

Estimating group size from acoustic footprint to improve Blainville's beaked whale abundance estimation



Tiago A. Marques^{b,*}, Patrícia A. Jorge^a, Helena Mouriño^a, Len Thomas^c, David J. Moretti^d, Karin Dolan^d, Diane Claridge^e, Charlotte Dunn^e

^a Departamento de Estatística e Investigação Operacional, Faculdade de Ciências da Universidade de Lisboa, Portugal

^b Centre for Research into Ecological and Environmental Modelling, University of St Andrews, United Kingdom, Centro de Estatística e Aplicações, Faculdade de Ciências da Universidade de Lisboa, Portugal

^c Centre for Research into Ecological and Environmental Modelling, University of St Andrews, United Kingdom

^d Naval Undersea Warfare Center, United States

^e Bahamas Marine Mammal Research Organisation, Bahamas

ARTICLE INFO

Article history:

Received 14 June 2018

Received in revised form 17 May 2019

Accepted 31 July 2019

Keywords:

Blainville's beaked whales

Echolocation

Dive counting

Density estimation

Group size

Passive acoustic

ABSTRACT

The numbers of animals in groups and the density of Blainville's beaked whale *Mesoplodon densirostris* (*Md*) were estimated using passive acoustic data collected on the Atlantic Undersea Test and Evaluation Center (AUTEK). *Md* typically associate in groups, producing ultrasonic echolocation signals when foraging, and are routinely detected year-round on the AUTEK range. AUTEK includes a large network of hydrophones cabled to shore that can be used to detect *Md* echolocation signals. Using a first data set, with known group sizes, we used generalized linear models (GLMs) to model group size as a function of the acoustic footprint of a detected deep dive as perceived on the AUTEK hydrophones. The most important variable to explain group size was the detected click rate (total number of clicks detected divided by total length of vocal period duration). Using a second data set, covering 3 separate time periods in 2011 with automated group dive detections, we estimated beaked whale density using a dive counting approach. False positives were removed through manual inspection, removing dives with biologically infeasible characteristics. This led to a total of 8271 detections of beaked whale deep dives, with the average number per day in the three time periods considered being 75, 80 and 76 respectively. Using the selected GLM, the mean estimated group size was 2.36 (95% CI 2.15–2.60), 2.30 (95% CI 2.08–2.56), and 2.33 (95% CI 2.19–2.58) whales/group for the 1st, 2nd and 3rd time period. *Md* density was estimated at 15.8 (95% CI 13.6–21.9), 16.5 (95% CI 13.8–22.4), and 15.8 (95% CI 13.2–21.2) whales/1000 km², respectively. These results support findings from previous studies, and will allow a more precise estimation of group sizes and densities for *Md* in future research.

© 2019 Published by Elsevier Ltd.

1. Introduction

Mesoplodon densirostris (*Md*) is perhaps one of the best documented beaked whale species, although it spends little time at the surface and is difficult to observe in all but low sea-state conditions [3]. Therefore, traditional abundance estimation methods, like visual line transect distance sampling, may lead to estimates which have low precision and/or are potentially biased. These whales typically associate in groups of a few individuals and, when foraging, perform synchronized dives to great depths [2,4,3]. During these deep foraging dives they produce abundant distinctive

ultrasonic echolocation signals, known as 'clicks'. The click is a short, $\approx 300 \mu\text{sec}$, up-sweep from approximately 25 kHz to 50 kHz, with an inter-click interval (ICI) of around 200–300 ms [8]. Note that during the final stages of approaching a prey item *Md* produce short sequences of clicks with a much smaller ICI, known as "buzzes" [7], but they are typically ignored in PAM studies due to their lower SNR making them far less detectable. *Md* click for almost 20% of their time [1]. These characteristics make them ideal candidates for Passive Acoustic Monitoring (PAM) [15].

The Atlantic Undersea Test and Evaluation Center (AUTEK) is a U.S. Navy testing and training range located in a deep (>1500 m) oceanic trough known as the Tongue of the Ocean (TOTO), in the Bahamas. *Md* clicks are routinely detected year-round on the AUTEK range [11,5]. Given the hydrophone spacing and sensitivity,

* Corresponding author.

E-mail address: tiago.marques@st-andrews.ac.uk (T.A. Marques).

combined with the animals' clicks source level and the large number of clicks produced per animal per dive [14], all the dives of a group occurring within the AUTECH range can be assumed to be detected with certainty by the AUTECH system [11]. This was the basis of the density estimation method of dive counting described by Moretti et al. [11].

