

Variations in received levels on a sound and movement tag on a singing humpback whale: Implications for caller identification

Alison K. Stimpert, Marc O. Lammers, Adam A. Pack, and Whitlow W. L. Au

Citation: *The Journal of the Acoustical Society of America* **147**, 3684 (2020); doi: 10.1121/10.0001306

View online: <https://doi.org/10.1121/10.0001306>

View Table of Contents: <https://asa.scitation.org/toc/jas/147/5>

Published by the [Acoustical Society of America](#)

ARTICLES YOU MAY BE INTERESTED IN

[Detection and classification of narrow-band high frequency echolocation clicks from drifting recorders](#)
The Journal of the Acoustical Society of America **147**, 3511 (2020); <https://doi.org/10.1121/10.0001229>

[Beluga whale acoustic signal classification using deep learning neural network models](#)
The Journal of the Acoustical Society of America **147**, 1834 (2020); <https://doi.org/10.1121/10.0000921>

[Modeling of the near to far acoustic fields of an echolocating bottlenose dolphin and harbor porpoise](#)
The Journal of the Acoustical Society of America **147**, 1790 (2020); <https://doi.org/10.1121/10.0000918>

[Modeling the acoustic repertoire of Cuvier's beaked whale clicks](#)
The Journal of the Acoustical Society of America **147**, 3605 (2020); <https://doi.org/10.1121/10.0001266>

[Automatic detectors for low-frequency vocalizations of Omura's whales, *Balaenoptera omurai*: A performance comparison](#)
The Journal of the Acoustical Society of America **147**, 3078 (2020); <https://doi.org/10.1121/10.0001108>

[Fin whale acoustic presence and song characteristics in seas to the southwest of Portugal](#)
The Journal of the Acoustical Society of America **147**, 2235 (2020); <https://doi.org/10.1121/10.0001066>



JASA
THE JOURNAL OF THE
ACOUSTICAL SOCIETY OF AMERICA

Special Issue:
Supersonic Jet Noise

Submit Today!

Variations in received levels on a sound and movement tag on a singing humpback whale: Implications for caller identification

Alison K. Stimpert,^{1,a)} Marc O. Lammers,² Adam A. Pack,³ and Whitlow W. L. Au^{4,b)}

¹*Bioacoustics and Vertebrate Ecology, Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California 95039, USA*

²*Hawaiian Islands Humpback Whale National Marine Sanctuary, National Oceanic and Atmospheric Administration, 726 South Kihei Road, Kihei, Hawaii 96753, USA*

³*Departments of Psychology and Biology and LOHE Bioacoustics Laboratory, University of Hawaii at Hilo, Hilo, Hawaii 96720, USA*

⁴*Hawaii Institute of Marine Biology, 46-007 Lilipuna Road, Kaneohe, Hawaii 96744, USA*

ABSTRACT:

Bio-logging devices are advancing the understanding of marine animal behavior, but linking sound production and behavior of individual baleen whales is still unreliable. Tag placement potentially within the near field of the sound source creates uncertainty about how tagged animal sounds will register on recorders. This study used data from a tagged singing humpback whale to evaluate this question of how sound levels present on a tag when calls are produced by a tagged animal. Root-mean-square (rms) received levels (RLs) of song units ranged from 112 to 164 dB re 1 μ Pa rms, with some, but not all, of the lower frequency units registering on the tag's 800 Hz accelerometer sensor. Fifty-nine percent of recorded units measured lower acoustic RLs than previously reported source levels for humpback song, but signal-to-noise ratios (SNRs) were 30–45 dB during periods of the dive with low noise. This research highlights that tag RL does not alone predict caller identity, argues for higher SNR thresholds if using SNR to inform decisions about the source of a call, and provides a baseline for future research identifying diagnostic properties of tagged animal calls in cetacean bioacoustic tag datasets.

<https://doi.org/10.1121/10.0001306>

(Received 20 November 2019; revised 2 May 2020; accepted 5 May 2020; published online 28 May 2020)

[Editor: Rebecca A. Dunlop]

Pages: 3684–3690

I. INTRODUCTION

Understanding the behavior of individual animals has been revolutionized over the past 50 years by rapid innovations in the field of bio-logging, the collection of biological data on individuals through animal-borne tags (e.g., Fehlmann and King, 2016; Kooyman, 2004; Naito, 2004; Wilmers *et al.*, 2015). In the marine environment, advances in bio-logging tag technology (Burgess, 2009; Burgess *et al.*, 1998; Johnson and Tyack, 2003; Schevill and Watkins, 1966; Watkins, 1978) have enabled the study of cetacean large-scale migratory movements as well as fine-scale motor movements that can both be placed into environmental and social contexts to address the proximate and ultimate causes of behavior patterns (e.g., Goldbogen *et al.*, 2008; Mate *et al.*, 1998; Tackaberry *et al.*, 2020).

