2013). Hubbs' beaked whale (*Mesoplodon carlhubsii*) echolocation pulses were characterized by Griffith et al. (2019) and were matched to species by Ballance et al. (unpublished data[1]). Another beaked whale pulse type (designated BWB) was described by Barlow et al. (2022) and may represent an undescribed beaked whale species. Because BW43 and BWB are difficult to distinguish and because both have not been definitively linked to a beaked whale species, we pool these in our analyses. We analyze Cuvier's beaked whales separately in the California Current and Pacific Islands regions.

Estimates of dive cycle durations were made by first identifying foraging dives. Adjacent 2 min recording periods with echolocation pulses from the same species were linked as "foraging dive events." Dive events with a period of silence greater than 33 min (the mean vocally active period for Cuvier's beaked whales; Tyack et al., 2006) were divided into two events at this break. Dive events shorter than 2 min (one recording period) were eliminated to avoid confusing short periods of echolocation (Warren et al., 2017) with a deep foraging dive. The resulting distributions of the dive event durations differed among species (Figure 1).

Next, histograms of times between adjacent dive events (of the same species) were plotted and the first mode of that distribution was used as a first approximation of the dive cycle duration. The distributions were found to have long tails (Figure 2), likely because a foraging dive may have been missed or another group might have been detected. To obtain a robust estimate of dive cycle durations, the median time between events was calculated only for those observations that were less than twice the first modal value (to avoid cases when one foraging dive was missed and the subsequent dive was detected). The resulting median values differ among species (Figure 2). Here we use the median time between successive dive events (excluding values greater than twice the mode) as an estimate of dive cycle duration.

In our study, the longest estimates of dive cycle durations are for Cuvier's beaked whales in the California Current (2.97 hr); however, the value for the same species in the Pacific Islands (2.60 hr) is less than that of two other species groups (Blainville's beaked whales in the Pacific Islands (2.75 hr) and unidentified *Mesoplodon* species in the California Current (2.83 hr)). The shortest dive cycles are for Stejneger's and Hubbs' beaked whales in the California Current (2.00 and 2.37 hr, respectively). Dive cycle durations appear to be correlated with acoustic encounter durations (Figure 3). Longer periods of echolocation may indicate longer foraging dives which would result in longer dive cycles, especially if those longer dives required longer IDDIs to recover oxygen stores for the next dive.

Our estimates of acoustic encounter durations (Figure 1) are likely to be biased under-estimates of the acoustically active period of beaked whale foraging dives. Our data were often duty cycled, which means that the actual beginning and ending of the acoustic period could be missed. Animals and our drifting recording systems are moving,