In passive acoustic density estimation, a number of multipliers might be necessary to correct the density of objects, be it cues or groups, to animal density (Marques et al., 2013). For group-based methods, as dive counting, the mean group size is a key multiplier. In Moretti et al. [11] the mean group size for dive counting was obtained from visual-based values available in the literature, and its estimation remains a challenge for group-based methods. The method described here assumes that the acoustic footprint of a detected dive, i.e. the pattern of detections across the AUTECH sensors over which a group performing a deep dive is detected, is correlated to the number of animals in the group. DiMarzio et al. [5] have shown that, not surprisingly, the acoustic footprint of a group is dependent on its group size. This was described for a very small number of groups with known size. Describing the group size distribution over time and space might bring additional knowledge about the effect of navy operations sonar usage on the considered species, which is known to be sensitive to sonar (e.g. Tyack et al., [16], McCarthy et al. [10]).

The present case study focuses on PAM to detect and classify *Md* echolocation clicks. It starts by using a first dataset to model group size as a function of the acoustic footprint of the group dives on the surrounding hydrophones on AUTECH. A model is proposed relating acoustic footprint statistics (e.g., click detection counts, number of hydrophones involved, etc) on AUTECH hydrophones to the group size. The statistical model will enable the development of a real-time algorithm to estimate and display group size information for support of routine density estimation (e.g., Marques et al. [9] and Moretti et al. [11]), providing support for exercises conducted on the range. Using this model over a second dataset we will estimate *Md* density on the AUTECH range for 3 time periods in 2011.

2. Methods

2.1. The AUTECH US Navy range

The AUTECH acoustic range consists of an array of 87 bottom-mounted, widely-spaced hydrophones. AUTECH hydrophones consist of two seven-hydrophone (six outside and a center hydrophone) hexagonal arrays with a baseline of 1.5 km (known as Whiskey arrays) and 73 hydrophones with a wider baseline of ≈ 4 km. The hydrophones are cabled to shore where the signals are digitized (96 kHz) and monitored, for a variety of sounds including beaked whale clicks, by an acoustic signal processor [6].

The Whiskey arrays were the first devices installed, and the newer Advanced Hydrophone Replacement Program (AHRP) array are based on more recent technology. The AHRP array is itself composed by two different types of hydrophones: bi-directional (transmit and receive) and uni-directional (receive only) hydrophones. The Whiskey and AHRP arrays have different hydrophone features and shore processing hardware, resulting in distinct *Md* detection characteristics. The bi-directional hydrophones have more electronic noise potentially leading to a higher frequency of false positive detections [6].

For the purpose of dive counting, we consider detections to occur within an area of 1291 km². This corresponds to the area defined by Moretti et al. [11] for the dive counting algorithm, which extends all but outermost line of hydrophones by a buffer of 6.5 km. This is required to exclude detections from outside this area (see details below).

2.2. The *Md* data

Two different datasets are considered: (1) the modelling dataset consists of the acoustic footprint of *Md* deep dives for detected dives for which group size was confirmed (see details below). It was used to build the model of the group size as a function of the group's dive acoustic footprint, via zero-truncated generalized linear models; and (2) the density estimation dataset which was employed after building the model, which consists of a time series of data from the AUTECH hydrophones, for which the *Md* average group size and density were estimated.

Beaked whale dives were identified using a MATLAB program, Autogrouper, to quickly identify whale dives and start and end times of the echolocations. This works by combining clicks within hydrophones into sequences of clicks, called click trains. It then associates click trains close in space and time, i.e., detected simultaneously in adjacent hydrophones, into vocal groups. Each vocal group detected corresponds to a *Md* foraging dive. Associated with each detected dive there is a set of available statistics that define the acoustic footprint of the group, such as the number of detected clicks and the number of hydrophones detecting each dive.

