

# Cetacean population density estimation from single fixed sensors using passive acoustics

Elizabeth T. Küsel<sup>a)</sup> and David K. Mellinger

Cooperative Institute for Marine Resources Studies (CIMRS), Oregon State University, Hatfield Marine Science Center, Newport, Oregon 97365

Len Thomas

Centre for Research into Ecological and Environmental Modelling, University of St. Andrews, St. Andrews KY16 9LZ, Scotland

Tiago A. Marques

Centro de Estatística e Aplicações da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

David Moretti and Jessica Ward

Naval Undersea Warfare Center Division, Newport, Rhode Island 02841

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Passive acoustic methods are increasingly being used to estimate animal population density. Most density estimation methods are based on estimates of the probability of detecting calls as functions of distance. Typically these are obtained using receivers capable of localizing calls or from studies of tagged animals. However, both approaches are expensive to implement. The approach described here uses a MonteCarlo model to estimate the probability of detecting calls from single sensors. The passive sonar equation is used to predict signal-to-noise ratios (SNRs) of received clicks, which are then combined with a detector characterization that predicts probability of detection as a function of SNR. Input distributions for source level, beam pattern, and whale depth are obtained from the literature. Acoustic propagation modeling is used to estimate transmission loss. Other inputs for density estimation are call rate, obtained from the literature, and false positive rate, obtained from manual analysis of a data sample. The method is applied to estimate density of Blainville's beaked whales over a 6-day period around a single hydrophone located in the Tongue of the Ocean, Bahamas. Results are consistent with those from previous analyses, which use additional tag data.

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## I. INTRODUCTION

Passive acoustic methods can be valuable tools for monitoring populations of marine mammals since many species produce loud and distinctive calls. Acoustic recordings of marine mammal vocalizations, including echolocation clicks, calls, and songs, sometimes used in conjunction with line-transect methods (e.g., Barlow and Taylor, 2005), are being used increasingly often to better understand a particular species' distribution and population density in a given geographic area (McDonald and Fox, 1999; Moretti *et al.*, 2006; Mellinger *et al.*, 2006, 2007; Marques *et al.*, 2009). Recently, Marques *et al.* (2009) presented a density estimation method based on counting the number of detected cues, where a cue is an effectively instantaneous event such as a single vocalization or the start of a vocalization sequence. The method also requires information on the probability of detecting a cue as a function of distance, the rate at which animals produce cues, and the fraction of false detections. This method was applied to estimate the density of Blainville's beaked whales (*Mesoplodon densirostris*) over a

6-day period in 2005 at the Atlantic Undersea Test and Evaluation Center (AUTEK) in the Tongue of the Ocean, Bahamas. Results of their analysis yielded an estimate of 25.3 [95% confidence interval (CI) 17.3–36.9] or 22.5 (95% CI 15.4–32.9) animals per 1000 km<sup>2</sup>, depending on assumptions about false positive detections.

Estimating the *detection function*, i.e., the probability of detecting a cue as a function of distance from a receiving sensor (Buckland *et al.*, 2001), is a key element required by the above density estimation method. The estimated detection function is integrated over the area of interest, which is equivalent to averaging over distance, assuming that animals are uniformly distributed around the sensors, to derive the estimated average probability of detection. One method for calculating the detection function from data recorded at widely spaced hydrophones in an array configuration is to use the time difference between arrivals of direct path signals at the sensors to estimate the positions of vocalizing animals, and hence, their distances with respect to the sensors. In their study, Marques *et al.* (2009) used data from 82 hydrophones from the AUTEK array. However, due to the narrow beam pattern of Blainville's beaked whales and the configuration of the hydrophones at AUTEK, clicks are normally detected at only one or two hydrophones simultaneously (Ward *et al.*, 2008). Such conditions make methods based on localization

<sup>a)</sup>Author to whom correspondence should be addressed. Electronic mail: kusele@alum.rpi.edu

difficult. One recently developed alternative (Marques *et al.*, 2010) makes use of multiple detections without precise time differences, and hence bypasses the need for localization. However, a reasonable number of multiple detections are required, and these are not obtained in the case of beaked whales. Consequently, to estimate the detection function for Blainville's beaked whales, Marques *et al.* (2009) made use of auxiliary data sets recorded with digital acoustic tags (DTAGs) (Johnson and Tyack, 2003) at AUTEK. Emitted clicks were detected both in data from individual tagged animals and in data from surrounding hydrophones. These detections were combined to localize precisely the animals using a hyperbolic fixing algorithm. The number of clicks detected on each hydrophone was measured and compared to the number produced by the animal to derive the probability of detection as a function of distance. Another important variable required for density estimation, the click production rate, was also estimated using DTAG data.

The goal of this work is to develop and demonstrate an alternative method of estimating animal density from acoustic recordings on separate, non-linked fixed hydrophones. By using separate, non-linked sensors, the method does not rely on localizing animals, a process that can be labor intensive even when it is feasible. Necessary information on animal vocal behavior is preferably obtained from the literature or derived from known information on similar species, instead of using acoustic tag data. Affixing acoustic tags to marine mammals is both difficult and expensive, and most often tag data from a specific population are not available. However, it should be noted that information available in the literature for certain species such as beaked whales, may come mostly from acoustic tag studies, although not necessarily from the same population or area being considered.