For marine species that are social, use of the acoustic channel for communication is essential and often preferred over the visual channel because of the efficiency of sound transfer and low acoustic absorption, as well as the limited and often relatively poor visibility compared to terrestrial environments (Herman and Tavolga, 1980). The ability to assign sound production to an individual and link those

sounds with the movement and/or physiology of that individual is key to understanding social interactions, as well as quantifying acoustic behavior such as individual call rates, which can be used to generate population density estimates with passive acoustic monitoring data. Toward these goals, many recent tag types include an acoustic recording feature (Burgess, 2009; Johnson and Tyack, 2003). In high-frequency echolocating odontocetes, when two hydrophones are present on a tag, the angle of arrival (AoA) of a given sound (generally an impulsive echolocation click, although high-frequency tonal calls have also been studied) can be calculated, and through comparisons of AoAs over time, click trains produced by the tagged animal can be identified (Arranz *et al.*, 2016; Jensen *et al.*, 2011; Johnson *et al.*, 2004; Johnson *et al.*, 2009; Oliveira *et al.*, 2016). Clicks produced by the tagged animal also often have additional low- or high-frequency components that, although they are acoustic artifacts, are diagnostic of the clicks having been produced by the tagged animal (Arranz *et al.*, 2016; Madsen *et al.*, 2005; Sorensen *et al.*, 2018). In these cases, behavioral data from movement sensors can be correlated with sound production of the tagged animal.

However, for low-frequency-producing baleen whales, although sound and movement (or hereafter, “acoustic”) tags provide a general acoustic context for behaviors, it is a challenge to definitively identify the individual producing a recorded sound based on the acoustic record alone when

^{a)}Electronic mail: astimpert@mlml.calstate.edu, ORCID: 0000-0002-9400-0305.

^{b)}Deceased.

more than one animal is present (Johnson *et al.*, 2009; Oleson *et al.*, 2007). Sounds produced by a whale and subsequently received on its tag are subject to undetermined propagation effects (often in shallow water), near-field effects, and potential body shading of the tag. In addition, questions remain about which parts of a whale's anatomy contribute to which types of sound emission, and how directivity, frequency, and sound level are influenced by the animal's body as well as tag placement (Madsen *et al.*, 2002; Reidenberg, 2018; Reidenberg and Laitman, 2007).

Despite these challenges, some attempts have been made to describe individual calling behavior in baleen whales. One recent technique is the discovery that very low-frequency calls produced by the tagged animal can appear on the accelerometer record of the tag, possibly through body vibration or some other mechanism (Goldbogen *et al.*, 2014). This technique has been used on fin whale data, *Balaenoptera physalus* (Stimpert *et al.*, 2015) and a modified version (including cross-correlating acoustic signals and accelerometer signals) on blue whale data, *Balaenoptera musculus* (Saddler *et al.*, 2017). Within the blue whale data, authors concluded that calls from other whales could register on a tagged whale's accelerometer (negating the base technique as a simple and foolproof method for identifying a calling animal), but also proposed that additional cross-correlation techniques across all three accelerometer axes might identify calls produced by a single source (potentially the tagged whale). In general, though, the mechanism for the phenomenon is not fully understood, be it particle-motion, body-motion, related to instrument sensitivity or tag placement, or some combination of all of these, and further vetting of the technique is needed. Researchers also have yet to demonstrate the calls of higher frequency-producing baleen whales (e.g., humpback whales, *Megaptera novaeangliae*, right whales *Eubalaena sp.*, and minke whales, *Balaenoptera acutorostrata*) registering on accelerometers.

In the absence of a high sampling rate accelerometer signal, baleen whale researchers have estimated which calls are likely produced by a tagged whale based on a combination of signal-to-noise ratio (SNR), received level (RL), swim speed, presence of harmonics, and distance to conspecifics (Oleson *et al.*, 2007; Parks *et al.*, 2011; Parks *et al.*, 2019). Unfortunately, varying propagation conditions, as mentioned above, and a documented propensity of individual baleen whales to vary their source level (SL) on a call-by-call basis (Au *et al.*, 2006; Parks *et al.*, 2010) may make sound level alone an unreliable indicator of range to the caller (Stimpert *et al.*, 2015). To our knowledge, there has not been to this point a baleen whale dataset with which to test this idea directly. Here we report on such a dataset, opportunistically obtained from a singing humpback whale. Singing by the tagged whale was verified independently of the tag recording, which allowed us to evaluate how song units produced by a tagged free-swimming baleen whale registered on the tag. We offer comparisons to RLs and SLs from previous studies and discuss implications for confirming the tagged animal as the source of the call in acoustic tag data.