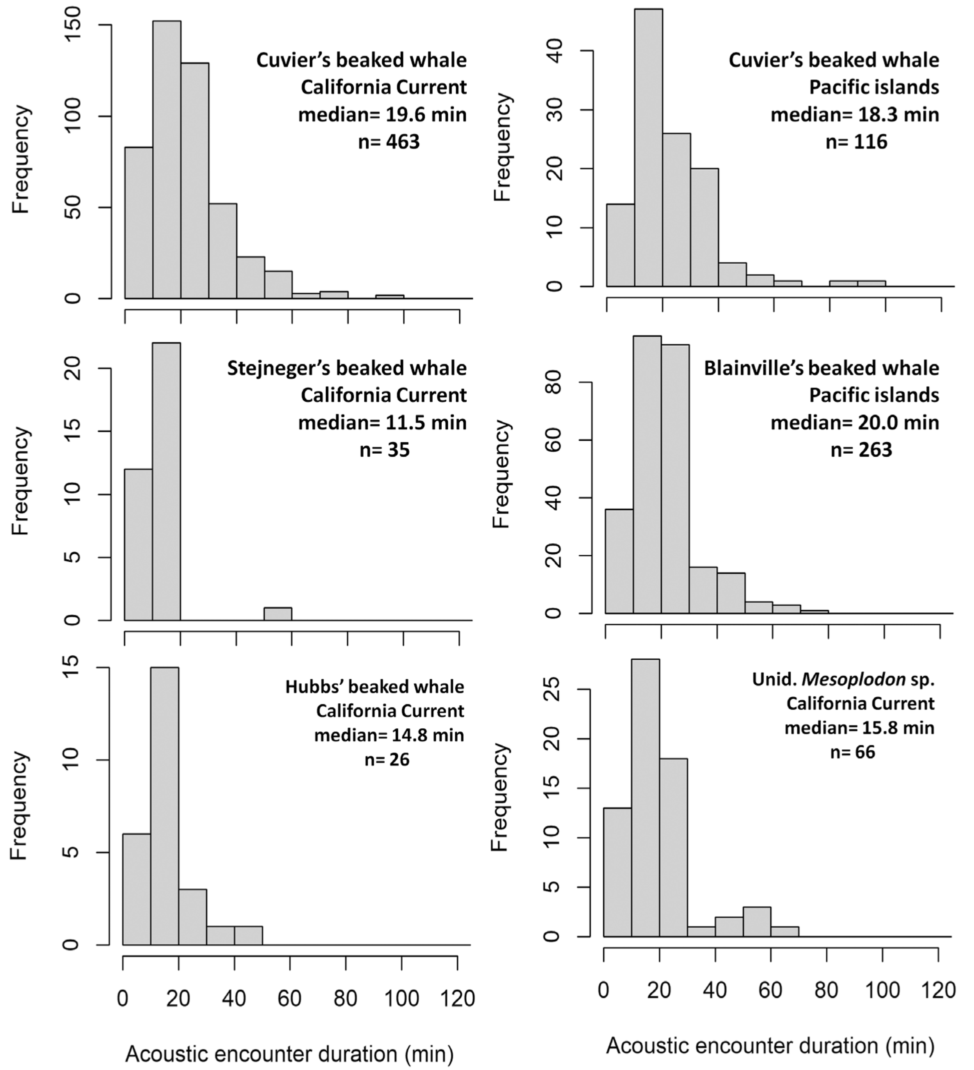

FIGURE 1 Distributions of acoustic encounter duration for beaked whale using drifting recording systems. Distributions include six beaked whale taxa in the California Current and Pacific Islands; unidentified *Mesoplodon* sp. represents a pooled category of acoustic detections that include the BW43 and BWB pulse types. Encounters of less than two min were excluded when calculating median encounter durations.

and animals might be outside the acoustic detection range of our recorders during part of an acoustically active period. Finally, animals are only likely to be detected if their echolocation beams are oriented in the general direction of the hydrophones, so acoustic encounter durations are likely to be shortened as animals turn during their foraging activities. However, we do not believe that our estimates of dive cycle duration are as likely to be affected by these factors. Although missing a true start time a first dive or a subsequent foraging dive would add error to the estimate of dive cycle duration, these errors should be unbiased if start times are equally likely to be missed for the first and for the subsequent acoustically active period. Clearly, however, the use of continuous recordings (avoiding duty cycles) is likely to reduce this source of error and improve estimates of dive cycle duration.

Results are generally consistent with estimates of dive cycle durations for tagged Cuvier's and Blainville's beaked whales (Figure 2). Tagging studies indicate that dive cycles for Cuvier's beaked whales in the California Current