The method developed here is applied to estimate the density of Blainville's beaked whales at AUTEK during the same time period analyzed by Marques *et al.* (2009), and the results are compared. The current study focuses on data from a single hydrophone and follows the methodology outlined by Zimmer *et al.* (2008) to estimate the detection function by application of the passive sonar equation. The probability of detecting a click as a function of distance from a single sensor is estimated by simulating clicks at a set of distances, predicting their signal-to-noise ratio (SNR) at the sensor using the sonar equation, and determining whether they would be detected at this SNR using information about the sensitivity of the detection and classification system. The use of the sonar equation requires knowledge of animal source level and characteristics of their sound beam pattern, including change in source level as a function of off-axis angle, propagation loss from source (whale) to receiver, and ambient noise levels at the receiver. Distributions of these parameters are used in a Monte Carlo algorithm to simulate the probability of detecting beaked whale clicks. The animal's location and orientation relative to the sensor must be simulated in order to estimate the acoustic off-axis angle and hence the attenuation of source level. The slant distance to the sensor is also important to infer sound transmission losses, which occur due to signal spreading and sound absorption. The on-axis source level, animal depth and orien-

tion, and click production rate are gathered from information available in the literature derived from acoustic tags, but not the same acoustic tag data sets used by Marques *et al.* (2009). The sensitivity of the detector is characterized by manually analyzing a short section of data to determine the SNR of all clicks, then analyzing the same data using the detector to determine which clicks were correctly detected and classified, and finally using this to build a regression curve of probability of detection versus SNR. The estimated average probability of detection from the simulated clicks is then used to estimate density of whales at AUTEK using the density estimation formula from Marques *et al.* (2009).

## II. BEAKED WHALES AT AUTEK

The family of beaked whales, Ziphiidae, is composed of 21 deep-diving species that spend little time at the surface and hence are difficult to observe and study (Barlow *et al.*, 2006). Until about a decade ago, little information was available on their ecology, behavior, or vocalizations. Strandings of two species, Cuvier's (*Ziphius cavirostris*) and Blainville's beaked whales, coincident with U.S. Navy sonar operations, prompted many efforts to study these species in more detail to understand their distributions, their use of sound, and the effects of sound on them (Barlow and Gisinier, 2006).

This paper is focused on Blainville's beaked whales, although references to Cuvier's beaked whales are made occasionally since both species have somewhat similar acoustics (Tyack *et al.*, 2006). These species produce high-frequency echolocation clicks with center frequency in the range of 30 to 40 kHz. They also produce two distinct types of clicks during foraging (Johnson *et al.*, 2006). One type, called a *regular click*, is frequency-modulated; the other, the *buzz click*, is believed to occur during the final stages of prey capture. Regular clicks have duration of approximately 250  $\mu$ s, while buzz clicks are distinctly different from regular clicks, having mean duration of 104  $\mu$ s. Buzz clicks are excluded from this analysis, as has been done elsewhere (Zimmer *et al.*, 2008; Marques *et al.*, 2009), and henceforth "click" refers to a regular foraging click.

Blainville's beaked whale data were obtained from AUTEK, which includes a U.S. Navy undersea tracking range with an extensive array of bottom-mounted hydrophones suspended approximately 4–5 m off the ocean bottom at depths of up to 2000 m. Recordings from AUTEK's hydrophones made with a sampling rate of 96 kHz and 16-bit resolution during a 6-day period in the spring of 2005 (April 26 to May 2) are used as the principal data set for this study. This is also the primary data set used by Marques *et al.* (2009) in a multi-sensor analysis to estimate density of Blainville's beaked whales at AUTEK. The hydrophone array configuration used for the study is shown in Fig. 1 and the single sensor chosen (H 57) for analysis is also indicated. The bandwidth ( $\pm 3$  dB) of the single sensor is 50 Hz to 45 kHz, though some energy was present up to 48 kHz. The detection and classification system used to extract Blainville's beaked whale clicks consisted of a multi-stage fast Fourier transform (FFT)-based energy detector. Detections of Blainville's beaked whale clicks were classified by comparing in-band

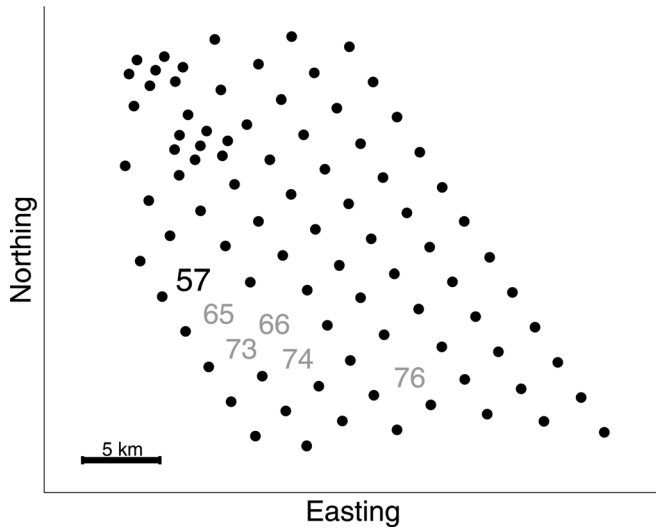


FIG. 1. Distribution of AUTEc's hydrophones showing the single sensor (#57) used in this paper's analysis, and the sensors used in ambient noise measurements.

(24–48 kHz) to out-of-band (0–24 kHz) energy (DiMarzio *et al.*, 2008; Ward *et al.*, 2008).