II. MATERIALS AND METHODS

On March 28, 2018, an Acousonde 3B (Burgess, 2009; Burgess *et al.*, 1998) was deployed on a humpback whale in the waters off Maui, Hawaii, in the United States. The Acousonde 3B is a self-contained underwater acoustic recorder. Its 16-bit low power acoustic channel was used for this study and sampled continuous acoustics at 12 226 Hz, auxiliary sensors at 40 Hz, and accelerometers at 800 Hz. The acoustic channel contained a 3 dB anti-alias cutoff at 4646 Hz and a 3 dB high-pass cutoff at 22 Hz. Hydrophone sensitivity was -187.2 dB re 1 V/ μ Pa, and the tag recording system included 2.4 dB of gain. The tag was placed behind the whale's blowhole, about 1 m forward of its dorsal fin and to the right of its centerline (Fig. 1). It remained attached to the whale for approximately 36 h. The tagged whale was initially tracked by a small outboard vessel using the tag's VHF transmitter, and surface behavior was recorded from the time the tag was attached at 10:01 Hawaiian Standard Time (HST) until approximately 17:30 HST on the same day. Approximately 30 min after tag deployment, the whale disassociated from a companion whale and began a singing bout that lasted 5.5 h, remaining largely stationary at approximately 22 meters in depth between surfacings, and unaccompanied by any other whales. Singing was verified by positioning the research vessel over the location of the singing whale such that the song could be heard in air through the vessel's hull, indicating close proximity (ca. within 100 m) to the source. This verification process continued between the whale's surfacings to breathe. The location of the tag on the whale did not change substantially during the period of singing analyzed, based on surface observations and inspection of the accelerometer record. No other whales were observed closer than 2 km during this period.

Images of the unique pattern on the ventral surface of the tagged whale's tail flukes were obtained and compared against the images in an archival catalog maintained by one of the co-authors (A.A.P). The tagged whale was first photographed as a male escort in Hawaii on February 22, 1979, indicating that at the time of tagging, it was sexually mature (Best, 2011) and a minimum of 41 years old.

The acoustic record logged by the Acousonde was manually scanned and the start and end points of individual song



FIG. 1. (Color online) Photo of tag placement on the right flank of the humpback whale.

units (i.e., the smallest continuous segments comprising phrases and themes within a song; [Au et al., 2006](#); [Herman, 2017](#); [Payne and McVay, 1971](#)) were marked within a custom auditing script in MATLAB 2019a. Background song was rarely noted. Root-mean-square (rms) RLs were calculated across the entire duration and full bandwidth of each unit. Calculations of SNR [defined as (signal+noise)/noise] values were initially attempted using a 100 ms segment taken immediately before each song unit to measure background noise; however, many units were closer than 100 ms to previous and following units. To avoid inflated noise values, we estimated background noise using 136 manually chosen 400 ms segments throughout the recording, selecting one segment during each 30-s panel when paging through the acoustic record. These segments were expressly chosen to exclude any portion of song units or surfacing sounds, and broadband rms RL was calculated over the full segment duration. Each song unit was then matched to its closest noise segment for calculation of SNR and was therefore always compared to a noise clip less than 30 s away.

III. RESULTS

We extracted song unit clips from approximately 1 h and 10 min of song recorded from the middle of the Acousonde deployment. Every distinguishable unit within this section was marked for a total of 3185 song units. This

time period encompassed just over three complete song cycles, so multiple examples of all unit types were included [one complete cycle is shown in Fig. 2(a)]. We did not classify units, as a subjective “type” designation was not relevant to this study. Generally, units ranged from short (<1 s) grunts and upsweeps, to low-frequency pulsed sounds similar to whups ([Stimpert et al., 2011](#); [Wild and Gabriele, 2014](#)), to short, repetitive broadband bursts (<0.1 s) grouped together, to higher frequency, modulated sounds, to longer duration tonal sounds (up to 8 s) [Fig. 2(a)].

The units ranged in mean RL across approximately 50 dB (130–163 dB re 1 μ Pa rms) excluding outliers. This wide variability is evident in the temporal representation of unit RL in Fig. 2(b) and broken down by peak frequency of the unit in Fig. 3(a). Unit peak frequencies fell well below the anti-alias cutoff of 4646 Hz, and units with peak frequencies between approximately 500 and 1500 Hz had the most consistency in RL (fewer outliers) [Fig. 3(a)].

Mean broadband background noise was 118 dB re 1 μ Pa rms. Figure 3(b) shows the much lower median value, but we include the mean here to acknowledge the substantial variation in background noise RL noted on a temporal scale, which was consistent with dive patterns of the whale surfacing to breathe. Either the slow swimming during surfacing or potentially higher sound levels near the surface raised received noise levels from approximately 111 to 135–145 dB re 1 μ Pa rms just before and after surfacing.