2.2.1. The modelling dataset

This dataset includes the Autogrouper routine output for 51 deep dives, detected between 2005 and 2008, that were confirmed either visually (41 dives) or by a very time consuming non-automated acoustical analysis (10 dives). This acoustic analysis involves a complex procedure to localize in 3D the majority of clicks produced by animals during a group deep dive and inferring from those the 3D tracks of all the animals in the group, and then counting the number of distinct tracks to get the number of animals in the group. This is the subject a separate paper under preparation. The group size in this modelling data ranged between 1 and 6 whales. We considered the following as potential explanatory variables: (1) K , the total number of the hydrophones over which the dive echolocation clicks were detected, (2) n , the total number of clicks detected across all hydrophones, (3) d , the duration of the echolocation period (time difference between the first click and the last click associated to the dive), and (4) the detected click rate ($\frac{n}{d}$). Additionally, we considered variables that, while not being related to group size per se, could affect the detected acoustic footprint and hence obscure the relationship between the acoustic footprint and the group size if ignored. These were binary variables indicating whether or not the particular dive had its clicks detected by at least one hydrophone located on the edge of the hydrophone array, or if whether or not at least one hydrophone belonged to the particular types of Whiskey or Bi-directional hydrophones.

2.2.2. The density estimation dataset

This second dataset considered a time series of AUTECH data from which density was estimated. It included 3 separate periods of time in 2011: (1) 61 days from the 28th of April to the 27th of June, (2) 18 days from the 20th of October to the 6th of November, and (3) 30 days from the 2nd to the 31st of December. These data were processed using the same procedure that generated the data for the group size model. This allowed us to count the number of dives that occurred on the AUTECH range during the recording period. This in turn allowed the estimation of density over time using an improved version of the dive counting method as described below.

To eliminate false positives, a pre-processing of the data was implemented, based on excluding detected dives with biologically infeasible characteristics: (1) dives occurring on a single hydrophone, and (2) dives with <400 clicks detected. This resulted in a much more biologically plausible distribution of observed vocal

duration per dive, matching what would be expected given described values in the literature. As noted above, we also excluded dives detected only on edge hydrophones, considering these would correspond to dives outside the 1291 km² area of inference.

For each of the dives detected, we used the model that predicts the group size as a function of the acoustic footprint to estimate the corresponding group size.

2.3. Modelling group size

To model the group size as a function of the acoustic footprint we considered the class of generalized linear models (GLMs). Generalized additive models (GAMs) [18] were used to explore non-linear relations, but no evidence of these was found and hence these were discarded. Because group size is a strictly positive number, we only considered zero-truncated GLMs. We considered the known group size for our sample of 51 dives as a Poisson response and the available covariates as explanatory variables. We used Akaike's Information Criteria (AIC) for model selection, and performed visual inspection of qq-plots and residual plots for absolute goodness-of-fit. Models were implemented in the R software [12], with the help of package VGAM [19].

2.4. Density estimation

Here we extend the previous approach from Moretti et al. [11] for group counting, where the proposed estimator of animal density in a period time k was given by:

$$\hat{D}_k = \frac{n_k \hat{s}}{\hat{r} T_k A} \quad (1)$$

where n_k represents the total number of deep dives detected during recording time T_k , \hat{s} is the estimated average group size (common to all groups), \hat{r} is the estimated average number of dives per unit time and A the area over which deep dives are assumed to be detected with certainty. As in Moretti et al. [11] we used $\hat{r} = 0.36$ dives per hour (with a standard error of 0.04) and $A = 1291$ km².

While Moretti et al. [11] used an estimated average group size (\hat{s}) common to all dives, this work used the results from Section 2.3 to estimate the number of individuals for each detected dive. Hence, instead of resorting to the total number of dives and multiplying that value for an estimated average group size based on literature, we suggest an alternative in which the estimator of density (\hat{D}) is obtained using the following equation:

$$\hat{D} = \frac{\sum_{i=1}^{n_k} \hat{s}_i}{\hat{r} T_k A}; \quad (2)$$

where \hat{s}_i corresponds to the estimated group size for group i detected on period k , and n_k represents the number of groups for the considered time period.

For the current case study, after estimating group size for each detected dive, Md density and associated precision measures were estimated per day over the time period for which recordings are available. We also estimated the mean density and the mean group size for each of the 3 survey time periods considered.

To propagate the variance in the model of group size and cue rate to the density estimates, while accounting for correlation in these parameters across daily estimates, we considered resampling methods. We implemented a bootstrap approach with a dual component, non-parametric for the group sizes (as we have the data for each of the detected dives in the modelling dataset) and parametric for the dive rate (as we only have a literature based mean and a standard error). We considered the dives in the first data set as the independent resampling units for the group size model component, and we drew samples from a Gaussian distribution with the

required parameters (i.e. mean and standard deviation) for the dive rate. From these, for each bootstrap iteration, we calculated the statistics of interest, i.e. the daily estimates and the mean estimates for each period of mean group size and density. We report 95% confidence intervals based on the percentile method.

