JASA ARTICLE

Click detection rate variability of central North Pacific sperm whales from passive acoustic towed arrays

Yvonne M. Barkley,[1,a)] Karlina P. B. Merkens,[2] Megan Wood,[2] Erin M. Oleson,[3] and Tiago A. Marques[4,5]

[1]*Cooperative Institute for Marine and Atmospheric Research, School of Ocean and Earth Science and Technology, University of Hawai'i at Mānoa, Honolulu, Hawaii 96822, USA*

[2]*Saltwater Inc., Anchorage, Alaska 99501, USA*

[3]*Pacific Islands Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, Hawaii 96818, USA*

[4]*Centre for Research into Ecological and Environmental Modelling, The Observatory, University of St Andrews, St Andrews, KY16 9LZ, Scotland*

[5]*Departamento de Biologia Animal, Centro de Estatística e Aplicações, Faculdade de Ciências da Universidade de Lisboa, Portugal*

ABSTRACT:
Passive acoustic monitoring (PAM) is an optimal method for detecting and monitoring cetaceans as they frequently produce sound while underwater. Cue counting, counting acoustic cues of deep-diving cetaceans instead of animals, is an alternative method for density estimation, but requires an average cue production rate to convert cue density to animal density. Limited information about click rates exists for sperm whales in the central North Pacific Ocean. In the absence of acoustic tag data, we used towed hydrophone array data to calculate the first sperm whale click rates from this region and examined their variability based on click type, location, distance of whales from the array, and group size estimated by visual observers. Our findings show click type to be the most important variable, with groups that include codas yielding the highest click rates. We also found a positive relationship between group size and click detection rates that may be useful for acoustic predictions of group size in future studies. Echolocation clicks detected using PAM methods are often the only indicator of deep-diving cetacean presence. Understanding the factors affecting their click rates provides important information for acoustic density estimation.
 https://doi.org/10.1121/10.0025540

(Received 16 October 2023; revised 8 March 2024; accepted 19 March 2024; published online 17 April 2024)

[Editor: Aaron M. Thode] Pages: 2627–2635

I. INTRODUCTION

Marine mammals emit a variety of calls for different ecological and behavioral purposes. Acoustic repertoires include different call types linked to foraging, reproduction, navigation, short- and long-range communication, and predator avoidance. Passive acoustic monitoring (PAM) makes it possible to detect and analyze these calls to infer a wide variety of biological and ecological applications, including the detection and identification of species (Baumgartner *et al.*, 2020; Oswald *et al.*, 2003; Robbins *et al.*, 2015), modeling spatiotemporal patterns in their movements and distribution (Davis *et al.*, 2017; Stanistreet *et al.*, 2017), and obtaining density and abundance estimates (Barlow and Taylor, 2005; Marques *et al.*, 2013; Westell *et al.*, 2022).

For deep-diving cetaceans, PAM is particularly useful given their usually inconspicuous behavior during the minimal time they spend at the surface, along with their frequent echolocation clicks produced at depth (Marques *et al.*, 2009; Moretti *et al.*, 2010). Cue-based density estimation using PAM data provides a method to convert the total number of acoustic cues detected at a set of sensors to animal density. This method requires knowing the average acoustic cue production rate, which must be a long-term average incorporating the proportion of time the animals are silent. However, relatively few studies have examined the acoustic cue production rates of marine mammals. While acoustic cue rate data from one species has been substituted to estimate the density of a similar species (Hildebrand *et al.*, 2015; Hildebrand *et al.*, 2019), having information about the acoustic cue rates for each species of interest would improve cue counting-based density estimates.

The definition of an acoustic cue rate is the average number of sounds of interest produced per animal per unit time. Therefore, a good understanding of a species' acoustic repertoire is critical. Acoustic cue rates may vary based on the call type, the time and location, or the behavioral context of the animals (Douglas *et al.*, 2005; Warren *et al.*, 2017). Animal-borne acoustic tags are one method to obtain cue rates directly from individual cetaceans to compute an average population-level cue rate (Johnson and Tyack, 2003). Acoustic tag data are challenging to collect due to the resources and conditions required to successfully deploy and

[a)]Email: yvonne.barkley@noaa.gov

retrieve the tags. Fortunately, other passive acoustic instrumentation exists to study the variability in acoustic cue rates, such as towed hydrophone arrays or seafloor acoustic recorders (Matthews *et al.*, 2023; Soldevilla *et al.*, 2010a,b).

In this study, we examine the variability in the acoustic cue rates of sperm whales located in waters surrounding the Hawaiian Archipelago, encompassing different demographic groups of sperm whales that exhibit a variety of behaviors (Barkley *et al.*, 2022; Thompson, 1982). Acoustic tags have not been deployed on sperm whales from this region, but a large towed hydrophone array data set exists. From this data set, we selected a subset of sperm whale encounters to gather information about acoustic cue production rates. The cues we focus on here are echolocation clicks. To emphasize that we do not observe cue rates directly, we refer to "click detection rates": this acknowledges that we cannot precisely assess the proportion of time the whales are silent from the towed array data, nor can we guarantee that all clicks produced are detected, and group sizes are estimated rather than known. Collectively, these factors contribute to blur our ability to directly observe cue rates. Nonetheless, acoustic data from towed arrays are useful for examining how whale behavior, distance from the array, group size (for visually observed encounters), and spatiotemporal variables affect these click detection rates. To our knowledge, this is the first analysis of the click rate behavior of sperm whales in the central North Pacific.

II. METHODS

To examine click detection rates of sperm whales, we used towed array passive acoustic data collected during shipboard line-transect cetacean abundance surveys within Hawaiian waters in 2013, 2016, and 2017. All surveys were conducted by the National Oceanic and Atmospheric Administration's (NOAA) Pacific Islands Fisheries Science Center (PIFSC) and followed systematic line-transect sampling protocols for simultaneous visual and passive acoustic data collection. Details about the visual data collection methods can be found in Yano *et al.* (2018). Briefly, observers rotated through three positions searching for cetaceans during daylight hours. Observers along the port and starboard sides searched using 25×150 mounted binoculars while a center observer searched with 7×50 binoculars and unaided eyes. If animals were seen within 5.6 km (3 nmi) of the track line, observers would direct the ship to turn towards the group to identify the species and obtain group size estimates. Upon sighting sperm whales, a special protocol was followed to account for the asynchronous diving behavior of subgroups and improve group size estimates. The protocol required three observers to spend the first 10 min counting whales, recording independent group size estimates, and noting the group's overall behavioral state. Next, a fourth observer joined the team to count whales for an additional 60 min to ensure that all subgroups were included in the estimates.