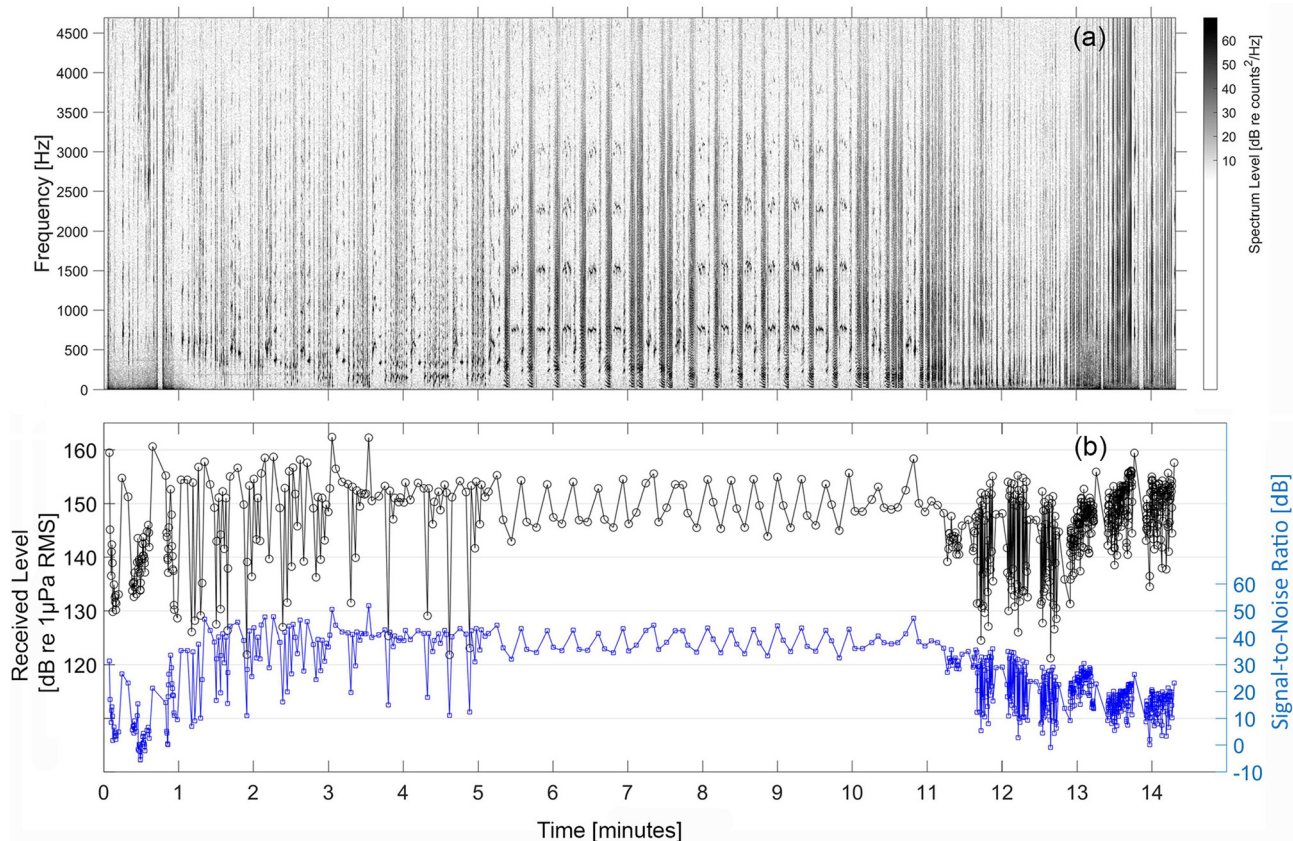


FIG. 2. (Color online) Overview of song structure and RL variability throughout one song cycle. (a) Spectrogram of one song cycle [Hanning window, Fast Fourier Transform (FFT) size 2048, 50% overlap] and (b) RLs (left axis) and SNRs (right axis) of each unit over time during the same song cycle.

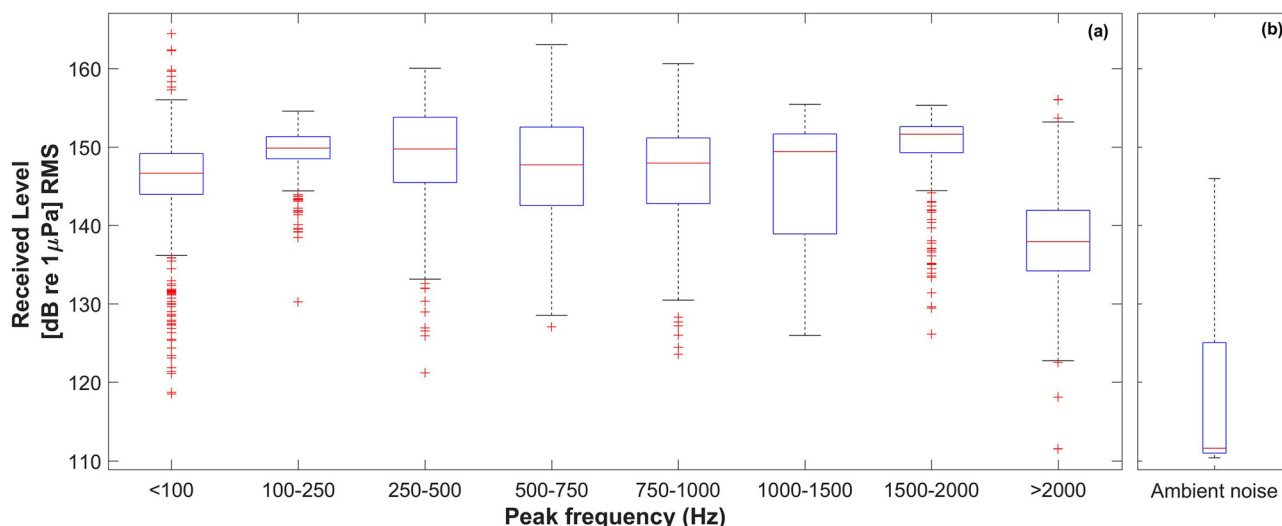


FIG. 3. (Color online) Boxplots showing variation in RL of song (by unit peak frequency) and noise clips. On each box, the central red line indicates the median, and the bottom and top edges of the box correspond to the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers, and the outliers are plotted individually using the “+” symbol (MATLAB 2019a). (a) Variation in rms RLs by peak frequency of the unit. RL was calculated over the entire duration of the unit and its full bandwidth. Peak frequencies were generally well below the anti-alias filter cutoff, and the most consistently intense units fell between 500 and 1500 Hz in peak frequency. (b) Full bandwidth rms RL of all background noise segments ($n = 136$), which were manually selected throughout the dataset (see Methods).