### III. DENSITY ESTIMATION

Marques *et al.* (2009) introduced a canonical formula for estimating the density of animals in a given area based on acoustic cue counting methods and on the formulation of Buckland *et al.* (2001). This formula is applied here, defining a cue as a foraging click, to estimate the spatial density of Blainville's beaked whales in the vicinity of a single sensor. The density estimation formula is given by

$$\hat{D} = \frac{n_c(1 - \hat{c})}{K\pi w^2 \hat{P} \hat{r}} \quad (1)$$

where  $\hat{D}$  is the density estimate,  $n_c$  is the number of detected clicks,  $\hat{c}$  is the estimated proportion of false positive detections,  $K$  is the number of sensors,  $w$  is the maximum detection distance beyond which we can safely assume that no clicks are detected,  $\hat{P}$  is the estimated average probability of detecting a click out to distance  $w$ ,  $T$  is the duration of the data set being analyzed, and  $\hat{r}$  is the estimated click production rate. Given variances on the input parameters, and assuming they are statistically independent, variance in estimated density can be obtained using the  $\delta$  method (Seber, 1982), and confidence limits can be obtained assuming the density estimate has a lognormal distribution (Marques *et al.*, 2009). Unlike Marques *et al.* (2009), who used multiple hydrophones that gave a spatial sample of a large area, here we focus on the area around a single hydrophone. Therefore, while there is no variance component associated with spatial variation in  $n_c$ , the variability in the number of detected clicks due to the randomness of the detection process needs to be accounted for. Here, counts were assumed to follow a Poisson distribution.

In the present analysis only data recorded on hydrophone 57 during the 6-day period are used and hence  $K$  in Eq. (1) equals 1. The total time of the recordings analyzed

from the 6-day period ( $T$ ) is the same as from Marques *et al.* (2009), i.e., 4961 min. From this data set, the number of all clicks automatically detected and classified ( $n_c$ ) as Blainville's beaked whale clicks on hydrophone 57 was 53 403. A maximum distance ( $w$ ) of 8 km is chosen to match that used by Marques *et al.* (2009), as detection distances of up to 6.5 km away from hydrophones at AUTEc have been reported for Blainville's beaked whales (Ward *et al.*, 2008). The estimation of the average probability of detecting a click ( $\hat{P}$ ) and the click production rate ( $\hat{r}$ ) are discussed in Secs. IV and V, respectively.

The proportion of false positive detections ( $\hat{c}$ ) comes from comparison of manual and automatic detections (Marques *et al.*, 2009). From the entire data set recorded during the 6-day period, 29 samples of 10 min each were used to estimate the false positive rate. The analysis of these samples yielded a total of 1958 sounds automatically detected on hydrophone 57, of which 1370 (almost 70%) were unambiguously identified as Blainville's beaked whale clicks by a trained analyst. The proportion of true positives,  $(1 - \hat{c})$ , is estimated to be 0.703, with a standard error (SE) of 0.0418 and corresponding coefficient of variation (CV) of 5.94%.

### IV. ESTIMATING CLICK DETECTION PROBABILITY

In this section the estimation of the probability of detecting foraging clicks from Blainville's beaked whales at a single fixed sensor is discussed. This is done by simulating animal sound production in an area around the sensor, then employing the passive sonar equation to estimate the SNR at the receiver. The estimated SNR is combined with the performance of the detection and classification system to estimate the probability that a given simulated vocalization is detected. Calculating a large number of these simulated vocalization events allows derivation of the detection function; calculating the average of this function over the area within distance  $w$  from a sensor results in the estimated average probability of detection ( $\hat{P}$ ). Repeating this process many times, each time sampling from a distribution of each input variable, allows calculation of the standard error of  $\hat{P}$ .

The SNR of a Blainville's beaked whale click at the receiver can be estimated by application of the passive sonar equation (Urlick, 1983), written in terms of acoustic intensity level (I), as follows:

$$\text{SNR} = \text{SL} - \text{DL} - \text{TL} - \text{NL}, \quad (2)$$

where SL is the whale's on-axis source level (measured in dB re 1  $\mu\text{Pa}$  at 1 m); DL is directivity loss, the attenuation (in dB) of the on-axis source level at a given angle from the animal's acoustic axis; TL is sound transmission loss as a function of distance between source (whale) and receiver (in dB); and NL is the ambient noise level (measured in dB re 1  $\mu\text{Pa}$ ). Equation (2) implies that the acoustic power per unit area (or acoustic intensity) of a received signal is averaged over the duration of the signal  $\tau_r$ . By considering the duration of the signal, a transient form of the passive sonar equation, written in terms of energy flux density (E), can also be written and used to estimate the received SNRs (Urlick, 1983;

Au, 1993). Energy flux density relates to the acoustic intensity by

$$I = E/\tau_i. \quad (3)$$

Considering the above relationship, the source level (SL) of a transient signal is defined as

$$SL = 10\log_{10}(E) - 10\log_{10}(\tau_i) = SL_E - 10\log_{10}(\tau_i), \quad (4)$$

where  $SL_E$  is the source energy flux density (measured in dB re  $1 \mu\text{Pa}^2 \text{ s}$ ), and hence, the energy-to-noise ratio (ENR) of a stationary signal is calculated as

$$ENR = SL_E - DL - TL - NL, \quad (5)$$

which is the transient form of the passive sonar equation. Equations (2) and (5) are then related by (Au, 1993)

$$ENR = SNR + 10\log_{10}(\tau_i). \quad (6)$$

Each parameter in Eq. (5) is characterized by a distribution used in a Monte Carlo model described below. Equation (6) is then used to convert the simulated ENR into SNR levels, for which the probabilities of detection are estimated. The detection and classification system is characterized by the probability of detecting a single click as a function of SNR, so that simulated SNRs from the Monte Carlo model can be used to estimate the average probability of detection  $\hat{P}$ . Note that the time window of measured and simulated SNRs must have the same duration.