For passive acoustic data collection, the hydrophone configuration of the towed arrays varied slightly between surveys. Generally, each array contained 4–7 hydrophones spaced 1–4 m apart with a frequency response of at least 2–40 kHz. A high-pass filter of 1.5 kHz was applied to recordings collected using a sample rate of at least 192 kHz and a bit depth of 16. Two acousticians used a suite of software to monitor real-time, continuous recordings aurally and visually for all cetacean species during daylight hours (ISHMAEL, Mellinger, 2002; PAMGuard, Gillespie *et al.*, 2009).

Acousticians used automatic classifiers in PAMGuard (Gillespie *et al.*, 2009) to classify cetaceans to either family, genus, or species when possible. Acoustic "encounters" were defined as the total time between the first and last click detected from a group. Most acoustic encounters were separated by at least one day. Any consecutive encounters within the same day were verified as distinct groups using geographic locations from acoustic localization data or sighting information in addition to a minimum separation of 30 min. The distinct characteristics of sperm whale echolocation clicks allowed for species classification by either the acoustician or automatic classifiers in PAMGuard (Backus and Schevill, 1966; Madsen *et al.*, 2022; Mohl *et al.*, 2003). When possible, vocalizing cetacean groups were localized in real-time using two-dimensional (2D) target motion analysis to obtain a perpendicular distance estimate from the group to the towed array. In a related study (Barkley *et al.*, 2021), sperm whale groups were localized again after the survey using a model-based approach to obtain more precise distance estimates with error bounds, which are used in this analysis to account for sound propagation effects on click detection rates. To examine any effects of distance on click detection rates, the perpendicular distance to all sperm whale encounters was calculated, using either acoustic localization or visual observations.

The sperm whale acoustic encounters were annotated for clicks using a combination of automated and manual methods. First, a Teager energy operator was used to automatically detect clicks using the TRITON software package in MATLAB (MathWorks, Inc., 2019; Roch *et al.*, 2011; Solsona-Berga, 2019; Wiggins, *et al.*, 2010). Due to varying levels of noise from different sources within the towed array data (i.e., ship propellers, small boats, electrical interference, and water flow), the automated detector frequently misclassified sperm whale clicks. Therefore, trained analysts (YB and MW) performed further manual validation using Raven Pro (Charif *et al.*, 2010) by formatting the timestamps of automatically detected clicks as a selection table. The analysts used the waveform and spectrogram [fast Fourier transform (FFT) = 512, Hann window, 50% overlap] to verify each individual sperm whale click in the recordings.

Sperm whale click characteristics vary depending on their behavioral state, which can affect the rate at which clicks are produced. Prior studies have demonstrated that the inter-click interval (ICI), or time between consecutive clicks, serves as a reliable indicator for categorizing distinct click types linked to specific behaviors (Jaquet *et al.*, 2001; Marcoux *et al.*, 2006; Solsona-Berga *et al.*, 2022; Watwood *et al.*, 2006; Whitehead and Weilgart, 1990). Regular clicks (0.5–1.2 s ICI) and creaks (0.01–0.1 s ICI) are associated with echolocation and foraging (Jaquet *et al.*, 2001; Miller *et al.*, 2004; Watwood *et al.*, 2006). Slow clicks are produced primarily by male sperm whales and may have a communication function (>2 s ICI; Madsen *et al.*, 2022; Oliveira *et al.*, 2013). Codas are repeated, stereotyped sequences of 3–40 clicks lasting approximately 3 s, can be highly variable and group specific and are believed to be linked to social behavior (Gero *et al.*, 2016; Hersh *et al.*, 2022; Oliveira *et al.*, 2016).

In this study, the analysts classified each click to a specific click type using the pattern of ICIs over time and the physical features of the click (e.g., amplitude, duration, frequency, etc.), and then further validated the click type with behavioral information from the visual observer data when available (e.g., dive information, group size, group composition, etc.). Once click types were assigned, the acoustic encounters were stratified into four "click-type groups," which included encounters with whales producing: (1) codas, (2) only regular clicks, (3) only slow clicks, and (4) a combination of regular and slow clicks. The codas click-type group often included encounters containing one or more of the other three click types. However, they were designated as "codas" because the other click types could not be consistently identified amidst the overlapping clicks, especially from larger groups. Additionally, encounters in the codas click-type group included such a large number of clicks that annotating the entire duration of these encounters in a timely manner was not feasible. Therefore, these encounters were subsampled by selecting 10-min periods of data separated by a 5-min gap, with a randomly selected start time within the first 5 min of the encounter. This resulted in significantly reducing the data processing time while still analyzing approximately 2/3 of data for each codas encounter. To ensure subsampling did not bias click detection rates, we compared a subset of fully-annotated codas encounters with their subsampled version of click data and found click detection rates to be very similar.

Since the true silent periods of sperm whales cannot be reliably assessed from the towed array data, we split each acoustic encounter into "click trains" to represent only the periods when clicks were detected to use as the unit for calculating the overall click detection rate. The minimum duration of a click train was identified using a threshold based on the percentile of all ICIs of each click-type group, which ranged between the 95th–99th percentile. The ICI results from previous studies were considered when determining the percentile to yield biologically consistent thresholds for each click-type group. Any ICIs exceeding the predetermined threshold indicated the start of a new click train, objectively removing periods of time when the whales were silent. Click detection rates were calculated per encounter by dividing the total number of clicks by the total duration of click trains (i.e., silent periods omitted). For comparison purposes, click detection rates were also computed by dividing the total number of clicks by the total time between the first and last click of the encounter (i.e., silent periods included). Encounter-level click detection rates from both methods were averaged to obtain a mean click detection rate for each click-type group. The same process was followed to calculate click detection rates using only the visually sighted encounters with group size estimates.