This resulted in unit SNRs that ranged from -13 to 52 dB, with a median value of 17 dB. The whale may also have been generally producing lower level sounds during this surfacing portion of the dive, as has been noted in early studies with humpback whale singers (Tyack, 1981). When estimating SNR during the period of lowest background noise (when the whale was presumably stationary), values ranged from 30 to 45 dB [Fig. 2(b)].

We did find evidence of song units registering in the accelerometer data, most clearly on the x -axis. While many low-frequency signals were present, some were not, and initial evidence does not suggest a strong relationship with unit RL. Many higher frequency acoustic signals also registered as an aliased version of the original signal in the accelerometer data, given the 800 Hz sampling rate of the accelerometer sensor. Figure 4 shows an example of four song units and the associated x -axis accelerometer signal. The first three units registered on the accelerometer, but the last one did not.

IV. DISCUSSION AND CONCLUSIONS

Here we have used an opportunistic dataset to describe how humpback whale song units present acoustically on a hydrophone attached to the singer. Wide variability was seen in RL, and SNRs were generally higher than previously reported.

In their 2006 study of the SLs of humpback whale song units, using a 5-element vertical hydrophone array, Au et al. (2006) measured 781 broadband unit SLs ranging from 149 to 169 dB re $1 \mu\text{Pa}$, a variation across 20 dB. This variation was speculated to result from variation in individual output (both within and between individuals), and may also have related to recording aspect combined with some level of the

directionality of song units. The maximum SL reported by Au et al. (2006) was 5 dB higher than the maximum level recorded on the tag in the current study. In the lower end of the range, however, there was more of a discrepancy. We measured levels as low as 112 dB from the tagged animal. Au et al. (2006) did not report SLs lower than 149 dB (recorded at ranges from 12 to 50 m from the singer). These authors were likely limited by SNR when recording in the far field since signals would be subject to transmission loss

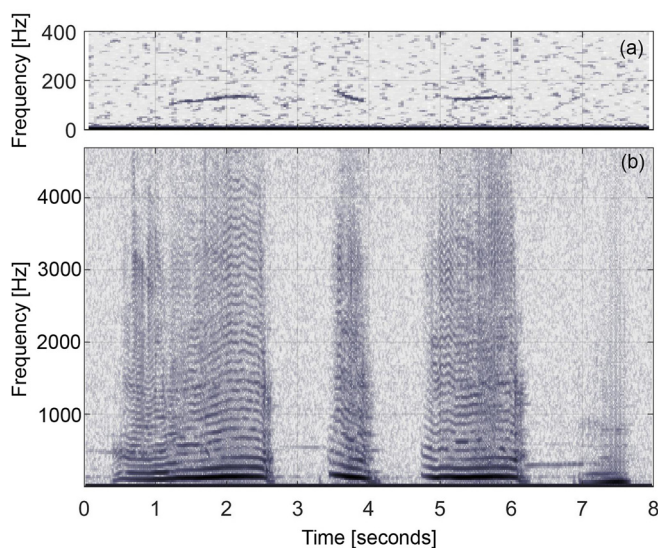


FIG. 4. (Color online) Occurrence of song units in the accelerometer data. (a) Spectrogram (Hamming window, FFT size 128, 75% overlap) of the x -axis of the accelerometer data, showing signals corresponding to the first three song units of the sequence of four in the bottom panel. (b) Spectrogram (Hamming window, FFT size 512, 75% overlap) of the acoustic record corresponding to the top panel, showing four consecutive song units.

and lower amplitude units may have attenuated before reaching the hydrophone. In fact, 59% of our tag-based RL measurements were below 149 dB. However, there are also other, unpredictable propagation effects at play within the tag's near field location that may raise or lower the RL in comparison to SL.

Although the current dataset does not include RLs on a tag from a confirmed, vocalizing *associate* whale, [Chen et al. \(2016\)](#) reported broadband RLs from a singing humpback whale escorting a humpback whale female and her calf in waters off Maui. Those levels were recorded on a tag attached to the calf and ranged from 126 to 158 dB re 1 μ Pa rms, with the singing escort estimated to be between 1 and 60 m away from the tag during the duration of the deployment. Those results combined with these in the current study indicate that little can be assumed about the precise origin of a call based on the level of the tag recording alone. A "low" level (such as 112 dB) does not necessarily indicate production by another individual (this study), nor does a "high" level (such as 158 dB) necessarily indicate production by the tagged animal ([Chen et al., 2016](#)).