To use Eq. (5) to estimate the SNR of received signals, the location of the sound source with respect to the receiver must also be simulated. Therefore, distributions of animal horizontal distances, clicking depths, and orientation angles with respect to the sensor were derived from the literature. These are required to calculate distributions of off-axis angles of an animal's acoustic beam, which in turn is required to estimate the off-axis attenuation of source level (DL). Animal-sensor geometry is also important when using a propagation model to calculate acoustic transmission loss (TL). The assumptions made about animal position and orientation, source level, off-axis attenuation, transmission loss, and noise levels are presented in Secs. IV A–IV E. Section IV F discusses how the detector (and classifier) was characterized. The combination of these distributions into Eq. (5) using a Monte Carlo simulation is then presented in Sec. IV G.

### A. Animal location and orientation

A first step in estimating the probability that a click will be detected at a given sensor is to simulate the position and orientation of the animal at the moment the click is produced. Detailed information on animal movement and vocalization behavior can be obtained from acoustic tag data. Here the goal is to estimate density without the use of local tag information, but information from the literature on both Blainville's and Cuvier's beaked whales is used to characterize the location and orientation of a whale with respect to a single hydrophone. It should be noted that the information

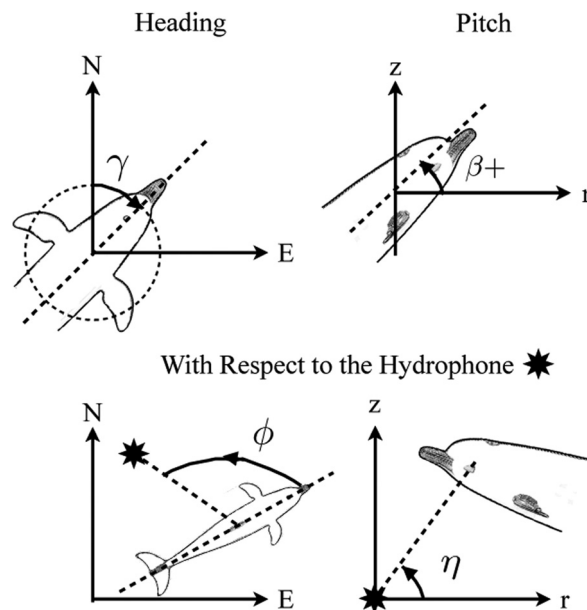


FIG. 2. Whale orientation and respective angles. Upper diagrams show whale heading and pitch, and lower diagrams show whale heading and elevation angle with respect to the hydrophone. These angles are necessary to estimate the acoustic off-axis angle between whale and hydrophone (see text).

found in the literature comes mostly from studies that utilized acoustic tags but that these studies were not done at AUTECH.

Discrete animal positions and orientations with respect to the sensor are derived from knowledge of the animal's diving behavior during vocal periods. Position is estimated in three dimensions ( $x$ ,  $y$ , and  $z$ ) and orientation in two (azimuth  $\gamma$  and pitch  $\beta$ , Fig. 2). The model used here assumes that beaked whales are randomly distributed in the horizontal plane ( $x$ ,  $y$ ) within a circle of radius  $w$  (defined earlier as  $w = 8$  km) centered on the sensor. The random distribution in  $x$  and  $y$  implies a triangular distribution of distances from the sensor, with larger distances corresponding to linearly larger areas. Azimuth, or whale heading  $\gamma$  with respect to magnetic north, is assumed to have a random uniform distribution around the circle ( $0^\circ$ – $360^\circ$ ). In other words, the whale is equally likely to be oriented in any horizontal direction anywhere within the specified circle.

To sample depth ( $z$ ) and whale pitch ( $\beta$ ), it is assumed that Blainville's beaked whales produce clicks at depths below 300 m during deep foraging dives (Tyack *et al.*, 2006). The vocal period is divided into three phases: descent, foraging, and ascent. The three phases and the proportion of clicks produced in each of them (Table I) are estimated from dive profiles with corresponding vocal periods that are found in the literature (Tyack *et al.*, 2006; Johnson *et al.*, 2006; Ward *et al.*, 2008). It is assumed that during each phase, a whale has certain distributions of depth and pitch. Depths are described by Gaussian distributions with mean and standard deviations estimated from published dive profiles (Johnson *et al.*, 2004; Madsen *et al.*, 2005; Tyack *et al.*, 2006; Ward *et al.*, 2008; Jones *et al.*, 2008). Whale pitch is measured from  $+90^\circ$  to  $-90^\circ$ , where negative angles correspond to downward orientation. Hence, during the descent



TABLE I. Values used to estimate whale clicking depth  $z$  and pitch  $\beta$  for three distinct dive phases. Click proportion is an estimate of the fraction of clicks produced during each dive phase. Mean depth and standard deviation (in parentheses) are used in Gaussian distributions for sampling clicking depths. Pitch distribution indicates the distribution used for each dive phase, the pitch range, and values used for the required distribution parameters. Negative pitch is measured downwards.

Dive Phase	Click Proportion	Mean Depth	Pitch Distribution
Descent	0.20	750 m ( $\pm 50$ )	Beta ( $-90^\circ \leq \beta \leq 0^\circ$ ) ( $a = 2, b = 5$ )
Foraging	0.72	1100 m ( $\pm 50$ )	Circular ( $\beta = 0^\circ$ ) ( $\kappa = 1$ )
Ascent	0.08	950 m ( $\pm 50$ )	Beta ( $60^\circ \leq \beta \leq 90^\circ$ ) ( $a = 3.5, b = 0.9$ )

phase, the mean pitch is downward (negative); during foraging, closest to horizontal; and during ascent upward (positive). Pitch is described by a beta distribution for the ascending and descending dive phases, with scaling parameters (Table I) that allow for the proportion of clicks to increase for decreasing angles in the descent phase, and for increasing angles in the ascent phase. During the foraging phase, pitch is described by a circular, or von Mises, distribution for which most pitch values are centered on the horizontal, but are also allowed to be oriented up or down (Table I).