Two sets of generalized additive models (GAMs) were implemented to evaluate the potential nonlinear effects of different factors on click detection rates calculated using the click trains and the total encounter duration. The first set of GAMs included all encounters and the second set included only sighted encounters with associated group size data from the visual observers. All four GAMs incorporated the same predictor variables, including the perpendicular distance to the animals, the click-type group, encounter latitude and longitude, Julian day, and survey year. The GAMS were fitted with the "mgcv" R package (v. 1.8–39; Wood, 2011) using a gamma distribution with a log link function. Thin-plate regression splines were restricted to three degrees of freedom (12 degrees of freedom for the spatial smoother using the latitude and longitude) to prevent overfitting. We optimized parameter estimates using restricted maximum likelihood and selected variables using a shrinkage approach to modify the smoothing penalty and remove non-significant variables from the model (Marra and Wood, 2011). To further simplify models, statistically non-significant predictors at the 0.05 significance level were also removed, and models were refit until only significant predictors remained. Model goodness of fit was assessed by inspection of the corresponding results, including visual inspection of residuals and q-q plots.

III. RESULTS

The variability in sperm whale click detection rates was evaluated using 49 towed array sperm whale encounters collected during three shipboard line-transect cetacean abundance surveys within the Hawaiian Archipelago, 20 of which were visually sighted (Fig. 1 and Table S1 in the supplementary material). For this analysis, the 49 sperm whale encounters resulted in a total duration of 54.5 h of acoustic data, of which 225 931 clicks within 1163 click trains were manually verified and annotated. Overall, sperm whale encounters lasted an average of 66.9 min (1.1–225.4 min) and produced an overall mean click detection rate per encounter of 1.39 clicks/s from the click trains data set and 0.74 clicks/s when using the total encounter duration. Click detection rates varied by click-type group, ranging from an average of 0.30 clicks/s for slow clicks to 2.87 clicks/s for codas (Table I). Encounter durations also varied across click-type groups, with the codas group lasting the longest amount of time and the groups producing only regular clicks having the shortest durations (Table I).

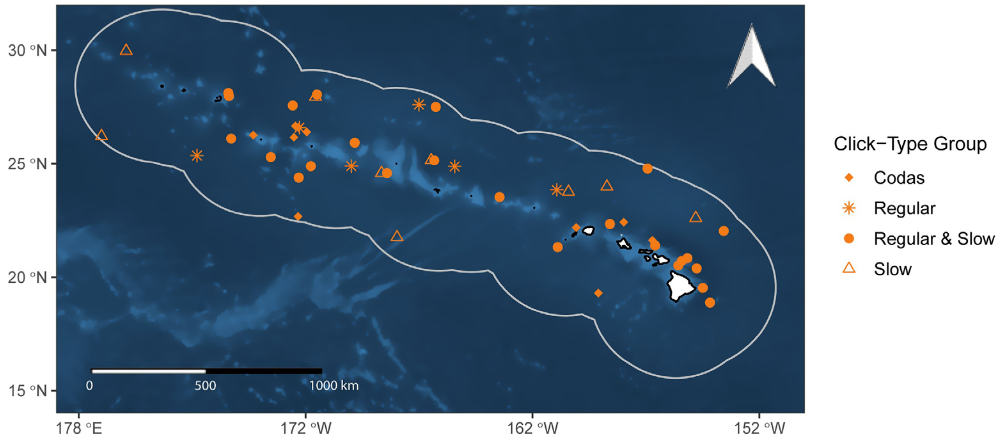

FIG. 1. (Color online) Study area with locations of sperm whale encounters included in the click detection rate analysis. The bathymetry of the study area is indicated using a blue color scale ranging from 0 to 6619 m, with lighter and darker shades depicting shallower and deeper depths, respectively.

After categorizing the encounters into one of four click-type groups using click spectral and temporal features, ICIs, and notes on the whales' behavioral state from visual observations, we further validated this grouping method by comparing the ICIs per group to previously published ICIs. Overall, the ICIs fell within the ranges reported in previous studies (Jaquet *et al.*, 2001; Watwood *et al.*, 2006; Weilgart and Whitehead, 1997) with the majority of the codas click-type groups having the shortest ICIs (keeping in mind this group included other click types), followed by those with regular clicks, then those with regular and slow clicks combined, and finally the slow click-type groups having the longest ICI (Table I, Fig. 2).

We compared click detection rates calculated from both the click trains and the total encounter duration data sets to gain a better understanding of the overall clicking behavior of the sperm whales. As expected, based on how these parameters were calculated, mean click detection rates were higher for the click trains data set as they included less silent time than the total encounter duration data set (Fig. 3, Table I). Even though the click trains data set produced higher standard deviations in the click detection rates than the total encounter duration data set (Table I), the within-group variability was similar between the two data sets for each click-type group (Fig. 3). For the sighted acoustic encounters, standardizing the click detection rates by group size estimates helped visualize the effects of other variables, such as distance from the ship (which nonetheless had no effect), and reduced the overall variability within click-type groups (Fig. 4).

GAMs were applied to assess the effects of multiple factors on click detection rates. The first set of GAMs incorporated all sperm whale encounters. The first model included click detection rates from click trains as the response variable and the second model included click detection rates from the total encounter duration. The click-type group was the only predictor variable retained in both models, finding all four groups to be statistically significantly different and deviating from the reference group (codas click-type group) in a similar pattern (Fig. 5). The first model produced a higher explained deviance (64.7%) compared to the second model (56.7%), which indicates the click-type groups explained more of the variation in click detection rates from the click trains than the total encounter duration data set. For the second set of GAMs, with only sperm whale encounters that were both visually and acoustically detected, we found a positive relationship between click detection rates and group size estimates. Therefore, we divided the click detection rates by the group size to account for this effect prior to fitting the GAMs, effectively turning the number into a per-animal measure (Fig. 6). No explanatory variable was considered statistically significant for models that used the standardized click detection rates as the response variable.