Given this ambiguity in using RL alone to assign signals to a tagged baleen whale, many studies integrate RL information with behavioral context as well as additional acoustic parameters to narrow down the identity of the sound producer. For example, SNR has been used in combination with RL and evidence of a lack of nearby conspecifics to infer call production by the tagged animal ([Oleson et al., 2007](#); [Parks et al., 2010](#); [Parks et al., 2011](#); [Parks et al., 2019](#)). The results from our dataset (median SNR 17 dB) show SNR values for sounds from the singer that are generally higher than the thresholds often used in such studies, especially when the singer was stationary and mid-dive cycle. Previous studies have assigned calls to the tagged animal based on SNR values ranging from 5 to 10 dB ([Oleson et al., 2007](#); [Parks et al., 2010](#); [Parks et al., 2011](#); [Parks et al., 2019](#)). Though these studies also used additional factors, such as no conspecifics closer than 100 m–1 km (depending on the study) or presence of high-frequency harmonics in the call recording, our results argue for higher SNR thresholds when using this parameter to assist in determining caller identity. However, our dataset is from only one individual humpback whale, and this whale's lack of movement may have created a background noise level that was artificially low compared to many acoustic tag datasets, especially those from other baleen whale species, or from animals that are not exhibiting stationary singing behavior. It is also important to keep in mind that humpback whale non-song calls have been shown to be quieter than most songs ([Dunlop et al., 2013](#); [Fournet et al., 2018](#)), and song SLs appear to be lower than those estimated for larger blue and fin whales ([Sirovic et al., 2007](#); [Weirathmueller et al., 2013](#)). These contextual variables (species, call type, swimming behavior, and general behavioral context) must be taken into account when determining study-specific acoustic thresholds and interpreting tag data.

The benefit of the dataset in this paper is that we can assert that all sounds came from the tagged animal. In addition to describing acoustic parameters of song units, this scenario presents an interesting possibility to study the presentation of song units on the accelerometer, if present. While our data did include to our knowledge the first evidence of tagged humpback whale sounds registering on an accelerometer, we still do not know the mechanism for this phenomenon nor the ultimate criteria for which call visibility on an accelerometer signal actually indicates production by the tagged animal, since not all units were visible in the accelerometer data and they were visible to varying degrees. Further detailed analysis of accelerometer signals is planned using additional data from different animals as well as different tag types. Our data do argue, however, that a call may not have to be present on an accelerometer signal in order to have been produced by the tagged animal—depending on appropriate accelerometer sensitivity, sampling rate, and tag placement. This underlines the importance of also understanding how sound levels produced by a tagged animal present on a tag recording.

In conclusion, when analyzing bio-logging acoustic data from a tagged baleen whale with the intent of assigning calls to the tagged individual, several data streams must be considered in concert. Evidence of a call in the accelerometer record *and* continued visual verification (including under water, or potentially using Unmanned Aerial Vehicles over clear, shallow waters) of the lack of any conspecifics in the area (complete with propagation calculations of transmission loss from noted distances) is presently a strong argument for tagged whale call production. In addition, this study has shown that the SNR values often used (in combination with other factors such as RL, presence of high-frequency call components, and evidence of an animal being "alone") may not be high enough, and we suggest a threshold such as 15 or 20 dB (perhaps species- and behavioral context- dependent). Conservatively, however, most tag acoustic data from baleen whales will still need to be treated as group output, i.e., produced by the tagged whale or a close associate ([Lewis et al., 2018](#); [Nielsen et al., 2019](#); [Stimpert et al., 2012](#)), until a more definitive, tag-based method can be determined.

We recommend that future research replicate our analysis with other tagged singing humpback whales (one of the few baleen whales that can be easily identified as a sound producer by field observation) to understand the effects of individual variation in level production as well as the effect of tag placement by comparing RL/SNR for the same units in a song across different deployments, or by deploying two tags on the same animal. Perhaps more likely in other species, levels could also be compared within pairs of animals where both are tagged and both are soniferous. Lastly, there may exist diagnostic acoustic properties of tagged baleen whale sound recordings, similar to those acoustic artifacts noted in high-frequency odontocete recordings, which could be identified by combining far field acoustic recordings of tagged humpback singers recorded simultaneously with the

near field tag recordings. Identifying such diagnostic properties would improve our ability to discriminate tagged-animal vocalizations and would increase interpretive confidence in analysis of future and previous tag datasets. This analytical leap would greatly expand our understanding of the physiology of sound production and its role in baleen whale foraging and social systems.

ACKNOWLEDGMENTS

Research was carried out under NOAA Permit Nos. 19655 to AA Pack and 20043 to WWL Au. Tools for acoustic tag data analysis were developed through modification and customization of tools originally developed by M. Johnson, S. DeRuiter, and C. Miller. We thank the following staff members of the Hawaiian Islands Humpback Whale National Marine Sanctuary Staff for their assistance with fieldwork and logistics: E. Zang, S. Wood, A. Kuegler, and E. Lyman. We also thank J. Chen for equipment assistance and P. Madsen, S. Videsen, and two anonymous reviewers for comments on earlier versions of this manuscript.

Arranz, P., DeRuiter, S. L., Stimpert, A. K., Neves, S., Friedlaender, A. S., Goldbogen, J. A., Visser, F., Calambokidis, J., Southall, B. L., and Tyack, P. L. (2016). "Discrimination of fast click-series produced by tagged Risso's dolphins (*Grampus griseus*) for echolocation or communication," *J. Exp. Biol.* **219**, 2898–2907.