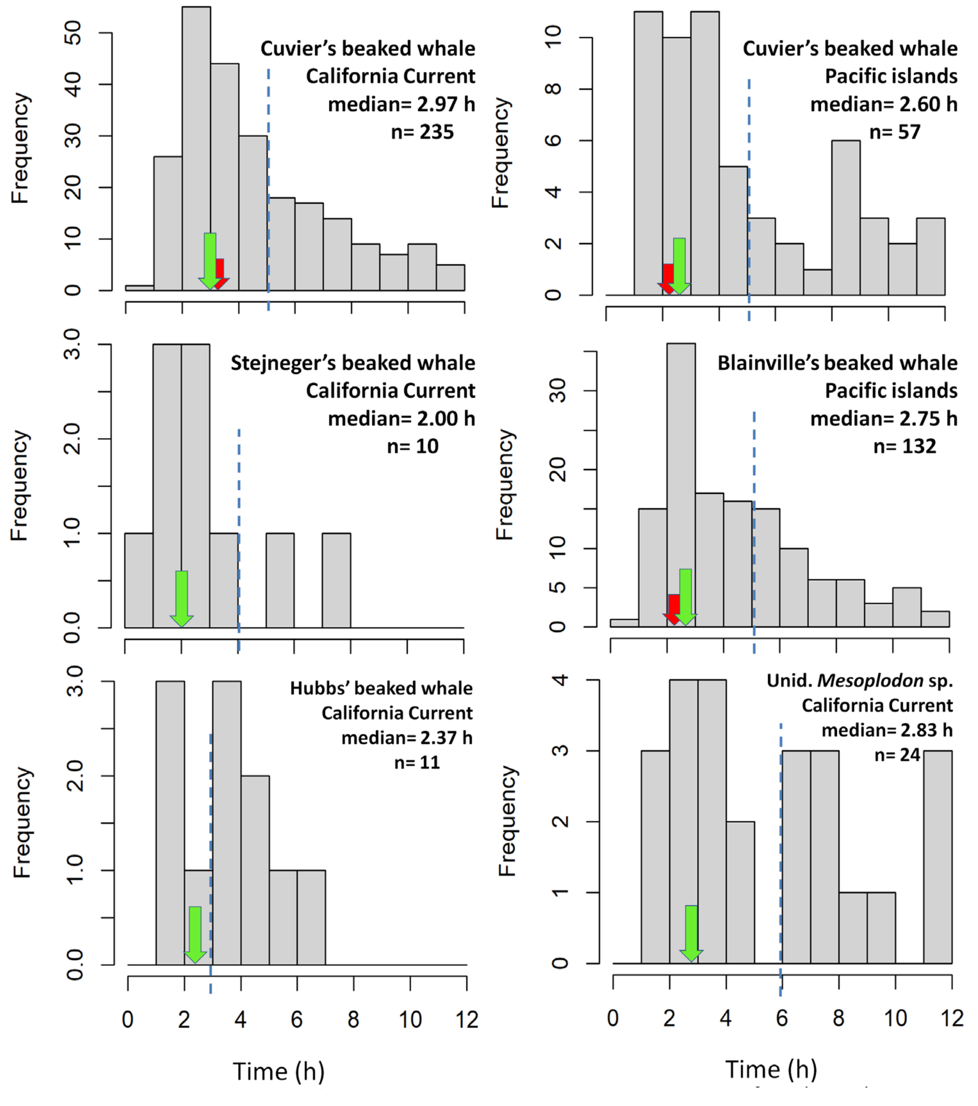

FIGURE 2 Distribution of times between the starts of echolocation for adjacent, acoustically-detected foraging dive events. Distributions include six beaked whale groups in the California Current and Pacific Islands; unidentified *Mesoplodon* sp. represents a pooled category of acoustic detections that include the BW43 and BWB pulse types. Median estimates of dive cycle duration (green arrows and text box within each plot) excluded times greater than twice the first mode (dashed line). Red arrows indicate the mean dive cycle durations estimated as the inverse of the dive rates measured from tagged whales in the given areas (Baird et al., 2008; Barlow et al., 2021a).

(Schorr et al., 2014) are longer than for the same species in Hawaii (Baird et al., 2008) and in the Ligurian Sea (Tyack et al., 2006). Regional difference in dive cycle durations for Cuvier's beaked whales are greater than some between-species differences.

No previous estimates of dive cycle durations or acoustic encounter durations are available for Stejneger's or Hubbs' beaked whales. It is also fair to assume that dive cycle durations have never been measured for the two unidentified *Mesoplodon* species that produce the BW43 and BWB acoustic pulse types.

Metabolic scaling models suggest that larger beaked whales should have longer maximum dive durations (Noren & Williams, 2000). Our estimates of dive cycle duration and acoustic encounter durations do not appear to