TABLE I. Summary results of sperm whale acoustic encounters from towed array data organized by click-type group. Mean encounter duration was calculated using the time difference between the first and last detected click. The ICI threshold percentile was used to obtain the ICI threshold as a cutoff value for determining the start of a new click train. The mean click detection rates (CDR) ± standard deviations were computed from the individual click trains, all click trains, and the total encounter duration are provided.

Click-type group	Total encounters	Mean encounter duration (min)	ICI threshold percentile	ICI Threshold (s)	Total click trains	Total clicks	Mean ICI (s)	Mean CDR of individual click trains (clicks/s)	Mean CDR of all click trains (clicks/s)	Mean CDR of total encounter time (clicks/s)
Codas	10	105	0.9987	7.38	251	189274	0.19 ± 0.32	2.87 ± 2.97	4.13 ± 2.36	2.48 ± 1.75
Regular	6	39	0.96	2.70	293	7932	0.80 ± 0.39	2.23 ± 1.58	1.40 ± 0.45	0.61 ± 0.25
Regular & Slow	24	66	0.98	13.66	526	25938	1.46 ± 1.64	0.74 ± 0.86	0.65 ± 0.37	0.30 ± 0.28
Slow	9	47	0.95	25.94	92	1589	3.72 ± 2.85	0.30 ± 0.10	0.27 ± 0.10	0.11 ± 0.08

JASA
https://doi.org/10.1121/10.0025540

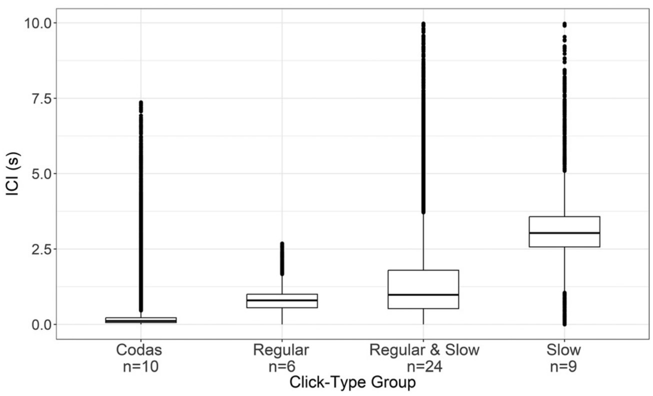

FIG. 2. Box plots show the minimum, first quartile, median, third quartile, and maximum values of the ICI in seconds for each encounter in each click-type group. Black dots represent extreme observations. The total number of acoustic encounters within each click-type group is represented by n. Note that the clicks used to calculate these ICIs are not strictly independent but clustered by encounter.

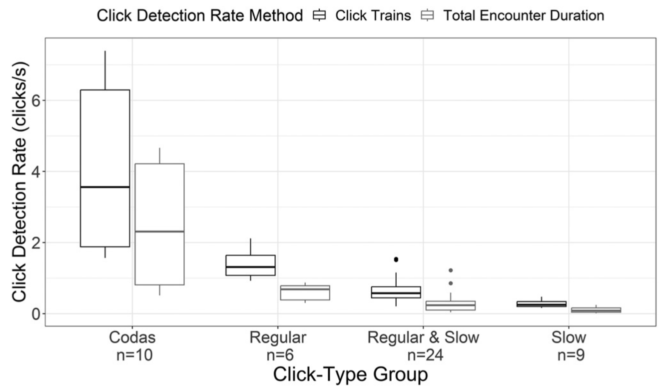

FIG. 3. Box plots of all sperm whale encounters show the minimum, first quartile, median, third quartile, maximum values, and outliers (dots) of the overall click detection rates calculated using only click trains (black) and the total encounter duration (gray) for each click-type group. The total number of acoustic encounters within each click-type group is represented by n.

IV. DISCUSSION

Estimating density using acoustic cues is ideal for deep-diving cetaceans that spend the majority of their life underwater, but an accurate acoustic cue rate is essential for obtaining a reliable estimate. No acoustic tag data exists to calculate acoustic cue rates for sperm whales in the North Pacific Ocean despite their endangered status and well-documented, highly acoustic behavior. In this analysis, the click detection rates of sperm whale groups in Hawaiian waters were computed using towed array data to examine the effects of distance from the track line, group size, day, year, location, and click-type group. Generalized additive models found click-type group to have the only statistically significant effect on click detection rates. Therefore, given the link between click types and different sperm whale behaviors (Goold and Jones, 1995; Miller *et al.*, 2004; Oliveira *et al.*, 2013; Oliveira *et al.*, 2016; Watkins, 1980; Weilgart and Whitehead, 1993), our results show that click detection rates change depending on the behavioral state of the group, which should be taken into account when using PAM to estimate their density. If behavior changes over space and time, then changes, or lack thereof, in observed density based on a single cue rate might be a consequence of different behavior, not just corresponding to different densities. This has been clearly discussed as a potential issue for other species, most notably in a recent, compelling example for harbour porpoise by Macaulay *et al.* (2023).

Part of the data selection criteria for choosing the sperm whale acoustic encounters required that reliable distance information must be obtained in order to evaluate the effect of distance on click detection rates. When models did not select the distance variable, we found this counter-intuitive since we know detectability alone should lead to a decrease in detected cue rates with distance. Therefore, we reexamined whether our criterion for distance information may have introduced bias by favoring groups closer to the track line, causing more of the produced clicks to be detected. Upon reviewing the distances of the selected acoustic encounters, 95% of them occurred within 15 km with a