The heading of the whale with respect to the hydrophone also matters; it is assumed that the whale can be located in any direction  $\varphi$  around the hydrophone, where  $\varphi$  is sampled uniformly in the circle ( $0^\circ$ – $360^\circ$ ), with  $0^\circ$  being north (Fig. 2). We also define the elevation angle  $\eta$  (Fig. 2) between hydrophone and whale as

$$\eta = \arctan\left(\frac{z_h - z}{r_{hw}}\right), \quad (7)$$

where  $z_h$  is the depth of the hydrophone,  $z$  is the depth of the whale as defined above, and  $r_{hw}$  is the horizontal distance between whale and hydrophone.

Animal position and orientation in space with respect to the hydrophone is required to calculate the acoustic off-axis angle  $\theta$ . This is used to estimate the source level off-axis attenuation due to the animal's beam pattern and is discussed in Sec. IV C. Following the approach described by Zimmer *et al.* (2008) and the assumptions made above, the direction vector of the whale is described as

$$\mathbf{a} = \begin{pmatrix} a_x \\ a_y \\ a_z \end{pmatrix} = \begin{pmatrix} \sin \gamma \cos \beta \\ \cos \gamma \cos \beta \\ \sin \beta \end{pmatrix}, \quad (8)$$

and the direction vector of the hydrophone, as seen by the whale, as

$$\mathbf{b} = \begin{pmatrix} b_x \\ b_y \\ b_z \end{pmatrix} = \begin{pmatrix} \cos \eta \sin \phi \\ \cos \eta \cos \phi \\ \sin \eta \end{pmatrix}. \quad (9)$$

The off-axis angle  $\theta$  is then calculated by taking the dot product of  $\mathbf{a}$  with  $\mathbf{b}$ ,

TABLE II. Source levels of beaked whales, *Ziphius cavirostris* (Zc) and *Mesoplodon densirostris* (Md), available in the literature. Source levels are in dB re 1  $\mu\text{Pa}$  at 1 m. Note that RMS values can vary depending on the window length used.

Source Level	Species	Reference
200 dB <sub>rms</sub>	Zc, Md	Zimmer <i>et al.</i> (2008)
199 dB <sub>rms</sub>	Zc	Tyack <i>et al.</i> (2006)
Up to 214 dB <sub>pp</sub>	Zc	Zimmer <i>et al.</i> (2005b)
220 dB <sub>pp</sub>	Md	Madsen <i>et al.</i> (2005)
200–220 dB <sub>pp</sub>	Zc, Md	Johnson <i>et al.</i> (2004)

$$\cos \theta = \mathbf{a}^T \mathbf{b}. \quad (10)$$

Estimations of animal vocalizing depths and distances from the receiving sensor are also used in calculating sound transmission loss (Sec. IV D) between source and receiver, and ultimately the probability of detection with distance.

## B. Source level

The on-axis source level is a critical parameter for estimating the SNR of a click using the sonar equation [Eq. (2)]. However, a literature search for source levels of beaked whales reveals only a few estimates, summarized in Table II. All are derived from either acoustic tag data (Zimmer *et al.*, 2005b), inferences based on tag data (Johnson *et al.*, 2004), or comparisons with echolocation signals from well-studied delphinid species (Madsen *et al.*, 2005). Tyack *et al.* (2006) suggested that Cuvier's and Blainville's beaked whales have similar source levels but different source apertures due to size differences, and that Blainville's have less directional clicks. It should be noted that source levels are not constant (Zimmer *et al.*, 2008; Madsen *et al.*, 2005), and that the average levels reported also contain uncertainty in their estimations. Another important factor to consider when using source level estimates to calculate the SNR of received levels, which are then compared to measured SNRs, is the time window in which the source level measurement was made. Therefore, a more general parameter to describe source level is source energy flux density [ $SL_E$ , used in Eq. (5)]. Zimmer *et al.* (2005b) measured  $SL_E$  from tagged Cuvier's beaked whales and reported a maximum level of 164 dB re 1  $\mu\text{Pa}^2$  s. For modeling purposes a distribution of levels that reflect the uncertainties in measurement is needed. A Gaussian distribution of source energy flux densities was assumed with mean 164 dB re 1  $\mu\text{Pa}^2$  s and standard deviation 1.769 dB re 1  $\mu\text{Pa}^2$  s. The standard deviation was estimated by measuring the three highest values from Fig. 6 (left) in Zimmer *et al.* (2005b), which are believed to be on-axis levels from a single scan of the whale's sonar beam across the hydrophone.

## C. Off-axis attenuation of source level

The off-axis angle is the angle between the acoustic axis of the whale and the ray that reaches the receiving sensor. For simplicity, the acoustic axis is often assumed to be aligned with the animal's body axis (Zimmer *et al.*, 2005b). However, the acoustic and body axes may not coincide;

Zimmer *et al.* (2005b) point out that both Cuvier's and Blainville's beaked whales have been observed to move their heads, and hence the acoustic axis, separately from their bodies while swimming.

Here, the model for a circular piston was used to estimate the attenuation of a beaked whale's source level as a function of its off-axis angle with respect to the hydrophone. Such a model has been used to estimate the acoustic beam pattern of odontocete species including dolphins (Au, 1993; Rasmussen *et al.*, 2004), sperm whales (Møhl *et al.*, 2003; Zimmer *et al.*, 2005a), and beaked whales (Zimmer *et al.*, 2005b, 2008). For beaked whales, Zimmer *et al.* (2005b) have shown reasonably good agreement between the piston model and measured apparent source levels from two tagged Cuvier's beaked whales.