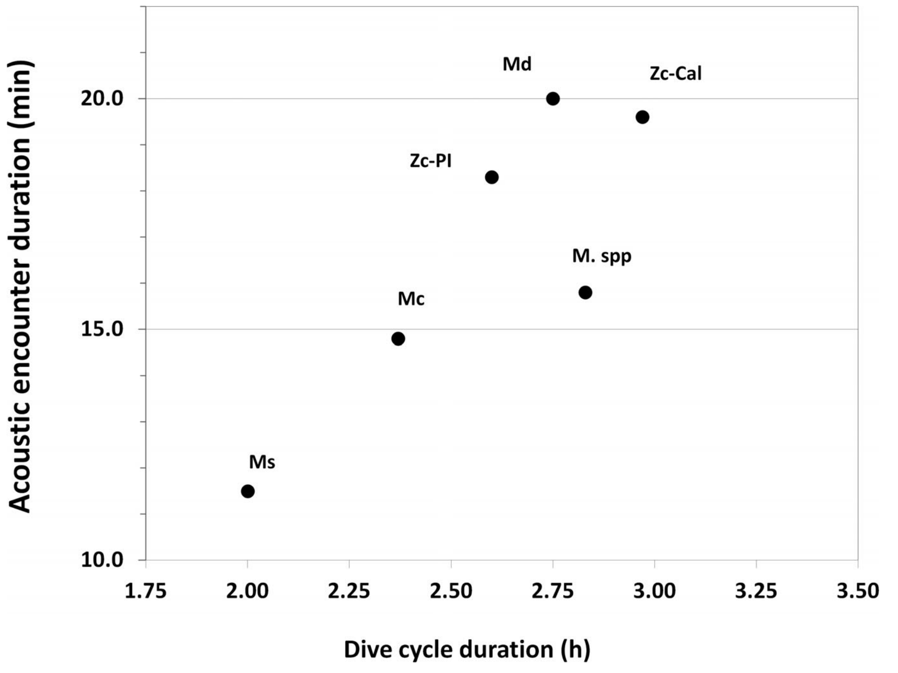

FIGURE 3 Empirical relationship between estimates of dive cycle duration and acoustic encounter durations for Cuvier's beaked whales in the California Current (Zc-Cal) and in the Pacific islands (Zc-PI), Blainville's beaked whale (Md), Hubbs' beaked whale (Mc), Stejneger's beaked whale (Ms), and unidentified *Mesoplodon* species (M. spp).

be related to body size. Although the largest beaked whale in our study (Cuvier's beaked whale) has the greatest values, the two larger *Mesoplodon* species (Stejneger's and Hubbs' beaked whales; Pitman 2009) have shorter dive cycles and acoustic encounter durations than Blainville's beaked whale (Figures 2 and 3). Typical dive times of beaked whales are much shorter than the maximum documented dive times (Schorr et al., 2014), and may be influenced more by local foraging conditions than by metabolic constraints. Although metabolic scaling may hold true at higher levels of analysis, local factors may be more important at local scales.

Dive cycle duration is an important parameter in estimating acoustic availability, which is used in acoustic estimates of population density (Barlow et al., 2021), and may be an important descriptor of beaked whale life history strategies. Previous estimates of dive cycles required data from tagged animals; however, only a few of the 24 species of beaked have been tagged. Our acoustic-only estimation method opens the door to obtaining estimates for many more species. Although our sample sizes are small for some species, we can still discern differences among species. Our estimates are similar to tag-based estimates for the species that have been tagged. If the observed relationship between acoustic encounter duration and dive cycle duration (Figure 3) is found to hold for more species, dive cycle times may be also estimated from this relationship, perhaps with a regression-based estimator.

AUTHOR CONTRIBUTIONS

Jay Barlow: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Jennifer L. K. McCullough:** Conceptualization; data curation; resources; supervision; validation; visualization; writing – review and editing.

ACKNOWLEDGMENTS

Acoustic data used in this note were from research surveys led by Eric Archer, Lisa Ballance, Amanda Bradford, Jim Caretta, Gustavo Cárdenas-Hinojosa, Karin Forney, E. Elizabeth Henderson, Marie Hill, Jeff Moore, Erin Oleson, Shannon Rankin, Greg Schorr, and J.B. We also thank Ann Allen, Annette Henry, Erik Norris, Eva Hidalgo Pla, Shannon Rankin, Juan Carlos Salinas, and Kym Yano for recorder deployment and logistic help associated with those surveys. We thank the PIFSC Science Operations Division MAKER Lab for acoustic instrument improvements and construction and the officers and crew of the Research Vessels *Oscar Elton Sette*, *Bell M. Shimada*, *Reuben Lasker*, *Martin Sheen*, and *Pacific Storm* for their efforts in deployment and retrieval of DASBRs. Acoustic data were collected under Marine Mammal Protection Act permits 19091 and 20311. Data in Mexico were collected under permits SGPA/DGVS/000374/20, and SGPA/DGVS/000969/20 issued by Direccion General de Vida Silvestre, Secretaría de Medio Ambiente y Recursos Naturales, and under permits F00.DRPBCPN.RBIPPBC.-112/2020, F00.DRPBCPN.RBIPPBC.-113/2020, and F00.DRPBCPN.RBIPPBC.-117/2020 issued by Reserva de la Biosfera Islas del Pacífico de la Península de Baja California of the Comision Nacional de Areas Naturales Protegidas (CONANP). Funding was provided bythe Pacific Islands and Southwest Fisheries Science Centers, Bureau of Ocean Energy Management (Interagency Agreement (IAA) M17PG00024/NMFS-PIC-17-005), U.S. Navy Pacific Fleet Environmental Readiness Division (IAA N0007018MP4C587-01/NMFS-PIC-18-005), Chief of Naval Operations N45 (IAA N0002518GTC032-06/NMFS-NEC-16-011-06), Naval Information Warfare Center San Diego (NAVSEA N0025320WX00369), Sea Shepherd Conservation Society, and Oregon State University. This paper was improved by helpful comments from Jeff Moore, Elizabeth Henderson, and three anonymous reviewers.