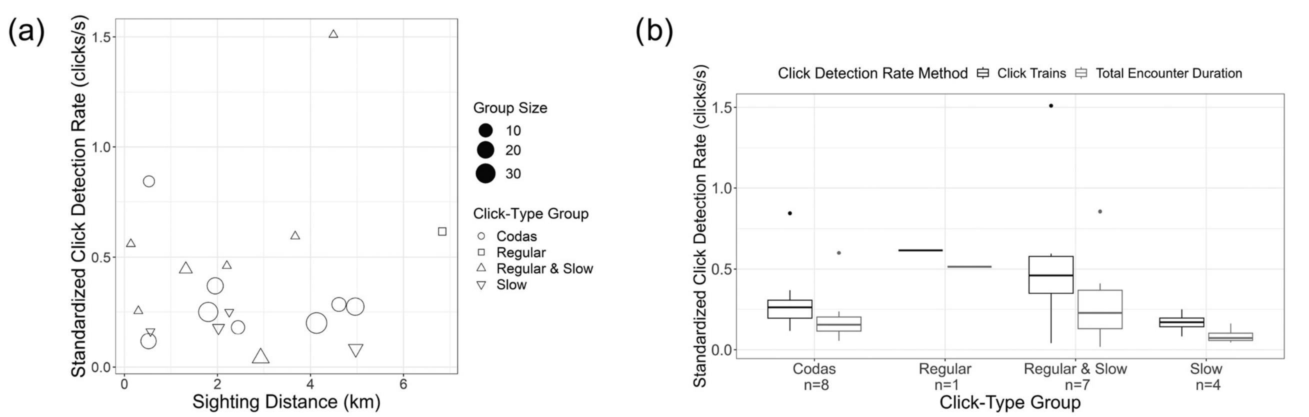

FIG. 4. (a) A scatterplot showing the sighting distance of sperm whale encounters with corresponding click detection rates standardized by group size. Most sighted sperm whale encounters occurred at distances ranging from 2 to 5 km from the ship, with the codas click-type groups consisting of larger group sizes. (b) Box plots of sighted sperm whale encounters show the minimum, first quartile, median, third quartile, maximum values, and outliers (dots) of the click detection rates (standardized by group size), calculated using only click trains (black) and the total encounter duration (gray) for each click-type group. The total number of sighted encounters within each click-type group is represented by *n*.

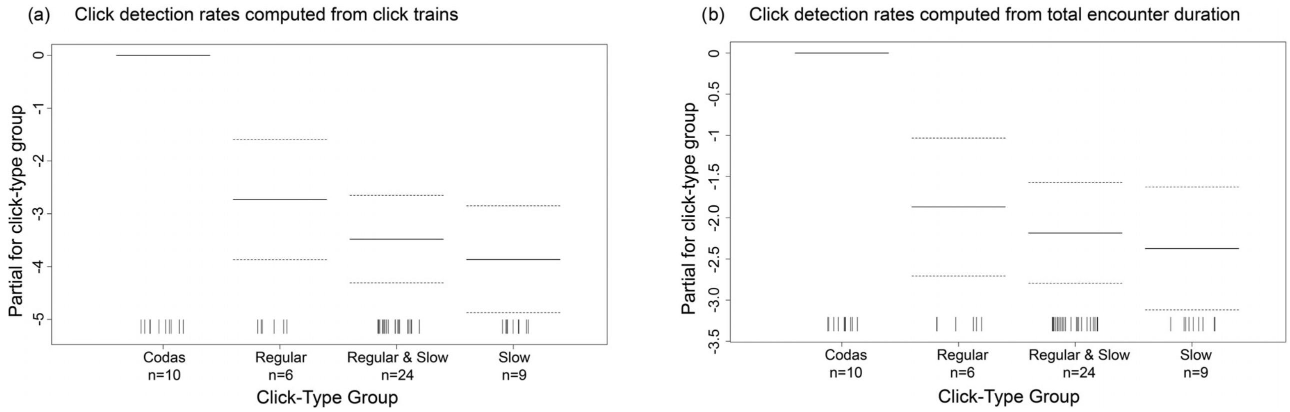

FIG. 5. Two generalized additive models including all acoustic encounters resulted in click-type group as the only significant predictor of sperm whale click detection rates calculated from a) click trains and (b) the total encounter duration. Models included 49 towed array sperm whale encounters.

maximum distance of 19.5 km. All sighted encounters occurred within 7 km. Sperm whale groups are routinely detected from towed surveys at distances well over 20 km, even up to 37 km, with click detectability generally decreasing at much farther distances (e.g., > 20 km) (Barlow and Taylor, 2005; Hastie *et al.*, 2023; Lewis *et al.*, 2018; Lewis *et al.*, 2007). Since the majority of our distances fall within 10 km, we were satisfied that all groups should have similar detectability and, therefore, it is reasonable that the models did not identify distance as a significant predictor variable. The type of clicks produced can also play a role in their detectability. For example, slow clicks are typically detected at greater distances than regular clicks due to their different acoustic characteristics (Barlow and Taylor, 2005). However, we still did not find the distance to influence the click detection rates despite having different click types present within the data set.

The amount of variability in click detection rates of the full data set ($n = 49$) differed between click-type groups and also depended on how they were computed, whether using click trains or the total encounter duration. The lower explained deviance of the GAMs using the total encounter duration indicated more unexplained variability likely due to the addition of more silent periods compared to using only click trains. Among all the click detection rates, the codas click-type group exhibited the widest range of values when incorporating all acoustic encounters (Fig. 3). This is partly due to the various click types overlapping among the codas and also likely related to the high variability in group sizes. The click-type groups containing only regular clicks and those with regular and slow clicks exhibited similar patterns in variability. This was not surprising since the slow clicks were less frequent compared to the regular clicks when they were both detected within the same encounter, thus they had less influence on the overall click detection rates. Sperm whales producing only slow clicks demonstrated the lowest click detection rates and least amount of variability compared to the other click-type groups [Figs. 3 and 4(a)]. The steady click rate of the slow clicks has been linked to long-distance communication by males who are likely keeping track of conspecifics while they are separated from larger groups (Oliveira *et al.*, 2013). A consistent, slower click rate might facilitate that communication. Since visual observations and acoustic localization data often confirm the presence of a single whale when slow clicks are detected (Table S1; unpublished acoustic data, see supplementary material), the click detection rates for the slow click-type group may be indicative of the click rate per whale in this behavioral state, information that is integral for estimating the average cue production rate for the population.