Au, W. W. L., Pack, A. A., Lammers, M. O., Herman, L. M., Deakos, M. H., and Andrews, K. (2006). "Acoustic properties of humpback whale songs," *J. Acoust. Soc. Am.* **120**, 1103–1110.

Best, P. B. (2011). "A note on the age at sexual maturity of humpback whales," *J. Cetacean Res. Manag.* **3**, 71–73.

Burgess, W. C. (2009). "The Acousonde: A miniature autonomous wide-band recorder," *J. Acoust. Soc. Am.* **125**, 2588.

Burgess, W. C., Tyack, P., Le Boeuf, B. J., and Costa, D. P. (1998). "A programmable acoustic recording tag and first results from free-ranging northern elephant seals," *Deep. Res. Part II Top. Stud. Oceanogr.* **45**, 1327–1351.

Chen, J., Pack, A. A., Au, W. W., and Stimpert, A. K. (2016). "Measurements of humpback whale song sound levels received by a calf in association with a singer," *J. Acoust. Soc. Am.* **140**, 4010–4015.

Dunlop, R. A., Cato, D. H., Noad, M. J., and Stokes, D. M. (2013). "Source levels of social sounds in migrating humpback whales (*Megaptera novaeangliae*)," *J. Acoust. Soc. Am.* **134**, 706–714.

Fehlmann, G., and King, A. J. (2016). "Bio-logging," *Curr Biol* **26**, R830–R831.

Fournet, M. E. H., Matthews, L. P., Gabriele, C. M., Mellinger, D. K., and Klinck, H. (2018). "Source levels of foraging humpback whale calls," *J. Acoust. Soc. Am.* **143**, EL105–EL111.

Goldbogen, J. A., Calambokidis, J., Croll, D. A., Harvey, J. T., Newton, K. M., Oleson, E. M., Schorr, G., and Shadwick, R. E. (2008). "Foraging behavior of humpback whales: Kinematic and respiratory patterns suggest a high cost for a lunge," *J. Exp. Biol.* **211**, 3712–3719.

Goldbogen, J. A., Stimpert, A. K., DeRuiter, S. L., Calambokidis, J., Friedlaender, A. S., Schorr, G. S., Moretti, D. J., Tyack, P. L., and Southall, B. L. (2014). "Using accelerometers to determine the calling behavior of tagged baleen whales," *J. Exp. Biol.* **217**, 2449–2455.

Herman, L. M. (2017). "The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: Review, evaluation, and synthesis," *Biol. Rev.* **92**, 1795–1818.

Herman, L. M., and Tavolga, W. N. (1980). "The communication systems of cetaceans," in *Cetacean Behavior: Mechanisms and Function*, edited by L. M. Herman (John Wiley & Sons, Inc., New York).

Jensen, F. H., Perez, J. M., Johnson, M., Aguilar de Soto, N., and Madsen, P. T. (2011). "Calling under pressure: Short-finned pilot whales make social calls during deep foraging dives," *Proc. R. Soc. Biol. Sci. Ser. B* **278**, 3017–3025.

Johnson, M., Aguilar de Soto, N., and Madsen, P. T. (2009). "Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: A review," *Mar. Ecol. Prog. Ser.* **395**, 55–73.

Johnson, M., Madsen, P. T., Zimmer, W. M. X., de Soto, N. A., and Tyack, P. L. (2004). "Beaked whales echolocate on prey," *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **271**, S383–S386.

Johnson, M. P., and Tyack, P. L. (2003). "A digital acoustic recording tag for measuring the response of wild marine mammals to sound," *IEEE J. Ocean. Eng.* **28**, 3–12.

Kooyman, G. L. (2004). "Genesis and evolution of bio-logging devices: 1963–2002," *Mem. Natl. Inst. Polar Res.* **58**, 15–22.

Lewis, L. A., Calambokidis, J., Stimpert, A. K., Fahlbusch, J., Friedlaender, A. S., McKenna, M. F., Mesnick, S. L., Oleson, E. M., Southall, B. L., Szesciorcka, A. R., and Širović, A. (2018). "Context-dependent variability in blue whale acoustic behaviour," *R. Soc. Open Sci.* **5**, 180241.

Madsen, P. T., Johnson, M., de Soto, N. A., Zimmer, W. M. X., and Tyack, P. (2005). "Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*)," *J. Exp. Biol.* **208**, 181–194.

Madsen, P. T., Payne, R., Kristiansen, N. U., Wahlberg, M., Kerr, I., and Mohl, B. (2002). "Sperm whale sound production studied with ultrasound time/depth-recording tags," *J. Exp. Biol.* **205**, 1899–1906.

Mate, B. R., Gisiner, R., and Mobley, J. (1998). "Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry," *Can. J. Zool.* **76**, 863–868.

Naito, Y. (2004). "New steps in bio-logging science," *Mem. Natl. Inst. Polar Res.* **58**, 50–57.