3. Results

The fitted GLMs reveal that group size can be predicted from acoustic footprint of the detected dive via available covariates. The most parsimonious model according to AIC (Model M1 Table 1) includes a single variable to explain group size: the detected click rate, corresponding to the sum of the number of clicks detected in all hydrophones that detected a group divided by total length of vocal period duration. The relation is shown in Fig. 1. Residuals and qq-plots did not show any reasons for concern. Two other models were close competitors in the sense of having only slightly higher values of AIC, but we ignored them for inference for the sake of parsimony as (1) results in terms of density estimates were insensitive to model choice, (2) and the interpretation of the models was less straightforward.

After pre-processing the dataset for the removal of false positives we obtained 8271 detections of beaked whale deep dives. The first period of time recorded 4562 dives, with a mean of 75 dives per day; the second period showed 1439 dives with a mean of 80 dives per day; and the third one registered 2270 dives with a mean of 76 dives per day. The mean number of dives per day for the three periods was approximately 76.8. Based on the GLM model, the estimated mean group size per period was 2.36 (95% CI 2.15–2.60), 2.30 (95% CI 2.08–2.56), and 2.33 (95% CI 2.19–2.58) whales, respectively.

Density estimates (whales/1000 km²) for each day were obtained. The daily density estimates over the 3 periods considered show relatively low variability (Fig. 2), being relatively constant over time, excluding a couple of days with very large and 3 days with very low density estimates during the first survey period. The overall estimated mean density for all three periods was 15.91 whales/1000 km², with a mean value of 75.88 dives per day. Corresponding average Md density estimates over the three time periods were, respectively 15.8 (95% CI 13.6–21.9, daily range 5.64 to 30.27), 16.5 (95% CI 13.8–22.4, daily range 11.17 to 20.47), and 15.8 (95% CI 13.2–21.2, daily range 9.27 to 22.49) whales/1000 km².

4. Discussion

PAM presents us the chance of accurately estimating wild animal population size and density. For some species and scenarios, PAM greatly improves abundance and density estimates over more traditional visual based methods. Therefore, not surprisingly, PAM is becoming an increasingly important tool for ecology and conservation. Here we extended the conventional dive counting proposed by Moretti et al. [11] by estimating the size of the group involved in each deep dive detected. The group size estimates are of interest in themselves, and the values obtained here are in close agreement with previously reported estimates. From groups at AUTECH in which high quality photo identifications were collected from all individuals, median group size was 2 whales (range 1–5, mode 2, mean 2.34, SD 0.95, n = 73 encounters, Diane Claridge, unpublished data).

The density estimation formula (2) involves two random components, mean group size and mean dive rate. The method proposed here improves on the previous approach of Moretti et al. [11] by (1) allowing the estimation of a group size for each detected dive, and hence (2) allowing the estimation of a mean

Table 1

Models, variables considered (*cdur* = click duration, *nhyd* = number of hydrophones and *crate* = detected click rate), the corresponding coefficient value and respective P-value, as well as the Akaike's Information Criteria.

Model	Variable	Coefficient	P-value	AIC
M1	<i>crate</i>	0.002	0.030	150.55
M2	<i>nhyd</i>	−0.056	0.021	150.71
	<i>crate</i>	0.003	0.193	
M3	<i>cdur</i>	0.010	0.011	150.49
	<i>nhyd</i>	−0.093	0.071	
	<i>crate</i>	0.004	0.137	

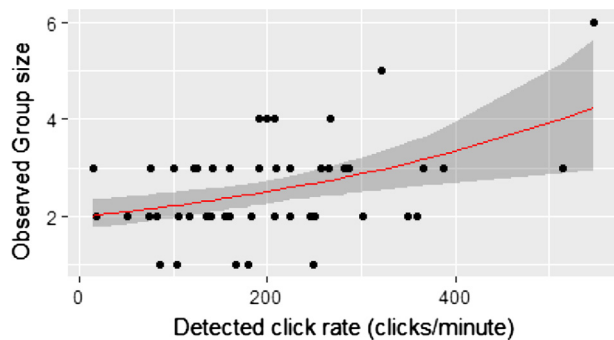


Fig. 1. Observed group sizes and corresponding detected click rate (black dots), along with the modelled relationship (red line), and the model's bootstrap 95% percentile interval for the mean group size (grey area). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