ORCID

Jay Barlow https://orcid.org/0000-0001-7862-855X
Jennifer L. K. McCullough https://orcid.org/0000-0003-4212-7846

ENDNOTE

[1] Cornwall, W. (2021, October 22). *They thought the expedition was lost. Then, they spotted a whale almost no one has seen*. Science News. https://www.science.org/content/article/they-thought-expedition-was-lost-then-they-spotted-whale-almost-no-one-has-seen

REFERENCES

Aguilar de Soto, N., Visser, F., Tyack, P. L., Alcazar, J., Ruxton, G., Arranz, P., Madsen, P. T., & Johnson, M. (2020). Fear of killer whales drives extreme synchrony in deep diving beaked whales. *Scientific Reports*, *10*(1), 1–9.

Baird, R. W., Webster, D. L., Schorr, G. S., McSweeney, D. J., & Barlow, J. (2008). Diel variation in beaked whale diving behavior. *Marine Mammal Science*, *24*(3), 630–642. https://doi.org/10.1111/j.1748-7692.2008.00211.x

Barlow, J., Cárdenas Hinojosa, G., Henderson, E. E., Breese, D., López Arzate, D., Hidalgo Pla, E., & Taylor, B. L. (2022). Unique morphological and acoustic characteristics of beaked whales (*Mesoplodon* sp.) off the west coast of Baja California, Mexico. *Marine Mammal Science*, *38*(1), 383–390. https://doi.org/10.1111/mms.12853

Barlow, J., Moore, J. E., McCullough, J. L. K., & Griffiths, E. T. (2021). Acoustic-based estimates of Cuvier's beaked whale (*Ziphius cavirostris*) density and abundance along the U.S. West Coast from drifting hydrophone recorders. *Marine Mammal Science*, *38*(2), 517–538. https://doi.org/10.1111/mms.12872

Barlow, J., & Schorr, G. (2018). *Drifting acoustic spar buoy recorder (DASBR) deployments in the San Nicolas Basin in January 2018* (NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-598). U.S. Department of Commerce.

Barlow, J., Schorr, G. S., Falcone, E. A., & Moretti, D. J. (2020). Variation in dive behavior of Cuvier's beaked whales with seafloor depth, time-of-day, and lunar illumination. *Marine Ecology Progress Series*, *644*, 199–214. https://doi.org/10.3354/meps13350

Baumann-Pickering, S., McDonald, M. A., Simonis, A. E., Solsona Berga, A., Merkens, K. P., Oleson, E. M., Roch, M. A., Wiggins, S. M., Rankin, S., Yack, T. M., & Hildebrand, J. A. (2013). Species-specific beaked whale echolocation signals. *Journal of the Acoustical Society of America*, *134*(3), 2293–2301. https://doi.org/10.1121/1.4817832

Gillespie, D., Mellinger, D. K., Gordon, J., McLaren, D., Redmond, P., McHugh, R., Trinder, P., Deng, X. Y., & Thode, A. (2009). PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localization of cetaceans. *Journal of the Acoustical Society of America*, *125*(4), 2547–2547. https://doi.org/10.1121/1.4808713

Griffiths, E.T., Keating, J.L., Barlow, J., Moore, J. E. (2019). Description of a new beaked whale echolocation pulse type in the California Current. *Marine Mammal Science*, *35*(3), 1058–1069. https://doi.org/10.1111/mms.12560

Johnson, M., Madsen, P. T., Zimmer, W. M., Aguilar de Soto, N., & Tyack, P. L. (2004). Beaked whales echolocate on prey. *Proceedings of the Royal Society of London B: Biological Sciences*, *271*(suppl_6), S383–SS386.