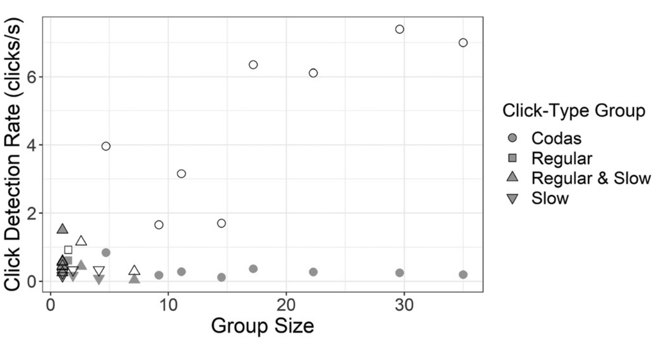

FIG. 6. Visually sighted sperm whale acoustic encounters show raw click detection rates from click trains (black) to be positively associated with group size, but this positive trend is removed when click detection rates are standardized by group size (solid gray).

We compared click detection rates from the towed array data set with click rates derived from a subsample of six acoustic tags collected from the Azores in the North Atlantic Ocean, a location with a similar latitude and bathymetry as the Hawaiian Islands. Since the tags only included regular clicks from individual whales, we selected only the four towed array encounters with single whales producing regular clicks as verified by acoustic localization methods. Click rates from tags and towed array encounters were computed using the total duration. The mean click rate from the six tags (1.24 clicks/s) was double that of the four towed array encounters (0.6 clicks/s). The difference in click rates may be evidence of the physical limitations of the towed array method, causing clicks to be missed due to different noise sources that were not present in the acoustic tag data (e.g., vessel noise). However, upon further inspection of the acoustic encounters, no obvious evidence of such masking sounds was found and all whales were localized less than 4 km from the towed array, well within their detectable range (Barkley *et al.*, 2021). While we cannot determine the exact reason for the discrepancy in click rates, it further emphasizes the importance of using click rates that are appropriate for the target population, ideally from the same time and place that a PAM density estimation survey might take place (e.g., Marques *et a*l., 2013; Marques *et al.*, 2023: Warren *et al.*, 2017).

One benefit of studying click rates using towed array data is the associated visual observer data that provides behavioral and group size information. For example, by standardizing the click detection rates of the sighted acoustic encounters by group size, we found a relationship between the two variables prior to fitting the GAMs. The strongest effect appeared to be on the larger groups producing codas, which further emphasizes the connection between click detection rates and a group's behavioral state. Since this result is based on a small sample size, additional data is needed to further explore this relationship. Nonetheless, this standardization process may act as a good starting point for estimating the number of individual whales within a group, a promising approach that also requires further investigation, but could prove to be essential for obtaining average acoustic cue production rates. Developing a model that can predict group sizes using sperm whale click rates from towed array data would also have important implications for abundance estimation within a distance sampling framework. A similar approach has been shown to be possible for beaked whales from bottom mounted arrays (Marques *et al.*, 2019).

This study contributes new information about sperm whale click detection rates in the central North Pacific Ocean with results clearly showing that the behavioral state of sperm whales affects their click detection rates for this region. Our results provide useful information about the variability in click detection rates that may be useful when applying cue-based density estimation methods to autonomous acoustic platforms. Ideally, future studies would deploy acoustic tags on sperm whales from this region to validate the amount of time whales are silent, as well as the amount of time they typically spend in different behavioral states. From this it could be determined to what degree the amount of time spent in each behavioral state affects the overall average cue production rate of the population, and consequently, cue-based density estimates. In the meantime, the available towed array data offers new insights into sperm whale acoustic behavior and provides a basis for future click rate studies of this endangered species in the central North Pacific Ocean.

SUPPLEMENTARY MATERIAL

See the supplementary material for a table of summary information of the towed array sperm whale encounters.

ACKNOWLEDGMENTS

This research was conducted under the ACCURATE project, funded by the U.S. Navy Living Marine Resources program (Contract No. N3943019C2176). T.A.M. thanks partial support by CEAUL (funded by FCT - Fundação para a Ciência e a Tecnologia, Portugal DOI: 10.54499/UIDB/00006/2020). This work was made possible by the officers and crew aboard the R/V Oscar Elton Sette and R/V Reuben Lasker. We would like to acknowledge the hard work of all the researchers who collected the towed array passive acoustic data. The funding for passive acoustic data collection during the cetacean line-transect surveys was provided by Pacific Islands Fisheries Science Center, Southwest Fisheries Science Center, NOAA Fisheries Office of Protected Resources, NOAA Fisheries Office of Science and Technology, Chief Naval Operation Environmental Readiness Division and Pacific fleet, and Bureau of Ocean Energy Management for HICEAS in 2017, and Pacific Islands Fisheries Science Center provided the funding for PACES in 2013 and HITEC in 2016. The DTAG data set used for the comparison of click detection rates was obtained through the financial support of the Danish Research Council; the Carlsberg Foundation; Fundação para a Ciência e a Tecnologia (FCT); Fundo Regional da Ciência, Tecnologia (FRCT) through research projects TRACE-PTDC/MAR/74071/2006 and MAPCET-M2.1.2/F/012/2011 [Fundo Europeu de Desenvolvimento Regional, the Competitiveness Factors Operational (COMPETE), Quadro de Referência Estratégico Nacional (QREN) European Social Fund, and Proconvergencia Açores/European Union Program]; Aarhus University; Woods Hole Oceanographic Institution; University of Southern Denmark and University of La Laguna. Ann Allen provided very useful comments on a draft of the manuscript.

AUTHOR DECLARATIONS

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Backus, R. H., and Schevill, W. E. (**1966**). "*Physeter* clicks," in *Whales, Dolphins, and Porpoises* (University of California Press, Berkley, CA), pp. 510–527.

Barkley, Y. M., Nosal, E.-M., and Oleson, E. M. (**2021**). "Model-based localization of deep-diving cetaceans using towed line array acoustic data," J. Acoust. Soc. Am. **150**(2), 1120–1132.

Barkley, Y. M., Sakai, T., Oleson, E. M., and Franklin, E. C. (**2022**). "Examining distribution patterns of foraging and non-foraging sperm whales in Hawaiian waters using visual and passive acoustic data," Front. Remote Sens. **3**, 940186.

Barlow, J., and Taylor, B. L. (**2005**). "Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey," Mar. Mammal Sci. **21**(3), 429–445.