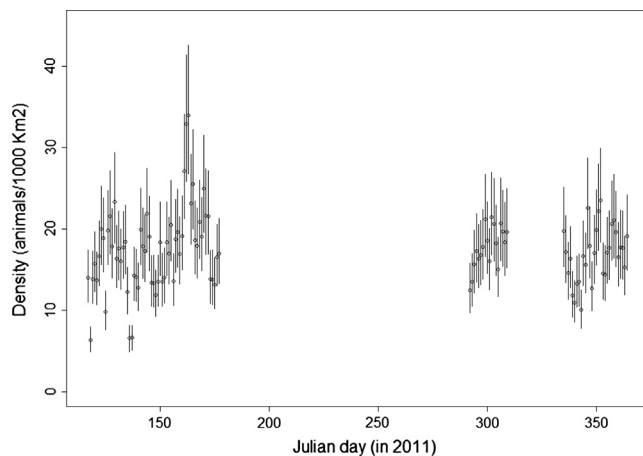


Fig. 2. Daily density estimates with the corresponding bootstrap 95% confidence intervals.

group size for each period of interest, and therefore (3) allowing relaxation of the implicit assumption that group size is constant over time and space. However, the same problem still applies to the dive rate, which is taken from the literature, based on a small sample of tagged animals [11], and assumed constant over time. It is possible that differences in dive rates are larger, over time and space, than differences in group sizes. Therefore, while being a useful step in obtaining more reliable density estimates, dealing with variation in group size might fall short from being enough to get reliable density estimates from dive counting methods. Additional studies looking at beaked whale dive rates, investigating how these might change in space (e.g., bottom depth dependent) and in time (e.g., seasonally), are fundamental to understand the reliability of dive counting methods. Assuming deep dives can be

identified, a good place to start investigating these issues further might be existing satellite tag data (e.g. Schorr et al., [13]), which currently provide much wider temporal and spatial scales than DTAGs.

Given the proposed density estimator assumes perfect detection of deep dives and hence a total count of deep dives, there is no variability associated with encounter rate. This is unusual for other density estimation methods, e.g. number of detections per unit effort in a distance sampling context. Hence, for dive counting, the only randomness in the density estimate is on the dive rate and on the estimated group sizes for the detected dives. The number of dives during that period is fixed. If one were to have a sample of days, but wishing to make inferences for a longer time period from which the days available would be a sample, then a variance component associated with encounter rate would be required.

In this work we assumed that there would be no false positives, i.e. events assumed to be detected deep dives of *Md* that would not correspond to *Md* deep dives. We also assume no false negatives, i.e. missed deep dives within the AUTECH range. These are fair assumptions, but we cannot be certain they hold all the time. A possible extension of these methods would be to include additional multipliers to deal with those two components. Naturally the key question then becomes how to estimate these multipliers, and the corresponding respective associated variances, for variance propagation to the density estimates. Manual validation of random subsets of the data by human analysts, taken as a gold standard, should be possible. A first way to investigate those, as suggested by a reviewer, would be to explore the distribution of the detected deep dive durations. Clearly, a deep dive detected exceeding what might be biologically plausible will be a good candidate for false positive (or contain clicks for more than one group which the Auto-grouper routine might have erroneously assigned to a single group).

We conclude that, based on the acoustic footprint of groups detected on AUTECH hydrophones, the variable detected click rate (sum of the number of clicks detected in all hydrophones that detected a group divided by total length of vocal period duration) appears to be the best descriptor of group size. However, when it comes to modelling, it is noticeable that more observations may be needed, as a small data set will never allow a complex model to be a parsimonious choice. Therefore, it is possible that with additional data more complex models might prove useful to describe group size from the corresponding deep dive(s) acoustic footprint. We note that results were insensitive to using just the visually verified data or using both the visually verified and acoustically verified data, and hence we decided to use all the data given the reduced sample size. Given that detected click rate was the single predictor in the model used for predicting group size, this variable might present a multi-modal distribution in the density estimation data set, where each group size would correspond to a mode. However, we plotted the variable and the multi-mode pattern was not present. This implies that while detected click rate can be used to predict group size, and might work quite well to

predict average group sizes over say a day, it might not be enough to accurately predict each detected dive group size.