Keating, J. L., Barlow, J., Griffiths, E. T., & Moore, J. E. (2018). *Passive acoustics survey of cetacean abundance levels (PASCAL-2016) final report* (OCS Study BOEM 2018–025). U.S. Department of the Interior, Bureau of Ocean Energy Management.

McCullough, J. L., Oleson, E. M., Barlow, J., Allen, A. N., & Merkens, K. (2021). *An acoustic survey in the main Hawaiian Islands using drifting recorders* (PIFSC Administrative Report, H-21-04). https://doi.org/10.25923/rzzz-0v38

McCullough, J. L., Wren, J. L., Oleson, E. M., Allen, A. N., Siders, Z. A., & Norris, E. S. (2021). An acoustic survey of beaked whales and *Kogia* spp. in the Mariana Archipelago using drifting recorders. *Frontiers in Marine Science*, *8*, 1–15. https://doi.org/10.3389/fmars.2021.664292

Noren, S. R., & Williams, T. M. (2000). Body size and skeletal muscle myoglobin of cetaceans: adaptations for maximizing dive duration. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *126*(2), 181–1191. https://doi.org/10.1016/S1095-6433(00)00182-3

Pitman, R., (2009). Mesoplodont whales:(*Mesoplodon* spp.). In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 721–726). Academic Press.

Schorr, G. S., Falcone, E. A., Moretti, D. J., & Andrews, R. D. (2014). First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLoS ONE*, *9*(3), Article e92633. https://doi.org/10.1371/journal.pone.0092633

Simonis, A. E., Trickey, J. S., Barlow, J., Rankin, S., Urbán, J., Rojas-Bracho, L., & Moore, J. E. (2020). *Passive acoustic survey of deep-diving odontocetes in the California Current ecosystem 2018: Final report* (NOAA Technical Memorandum NMFS-SWFSC-630). U. S. Department of Commerce.

Tyack, P. L., Johnson, M., Aguilar Soto, N., Sturlese, A., & Madsen, P. T. (2006). Extreme diving of beaked whales. *Journal of Experimental Biology*, *209*(21), 4238–4253. https://doi.org/10.1242/jeb.02505

Warren, V. E., Marques, T. A., Harris, D., Thomas, L., Tyack, P. L., Aguilar de Soto, N., Hickmott, L. S., & Johnson, M. P. (2017). Spatiotemporal variation in click production rates of beaked whales: Implications for passive acoustic density estimation. *Journal of the Acoustical Society of America*, *141*, 1962–1974. https://doi.org/10.1121/1.4978439

Yano, K. M., Oleson, E. M., McCullough, J. L. K., Hill, M. C., & Henry, A.E. (2020). *Cetacean and seabird data collected during the Winter Hawaiian Islands Cetacean and Ecosystem Assessment Survey (Winter HICEAS), January–March 2020* (NOAA Technical Memorandum NOAA-TM-NMFS-PIFSC-111). U.S. Department of Commerce. https://doi.org/10.25923/ehfg-dp78

Zimmer, W. M. X., Johnson, M. P., Madsen, P. T., & Tyack, P. L. (2005). Echolocation clicks of Cuvier's beaked whales (*Ziphius cavirostris*). *Journal of the Acoustical Society of America*, *117*(6), 3919–3927. https://doi.org/10.1121/1.1910225

Zimmer, W. M., Harwood, J., Tyack, P. L., Johnson, M. P., & Madsen, P.T. (2008). Passive acoustic detection of deep-diving beaked whales. *Journal of the Acoustical Society of America*, *124*(5), 2823–2832. https://doi.org/10.1121/1.2988277

How to cite this article: Barlow, J., & McCullough, J. L. K. (2023). Beaked whale dive cycle estimation based on acoustic data from drifting recording systems. *Marine Mammal Science*, *39*(2), 688–695. https://doi.org/10.1111/mms.12987