Baumgartner, M. F., Bonnell, J., Corkeron, P. J., Van Parijs, S. M., Hotchkin, C., Hodges, B. A., and Bruner, S. M. (**2020**). "Slocum gliders provide accurate near real-time estimates of baleen whale presence from human-reviewed passive acoustic detection information," Front. Mar. Sci. **7**, 100.

Charif, R. A., Waack, A., and Strickman, L. (**2010**). *Raven Pro 1.4* (The Cornell Lab of Ornithology, Ithaca, NY).

Davis, G. E., Baumgartner, M. F., Bonnell, J. M., Bell, J., Berchok, C., Bort Thornton, J., and Van Parijs, S. M. (**2017**). "Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014," Sci. Rep. **7**(1), 13460.

Douglas, L. A., Dawson, S. M., and Jaquet, N. (**2005**). "Click rates and silences of sperm whales at Kaikoura, New Zealand," J. Acoust. Soc. Am. **118**(1), 523–529.

Gero, S., Whitehead, H., and Rendell, L. (**2016**). "Individual, unit and vocal clan level identity cues in sperm whale codas," R. Soc. Open Sci. **3**(1), 150372.

Gillespie, D., Mellinger, D. K., Gordon, J., McLaren, D., Redmond, P., McHugh, R., Trinder, P., Deng, X.-Y., and Thode, A. (**2009**). "PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans," J. Acoust. Soc. Am. **125**(4), 2547.

Goold, J. C., and Jones, S. E. (**1995**). "Time and frequency domain characteristics of sperm whale clicks," J. Acoust. Soc. Am. **98**(3), 1279–1291.

Hastie, G. D., Swift, R. J., Gordon, J. C. D., Slesser, G., and Turrell, W. R. (**2023**). "Sperm whale distribution and seasonal density in the Faroe Shetland Channel," J. Cetacean Res. Manage. **5**(3), 247–252.

Hersh, T. A., Gero, S., Rendell, L., Cantor, M., Weilgart, L., Amano, M., and Kerr, I. (**2022**). "Evidence from sperm whale clans of symbolic marking in non-human cultures," Proc. Natl. Acad. Sci. U.S.A. **119**(37), e2201692119.

Hildebrand, J. A., Baumann-Pickering, S., Frasier, K. E., Trickey, J. S., Merkens, K. P., Wiggins, S. M., McDonald, M. A., Garrison, L. P., Harris, D., Marques, T. A., and Thomas, L. (**2015**). "Passive acoustic monitoring of beaked whale densities in the Gulf of Mexico," Sci. Rep. **5**, 16343.

Hildebrand, J. A., Frasier, K. E., Baumann-Pickering, S., Wiggins, S. M., Merkens, K. P., Garrison, L. P., Soldevilla, M. S., and McDonald, M. A. (**2019**). "Assessing seasonality and density from passive acoustic monitoring of signals presumed to be from pygmy and dwarf sperm whales in the Gulf of Mexico," Front. Mar. Sci. **6**, 66.

Jaquet, N., Dawson, S., and Douglas, L. (**2001**). "Vocal behavior of male sperm whales: Why do they click?," J. Acoust. Soc. Am. **109**(5), 2254–2259.

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. Oceanic Eng. **28**(1), 3–12.

Lewis, T., Boisseau, O., Danbolt, M., Lacey, C., Leaper, R., Matthews, J., and Moscrop, A. (**2018**). "Abundance estimates for sperm whales in the Mediterranean Sea from acoustic line-transect surveys," J. Cetacean Res. Manage. **18**(1), 103–117.

Lewis, T., Gillespie, D., Lacey, C., Matthews, J., Danbolt, M., Leaper, R., McLanaghan, R., and Moscrop, A. (**2007**). "Sperm whale abundance estimates from acoustic surveys of the Ionian Sea and Straits of Sicily in 2003," J. Mar. Biol. Ass. **87**(1), 353–357.

Macaulay, J. D. J., Rojano-Doñate, L., Ladegaard, M., Tougaard, J., Teilmann, J., Marques, T. A., Siebert, U., and Madsen, P. T. (**2023**). "Implications of porpoise echolocation and dive behaviour on passive acoustic monitoring," J. Acoust. Soc. Am. **154**, 1982–1995.

Madsen, P. T., Payne, R., Kristiansen, N. U., Wahlberg, M., Kerr, I., and Mohl, B. (**2022**). "Sperm whale sound production studied with ultrasound time/depth-recording tags," J. Exp. Biol. **205**, 1899–1906.

Marcoux, M., Whitehead, H., and Rendell, L. (**2006**). "Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*)," Can. J. Zool. **84**(4), 609–614.

Marques, T. A., Jorge, P. A., Mouriño, H., Thomas, L., Moretti, D. J., Dolan, K., Claridge, D., and Dunn, C. (**2019**). "Estimating group size from acoustic footprint to improve Blainville's beaked whale abundance estimation," Appl. Acoust. **156**, 434–439.

Marques, T. A., Marques, C. S., and Gkikopoulou, K. C. (**2023**). "A sperm whale cautionary tale about estimating acoustic cue rates for deep divers," J. Acoust. Soc. Am. **154**(3), 1577–1584.

Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Moretti, D. J., Harris, D., and Tyack, P. L. (**2013**). "Estimating animal population density using passive acoustics," Biol. Rev. Cambridge Philos. Soc. **88**(2), 287–309.

Marques, T. A., Thomas, L., Ward, J., DiMarzio, N., and Tyack, P. L. (**2009**). "Estimating cetacean population density using fixed passive acoustic sensors: An example with Blainville's beaked whales," J. Acoust. Soc. Am. **125**(4), 1982–1994.

Marra, G., and Wood, S. N. (**2011**). "Practical variable selection for generalized additive models," Comput. Stat. Data Anal. **55**(7), 2372–2387.

MATLAB (**2019**). Version 9.5.0 (R2019b) (MathWorks Inc., Natick, MA).

Matthews, J., Brown, S., Gillespie, D., Johnson, M., McLanaghan, R., Moscrop, A., Nowacek, D., Leaper, R., Lewis, T., and Tyack, P. (**2023**). "Vocalisation rates of the North Atlantic right whale (*Eubalaena glacialis*)," J. Cetacean Res. Manage. **3**(3), 271–282.