Other variables influence sound production, and hence the acoustic footprint detected, besides group size. One possible example would be the presence or absence of calves in the group. This would add noise to the relation between group size and acoustic footprint. However, since we do not have that information for groups which are not verified (i.e. for the survey data), it would not be possible to use this in a model for prediction of group size as a function of the detected acoustic footprint. Additionally, other factors not accounted for could influence the click detectability, and hence induce noise in the relationship found. It is possible that ambient noise might also induce changes in click detectability, further obscuring a relationship between acoustic footprint and group size. Including measurements on ambient noise in the regression model would allow to test that. However, Ward et al. [17] investigated the effects of ambient noise on beaked whale click detectability on AUTEK's hydrophones, and suggest that, for sounds produced at depth, and detected on deep moored sensors, the impact will be minor. It is likely that with shallower sensors that would be a relevant constraint.

In terms of the estimated group sizes and densities, the results presented here are well in line with those from previous studies. Nonetheless, the present work obtained a smaller mean group size estimate than the one from literature (2.35, vs 2.62 used in Moretti et al. [11]). The difference is higher when considering the values reported in Claridge [4] and Baird et al. [2], 4.1 and 3.6 animals per group, respectively, but that is not necessarily surprising since those were for different geographic areas.

The present work estimates a mean density of around 16 whales/1000 km² across all time periods. Sonar might lead to reductions in beaked whale foraging activity, and hence perceived differences in density if animals would stop clicking following sonar use. It is presumed that no major sonar activity took place during the survey period, although small activities can not be ruled out, both during this study, before or after. A lower number of detections could be attributed to sonar use (e.g. Tyack et al., [16], McCarthy et al., [10]) and not necessarily reflect a real change in density, interpreting the results would be easier knowing times of sonar emission. The average density values reported by Moretti et al. [11], 16.99, 4.76, 8.67 and 24.76 whales/1000 km², were calculated considering much shorter time periods (65 h, 68.13 h, 65 h and 43.23 h, respectively), for which the impact from the sonar activity may have become more perceptible. Therefore, localized sonar activity occurring for the present three time periods (1464 h, 432 h and 720 h, respectively) would probably not reflect on the average estimated densities, although it might on daily estimates. This may indicate that reactions are fast, and that a larger scale effect of the sonar activity on *Md* density might be hard to detect from our data, given we have not considered when naval activities were taking place. Future work could involve whether daily patterns in density as observed here are related to existing naval activities.

Additionally, the average number of dives detected per day appears to be consistent across the three time periods (74.8, 79.9 and 75.7, respectively), with a global mean of 75.9 dives/24 h. Moretti et al. [11] results for before, during and after sonar activities seem to exhibit larger differences (97.1, 32.8 and 24.0 groups/24 h, respectively). That might be again explained by the shorter time periods analysed by those authors (65 h, 68 h and 365 h, respectively), and the fact that sonar activities were occurring, likely decreasing *Md* click rates on the range as described by McCarthy et al. [10].

One advantage of the proposed method is to be able to provide a mean group size estimate for any time period that one might consider, naturally provided that period is long enough such that

the average is sensible. These differences would be averaged out when making comparisons across time points having to share the same mean estimate obtained from the literature. This kind of data could be used in itself to derive spatio-temporal models of group size at AUTEK.

If these types of studies are to be used to inform conservation directives, it is important to acknowledge their importance and their necessity to be constantly updated. A species' density fluctuation over time may be due to several external factors, which may also include human disturbance. Describing group size over time may contribute to a better understanding of *Md* habits, leading to enhanced conservation measures. Especially at the current pace that species are being affected by habitat deterioration, method's improvements are vital, as they provide more accurate information contributing to evidence based decisions and an effective management of ecosystems.

5. Research data for this article

The data used in this paper as well as the bootstrap results and code to permit readers to reproduce the figures presented have been submitted to the Mendeley Data repository, under DOI: <https://doi.org/10.17632/r3xpn3mccc.2>.

Acknowledgments

This work was conducted using data collected under the project GROUPAM, funded by the Office of Naval Research of the United States of America via award numbers N000141512648 to UStA, N0001416WX00450/ N0001415WX01715 to NUWC and N000141512649 to BMMRO. We thank the remaining large NUWC M3R team, for providing the raw acoustic data in a format that we could use. In particular we thank Jessica Shaffer who originally led the GROUPAM project, and Sarah Blackstock who contributed directly to some of the data processing. TAM thanks partial support by CEAUL (funded by FCT - Fundação para a Ciência e a Tecnologia, Portugal, through the project UID/MAT/00006/2013). Two anonymous reviewers provided excellent comments that led to a substantially improved paper. AA's Editor-in-Chief contribution is kindly noted, as is the support of the associate editor Neil Ferguson. Nancy DiMarzio provided a review of the final draft which allowed several corrections and clarifications.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.apacoust.2019.07.042>.