Sound radiated by a circular piston is mathematically described by (Zimmer *et al.*, 2005b; Au and Hastings, 2008)

$$P(x) = 2P_0 \frac{J_1(x)}{x} \quad \text{and} \quad x = \frac{2\pi a \sin(\theta)f}{c}, \quad (11)$$

where  $P$  is pressure,  $P_0$  is a reference source level,  $J_1$  is the Bessel function of the first kind and order 1,  $a$  is the piston radius,  $\theta$  is the off-axis angle,  $f$  is frequency, and  $c$  is the speed of sound in seawater. In this analysis,  $P_0$  was set to 200 dB re 1  $\mu\text{Pa}$  at 1 m (see Table II),  $a$  was assumed to be 16 cm which implies a head diameter of 32 cm,  $\theta$  ranged from  $+90^\circ$  to  $-90^\circ$ ,  $f$  spanned the 24 to 48 kHz frequency range, and  $c$  was set to 1500 m/s.

The broadband beam pattern for Blainville's beaked whales is then approximated by integrating Eq. (11) with respect to frequency, using a Gaussian weighting function to account for the variation of source level with frequency (Zimmer *et al.*, 2005b). For the weighting function a center frequency of 38.3 kHz and RMS bandwidth of 6.9 kHz was used based on values reported by Johnson *et al.* (2006, Table D). The resulting broadband attenuation of source levels as a function of off-axis angle is shown in Fig. 3

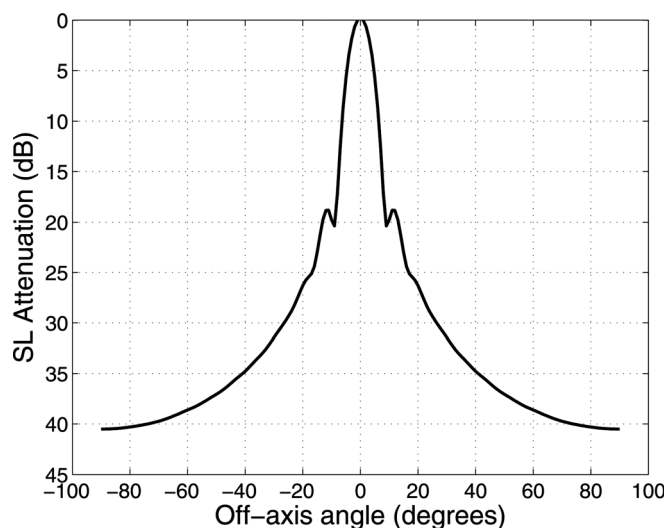


FIG. 3. Attenuation of source level as a function of off-axis angle for Blainville's beaked whales, estimated by using a piston model with radius of 16 cm.

where the symmetry about  $0^\circ$  (on-axis) can be observed. It is also observed that off-axis clicks will be attenuated by as much as 40 dB. According to Johnson *et al.* (2006), if Blainville's have a similar beam pattern to delphinids and Cuvier's beaked whales, their on-axis clicks will be at least 30 dB stronger than their weakest off-axis clicks.

#### D. Transmission loss

Sound transmission loss (TL) was calculated using the Gaussian beam tracing model Bellhop (Porter and Bucker, 1987) to model the high frequency clicks of beaked whales. Even though the clicks are broadband in nature, for simplicity a center frequency of 38.3 kHz (Johnson *et al.*, 2006) was used in the transmission loss calculations. A spring sound speed profile representative of the conditions encountered at AUTEK when the data set was recorded is used as input in the propagation model, and is shown in Fig. 4. The bottom properties for the AUTEK basin, which were also required as input parameters, were adapted from Kennedy and Szlyk (1989). The bottom sound speed, density, and attenuation used in the calculations were 1535 m/s, 1.93 g/cm<sup>3</sup>, and 0.014 dB/m/kHz, respectively. Use was made of the acoustic reciprocity principle, which states that the received signal will not change when the locations of source and receiver are interchanged in an unchanging environment (Kinsler *et al.*, 1999). Therefore, for ease of calculation, the hydrophone is assumed to be the source and the modeled whale locations are the receivers. Within an 8 km radius of the hydrophone, bathymetric features are smooth. Therefore a single propagation run is performed in a randomly chosen direction from the hydrophone. The resulting matrix of TL values as a function of range and depth is used as input to Eq. (5).

At high frequencies, the sound field is very sensitive to the properties of the medium, and the interference patterns are less stable than at low frequencies (Jensen *et al.*, 1994). Hence, both coherent and incoherent acoustic fields were calculated, where incoherent means that the phase of the pressure, or the interference pattern, is ignored, giving a smoother result. Both fields were also compared to the commonly used spherical spreading law, which approximates

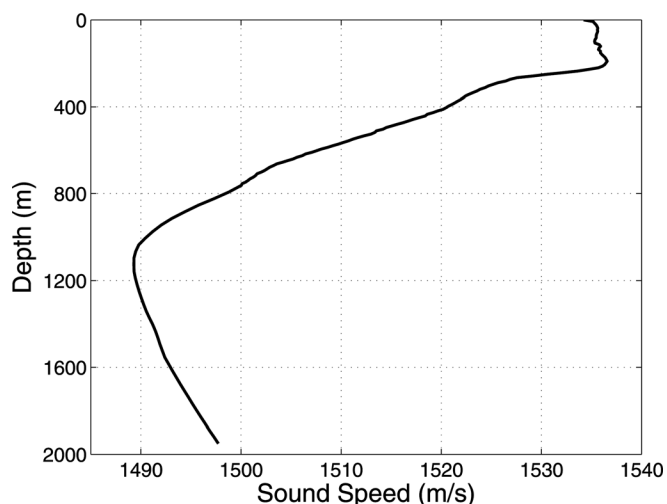


FIG. 4. Sound speed as a function of depth measured in spring at the AUTEK range and used as input for the transmission loss calculations.