Mellinger, D. (**2002**). Ishmael: 1.0 user's guide; Ishmael: integrated system for holistic multi-channel acoustic exploration and localization.

Miller, P. J., Johnson, M. P., and Tyack, P. L. (**2004**). "Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture," Proc. R. Soc. London, Ser. B **271**(1554), 2239–2247.

Mohl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A., and Lund, A. (**2003**). "The monopulsed nature of sperm whale clicks," J. Acoust. Soc. Am. **114**(2), 1143–1154.

Moretti, D., Marques, T. A., Thomas, L., DiMarzio, N., Dilley, A., Morrissey, R., McCarthy, E, Ward, J., and Jarvis, S. (**2010**). "A dive counting density estimation method for Blainville's beaked whale (*Mesoplodon densirostris*) using a bottom-mounted hydrophone field as applied to a Mid-Frequency Active (MFA) sonar operation," Appl. Acoust. **71**(11), 1036–1042.

Oliveira, C., Wahlberg, M., Johnson, M., Miller, P. J., and Madsen, P. T. (**2013**). "The function of male sperm whale slow clicks in a high latitude habitat: Communication, echolocation, or prey debilitation?," J. Acoust. Soc. Am. **133**(5), 3135–3144.

Oliveira, C., Wahlberg, M., Silva, M. A., Johnson, M., Antunes, R., Wisniewska, D. M., Fais, A., Goncalves, J., and Madsen, P. T. (**2016**). "Sperm whale codas may encode individuality as well as clan identity," J. Acoust. Soc. Am. **139**(5), 2860–2869.

Oswald, J. N., Barlow, J., and Norris, T. F. (**2003**). "Acoustic identification of nine delphinid species in the Eastern Tropical Pacific Ocean," Mar. Mammal Sci. **19**(1), 20–037.

Robbins, J. R., Brandecker, A., Cronin, M., Jessopp, M., McAllen, R., and Culloch, R. (**2015**). "Handling dolphin detections from C-PODs, with the development of acoustic parameters for verification and the exploration of species identification possibilities," Bioacoustics **25**(2), 99–110.

Roch, M. A., Brandes, T. S., Patel, B., Barkley, Y., Baumann-Pickering, S., and Soldevilla, M. S. (**2011**). "Automated extraction of odontocete whistle contours," J. Acoust. Soc. Am. **130**(4), 2212–2223.

Soldevilla, M. S., Wiggins, S. M., and Hildebrand, J. A. (**2010a**). "Spatial and temporal patterns of Risso's dolphin echolocation in the Southern California Bight," J. Acoust. Soc. Am. **127**(1), 124–132.

Soldevilla, M. S., Wiggins, S. M., and Hildebrand, J. A. (**2010b**). "Spatio-temporal comparison of Pacific white-sided dolphin echolocation click types," Aquat. Biol. **9**(1), 49–62.

Solsona-Berga, A. (**2019**). "Advancement of methods for passive acoustic monitoring: A framework for the study of deep-diving cetacean," Ph.D. thesis, Universitat Politècnica de Catalunya, Barcelona, Spain.

Solsona-Berga, A., Posdaljian, N., Hildebrand, J. A., Baumann-Pickering, S., Scales, K., and Quick, N. (**2022**). "Echolocation repetition rate as a proxy to monitor population structure and dynamics of sperm whales," Remote Sens. Ecol. Conserv. **8**(6), 827–840.

Stanistreet, J. E., Nowacek, D. P., Baumann-Pickering, S., Bell, J. T., Cholewiak, D. M., Hildebrand, J. A., Hodge, L. E. W., Moors-Murphy, H. B., Van Parijs, S. M., and Read, A. J. (**2017**). "Using passive acoustic monitoring to document the distribution of beaked whale species in the western North Atlantic Ocean," Can. J. Fish. Aquat. Sci. **74**(12), 2098–2109.

Thompson, P. O. (**1982**). "A long term study of low frequency sounds from several species of whales off Oahu, Hawaii," Cetology **45**, 1–19.

Warren, V. E., Marques, T. A., Harris, D., Thomas, L., Tyack, P. L., Aguilar de Soto, N., and Johnson, M. P. (**2017**). "Spatio-temporal variation in click production rates of beaked whales: Implications for passive acoustic density estimation," J. Acoust. Soc. Am. **141**(3), 1962–1974.

Watkins, W. A. (**1980**). *Acoustics and the Behavior of Sperm Whales* (Springer, New York).

Watwood, S. L., Miller, P. J., Johnson, M., Madsen, P. T., and Tyack, P. L. (**2006**). "Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*)," J. Anim. Ecol. **75**(3), 814–825.

Weilgart, L., and Whitehead, H. (**1993**). "Coda communication by sperm whales (*Physeter macrocephalus*) off the Galapagos Islands," Can. J. Zool. **71**(4), 744–752.

Weilgart, L., and Whitehead, H. (**1997**). "Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales," Behav. Ecol. Sociobiol. **40**, 277–285.

Westell, A., Sakai, T., Valtierra, R., Van Parijs, S. M., Cholewiak, D., and DeAngelis, A. (**2022**). "Sperm whale acoustic abundance and dive behaviour in the western North Atlantic," Sci. Rep. **12**(1), 16821.

Whitehead, H., and Weilgart, L. (**1990**). "Click rates from sperm whales," J. Acoust. Soc. Am. **87**(4), 1798–1806.

Wiggins, S. M., Roch, M. A., and Hildebrand, J. A. (**2010**). "TRITON software package: Analyzing large passive acoustic monitoring data sets using MATLAB," J. Acoust. Soc. Am. **128**(4), 2299.

Wood, S. N. (**2011**). "Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models," J. R. Stat. Soc. B **73**(1), 3–36.

Yano, K. M., Oleson, E. M., Keating, J. L., Ballance, L. T., Hill, M. C., Bradford, A. L., Allen, A. N., Joyce, T. W., Moore, J. E., and Henry, A. (**2018**). "Cetacean and seabird data collected during the Hawaiian Islands cetacean and ecosystem assessment survey (HICEAS), July–December 2017," NOAA Technical Memorandum, NMFS-PIFSC-72 (NOAA, Washington, DC).