References

- [1] Arranz P, de Soto NA, Madsen PT, Brito A, Bordes F, Johnson MP. Following a foraging fish-finder: diel habitat use of Blainville's beaked whales revealed by echolocation. *PLoS ONE* 2011;6:e28353.
- [2] Baird RW, Webster DL, McSweeney DJ, Ligon AD, Schorr GS, Barlow J. Diving behavior of Cuvier's (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*) in Hawai'i. *Can J Zool* 2006;84:1220–8.
- [3] Claridge D. Population ecology of Blainville's beaked whales (*Mesoplodon densirostris*). University of St Andrews; 2013 (Ph.D. thesis).
- [4] Claridge DE. Fine-scale distribution and habitat selection of beaked whales. Scotland, U.K: University of Aberdeen; 2006. Master's thesis.
- [5] DiMarzio N, Moretti D, Ward J, Morrissey R, Jarvis S, Izzi AM, Johnson M, Tyack P, Hansen A. Passive acoustic measurement of dive vocal behavior and group size of Blainville's beaked whale (*Mesoplodon densirostris*) in the Tongue of the Ocean (TOTO). *Can Acoust* 2008;36:166–73.
- [6] Jarvis SM, Morrissey RP, Moretti DJ, Shaffer JA. Detection, localization, and monitoring of marine mammals in open ocean environments using fields of spaced bottom mounted hydrophones. *Mar Technol Soc J* 2014;48:5–20.
- [7] Johnson M, Madsen PT, Zimmer WMX, de Soto NA, Tyack PL. Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click

- types matched to different phases of echolocation. *J Exp Biol* 2006;209:5038–50.
- [8] Madsen PT, Johnson M, de Soto NA, Zimmer WMX, Tyack P. Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J Exp Biol* 2005;208:181–94.
- [9] Marques TA, Thomas L, Ward J, DiMarzio N, Tyack PL. Estimating cetacean population density using fixed passive acoustic sensors: an example with Blainville's beaked whales. *J Acoust Soc Am* 2009;125:1982–94.
- [10] McCarthy E, Moretti D, Thomas L, DiMarzio N, Morrissey R, Jarvis S, Ward J, Izzi A, Dille A. Changes in spatial and temporal distribution and vocal behavior of Blainville's beaked whales (*Mesoplodon densirostris*) during multiship exercises with mid-frequency sonar. *Mar Mammal Sci* 2011;27:E206–26.
- [11] Moretti D, Marques TA, Thomas L, DiMarzio N, Dille A, Morrissey R, McCarthy E, Ward J, Jarvis S. 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* 2010;71:1036–42.
- [12] Core Team R. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing; 2017. URL: <https://www.R-project.org/>.
- [13] Schorr GS, Falcone EA, Moretti DJ, Andrews RD. First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLoS ONE* 2014;9:e92633.
- [14] Shaffer JW, Moretti D, Jarvis S, Tyack P, Johnson M. Effective beam pattern of the Blainville's beaked whale (*Mesoplodon densirostris*) and implications for passive acoustic monitoring. *J Acoust Soc Am* 2013;133:1770–84.
- [15] Tyack PL, Johnson M, Soto NA, Sturlese A, Madsen PT. Extreme diving of beaked whales. *J Exp Biol* 2006;209(21):4238–53.
- [16] Tyack PL, Zimmer WMX, Moretti D, Southall BL, Claridge DE, Durban JW, Clark CW, D'Amico A, DiMarzio N, Jarvis S, McCarthy E, Morrissey R, Ward J, Boyd IL. Beaked whales respond to simulated and actual navy sonar. *PLoS ONE* 2011;6:e17009.
- [17] Ward J, Jarvis S, Moretti D, Morrissey R, DiMarzio N, Thomas L, Marques TA. Beaked whale (*Mesoplodon densirostris*) passive acoustic detection with increasing ambient noise. *J Acoust Soc Am* 2011;129:662–9.
- [18] Wood SN. Generalized Additive Models: an introduction with. R. CRC/Chapman & Hall; 2006.
- [19] Yee TW. The vgam package for categorical data analysis. *J Stat Softw* 2010;32:1–34.