Nielsen, M. L. K., Bejder, L., Videsen, S., Christiansen, F., and Madsen, P. T. (2019). "Acoustic crypsis in southern right whale mother-calf pairs: Infrequent, low-output calls to avoid predation?," *J. Exp. Biol.* **222**, 1–6.

Oleson, E. M., Calambokidis, J., Burgess, W. C., McDonald, M. A., LeDuc, C. A., and Hildebrand, J. A. (2007). "Behavioral context of call production by eastern North Pacific blue whales," *Mar. Ecol. Prog. Ser.* **330**, 269–284.

Oliveira, C., Wahlberg, M., Silva, M. A., Johnson, M., Antunes, R., Wisniewska, D. M., Fais, A., Gonçalves, J., and Madsen, P. T. (2016). "Sperm whale codas may encode individuality as well as clan identity," *J. Acoust. Soc. Am.* **139**, 2860–2869.

Parks, S. E., Cusano, D. A., Van Parijs, S. M., and Nowacek, D. P. (2019). "North Atlantic right whale (*Eubalaena glacialis*) acoustic behavior on the calving grounds," *J. Acoust. Soc. Am.* **146**, EL15–EL21.

Parks, S. E., Johnson, M., Nowacek, D., and Tyack, P. L. (2010). "Individual right whales call louder in increased environmental noise," *Biol. Lett.* **7**, 33–35.

Parks, S. E., Searby, A., Celerier, A., Johnson, M., Nowacek, D. P., and Tyack, P. (2011). "Sound production behavior of individual North Atlantic right whales: Implications for passive acoustic monitoring," *Endanger. Species Res.* **15**, 63–76.

Payne, R. S., and McVay, S. (1971). "Songs of humpback whales," *Science* **173**, 585–597.

Reidenberg, J. S. (2018). "Where does the air go? Anatomy and functions of the respiratory tract in the humpback whale (*Megaptera novaeangliae*)," *Madag. Conserv. Dev.* **13**, 91–100.

Reidenberg, J. S., and Laitman, J. T. (2007). "Discovery of a low frequency sound source in mysticeti (Baleen whales): Anatomical establishment of a vocal fold homolog," *Anat. Rec. Integr. Anat. Evol. Biol.* **290**, 745–759.

Saddler, M. R., Bocconcelli, A., Hickmott, L. S., Chiang, G., Landea-Briones, R., Bahamonde, P. A., Howes, G., Segre, P. S., and Sayigh, L. S. (2017). "Characterizing Chilean blue whale vocalizations with DTAGs: A test of using tag accelerometers for caller identification," *J. Exp. Biol.* **220**, 4119–4129.

Schevill, W. E., and Watkins, W. A. (1966). "Radio-tagging of whales," *Ref. No. WHOI-66-17*, Woods Hole, MA, pp. 1–15.

Širović, A., Hildebrand, J. A., and Wiggins, S. M. (2007). "Blue and fin whale call source levels and propagation range in the Southern Ocean," *J. Acoust. Soc. Am.* **122**, 1208–1215.

Sorensen, P. M., Wisniewska, D. M., Jensen, F. H., Johnson, M., Teilmann, J., and Madsen, P. T. (2018). "Click communication in wild harbour porpoises (*Phocoena phocoena*)," *Sci. Rep.* **8**, 9702–9713.

Stimpert, A. K., Au, W. W. L., Parks, S. E., Hurst, T., and Wiley, D. N. (2011). "Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring," *J. Acoust. Soc. Am.* **129**, 476–482.

- Stimpert, A. K., DeRuiter, S. L., Falcone, E. A., Joseph, J., Douglas, A. B., Moretti, D. J., Friedlaender, A. S., Calambokidis, J., Gailey, G., Tyack, P. L., and Goldbogen, J. A. (2015). "Sound production and associated behavior of tagged fin whales (*Balaenoptera physalus*) in the Southern California Bight," *Anim. Biotelemet.* **3**, 1–12.
- Stimpert, A. K., Peavey, L., Friedlaender, A. S., and Nowacek, D. P. (2012). "Humpback whale song and foraging behavior on an Antarctic feeding ground," *PLoS One* **7**, e51214–e51214.
- Tackaberry, J. E., Cade, D. E., Goldbogen, J. A., Wiley, D. N., Friedlaender, A. S., and Stimpert, A. K. (2020). "From a calf's perspective: Humpback whale nursing behavior on two US feeding grounds," *PeerJ* **8**, e8538.
- Tyack, P. (1981). "Interactions between singing Hawaiian humpback whales and conspecifics nearby," *Behav. Ecol. Sociobiol.* **8**, 105–116.
- Watkins, W. A. (1978). "A radio tag for big whales," *Oceanus* **21**, 48–54.
- Weirathmueller, M. J., Wilcock, W. S., and Soule, D. C. (2013). "Source levels of fin whale 20 Hz pulses measured in the Northeast Pacific Ocean," *J. Acoust. Soc. Am.* **133**, 741–749.
- Wild, L., and Gabriele, C. M. (2014). "Putative contact calls made by humpback whales (*Megaptera novaeangliae*) in Southeastern Alaska," *Can. Acoust.* **42**, 23–31.
- Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., and Yovovich, V. (2015). "The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology," *Ecology* **96**, 1741–1753.