transmission loss by  $20 \log(r)$ , where  $r$  is range expressed in meters. However, at the high frequency modeled, loss due to absorption is a dominant factor (Urlick, 1983). This was incorporated into the spherical spreading approximation by adding the frequency-dependent absorption coefficient  $\alpha_f$  expressed in dB/km, which gives

$$TL = 20 \log(r) + \alpha_f(r/1000). \quad (12)$$

A value of 8.9 dB/km (corresponding to a frequency of 38.3 kHz) was used for  $\alpha_f$  in the above approximation (Marques *et al.*, 2009). This absorption coefficient was calculated using the Francois-Garrison equation (Francois and Garrison, 1982) integrated from the depth of the whale to the hydrophone using pH, temperature, and salinity measured at AUTECH. Figure 5 shows transmission loss calculated using Eq. (12) together with Bellhop's coherent and incoherent results. Absorption was also incorporated into the Bellhop model, but through the frequency-dependent Thorp attenuation formula (Thorp, 1967). In Fig. 5 transmission loss curves as a function of range are shown for three different receiver depths corresponding to possible depths where beaked whales produce foraging clicks. Overall, it is observed that there are no significant differences in the transmission loss patterns and magnitudes among coherent, incoherent and spherical spreading calculations. Differences in TL observed at horizontal distances of less than 500 m are not regarded as important as the area surveyed within 500 m is very small compared with the total area surveyed, so inaccuracies here will have small effect on estimates of average detection probability. At ranges greater than 7 km, attenuation is so large that clicks are unlikely to be detected and no significant difference is observed for different depths. These results suggest that for areas where the environment is relatively constant in space and time, a simple spherical spreading law, plus absorption in high frequency cases, should be sufficient for estimating the transmission loss.

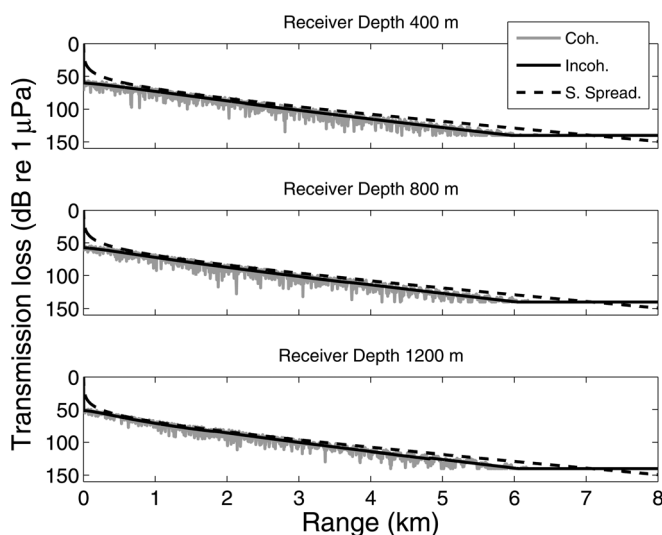


FIG. 5. Transmission loss as a function of range, or distance between source and receiver, for 3 different depths: (top) 400, (middle) 800, and (bottom) 1200 m. The different curves represent results of calculations for the coherent (gray) and incoherent (solid black) acoustic fields as well as the spherical spreading law with frequency-dependent attenuation  $\alpha = 8.9$  dB/km (dashed).

## E. Ambient noise levels

The Tongue of the Ocean represents an acoustically quiet environment due to deep water and the enclosed nature of the site. The main source of ambient noise is wind and wave activity at the surface. It has been observed that ambient noise levels decrease with increasing depth and frequency, most likely due to frequency-dependent acoustic absorption.

Ward *et al.* (2010) measured ambient noise power between 24 and 48 kHz on a subset of AUTECH's hydrophones, taking into account hydrophone sensitivity and system gain. These data were found to correlate well with the ambient noise spectrum predicted from historical wind speed measurements. However, at higher frequencies, the measured levels were found to be higher than predicted due to the electronic noise floor of the system. The ambient noise characterization was performed for the 6-day period considered in this study. The data analyzed consisted of manually picked periods of time with minimal biological or man made noise present. Figure 1 shows the 5 different hydrophones, labeled in gray, from which ambient noise measurements were used. They were chosen due to their close proximity to each other and to the single hydrophone used in this work (also shown in Fig. 1). The noise levels used in the analysis from all 5 hydrophones are presented in Fig. 6. It is observed that most of the measured ambient noise levels lie within an almost constant line between 64 and 66 dB re  $1 \mu\text{Pa}$ . The gaps in the noise levels, where no measurements are observed, are due to the way the data set was divided for analysis and the exclusion of some subsets that presented various problems in the recordings (Marques *et al.*, 2009).

## F. Detector characterization

To estimate the probability of detecting clicks received at a sensor, it is necessary to characterize the performance of the detector. This was done by measuring the probability of detecting a click as a function of SNR using the 6-day data set recorded on hydrophone 57. Here, detector performance

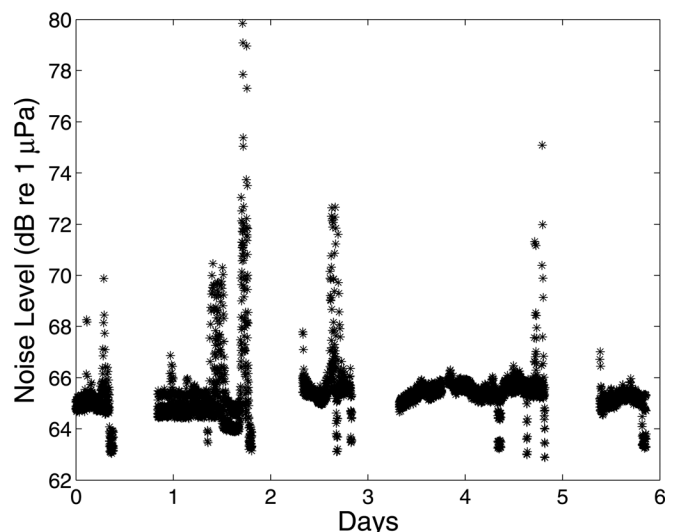


FIG. 6. High-frequency ambient noise levels, integrated over 24–48 kHz, measured at five different hydrophones at AUTECH and used in the Monte Carlo simulations.



is not as important as how well it can be characterized. However, it is noted that a detector with low performance will yield a lower number of detections, which contributes to high variance in the final density estimation.

To characterize the detector performance, a 6-min data sample taken from the 6-day data set recorded on hydrophone 57 was used. It was manually annotated (labeled) by a human analyst, who marked all Blainville's beaked whale clicks present. This yielded a total of 1474 clicks, assumed as ground truth. The SNR of each manually detected click was then measured by calculating the power of the click and comparing it to the background power. These measurements were performed in the time domain by band-pass filtering the sound file in the frequency interval between 24 and 48 kHz (Mellinger and Clark, 2006). For consistency, the power of each click was measured by centering the click on a time window with the same duration as the resolution of the FFT-based detector (20 ms), and the background power was measured from a time window between consecutive annotated clicks. The 6-min data sample was also analyzed by a beaked whale FFT-based detection and classification algorithm (Ward *et al.*, 2008), which picked up 659 of the ground truth clicks.

The measured SNRs from the manual detections were combined into a binary model by assigning a value of 1 if the same click was also detected and classified by the FFT algorithm, and 0 otherwise. A statistical model of detection probability  $P$  as a function of SNR was fit to the data using the binary generalized additive model (GAM) (Wood, 2006) implemented in R (R Foundation for Statistical Computing, 2009). This resulted in a model that predicts detection probability as a function of SNR. Uncertainty associated with the detector performance is measured by the residual variance of the GAM fit to the detector characterization data. The fitted curve (Fig. 7) shows near-zero probability of detection at SNR of approximately  $-5$  dB or below, followed by a rapid rise, to a maximum of 0.85 at 16 dB, and then a decline in detection probability at higher SNRs. The curve has wide confidence intervals at high SNRs due to the small number of observations at these levels. The observation that the probability of detection (and classification) never reaches 1.0 is not unexpected, given the relatively simple FFT-based energy detection and classification system used in this case study (Ward *et al.*, 2008). Received high-level transient signals, may contain considerable energy in the lower out-of-band frequencies, i.e., below 24 kHz for beaked whales. Such signals, which probably correspond to clicks produced at close ranges, are then misclassified, contributing to the declined detection probability with higher SNR.

It is noted that the choice of a 6-min period of data to characterize the detector is not optimal. Ideally, a systematic random sample from the whole time period (6-day dataset) would be chosen.

### G. Probability of detection: Monte Carlo simulations

The information described above was combined in a Monte Carlo simulation to estimate the average probability of detection as a function of distance. This simulation randomly samples from distributions of the sonar equation pa-

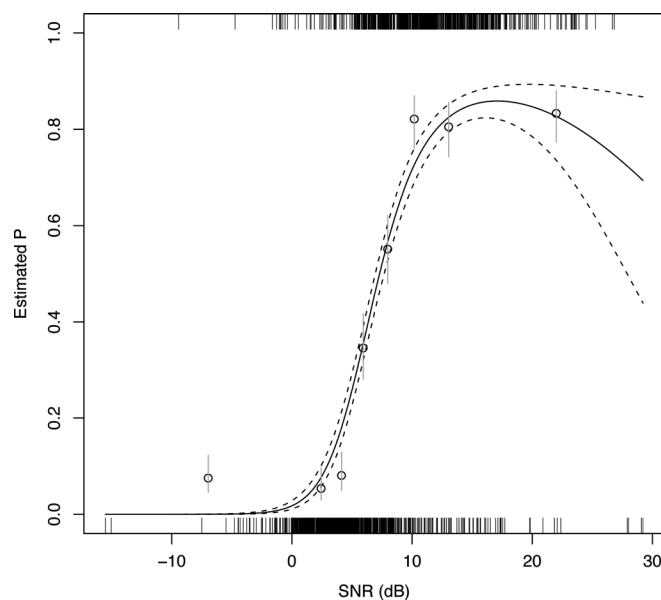


FIG. 7. Probability of detection ( $P$ ) as a function of signal-to-noise ratio (SNR), estimated by fitting a binary generalized additive model (GAM) to the manually annotated detections. The vertical lines on the top of the figure correspond to the manually detected clicks that were also detected by the FFT detector, and the ones at the bottom correspond to the manually detected clicks that were not detected by the FFT detector. Circles summarize the data, showing the proportion detected in 8 successive intervals, each containing 1/8 of the measured clicks; the vertical lines above and below each circle indicate 95% binomial confidence intervals for each proportion. Solid line shows estimate from the GAM, and dashed lines are 95% point-wise confidence intervals. The fall-off in detection probability at high SNR is discussed in the text.

rameters described above, then uses these sampled values to calculate the SNR of received clicks using Eqs. (5) and (6). Source level and detector characterization were randomly sampled 1000 times to incorporate the uncertainty of these parameters in the estimated detection probability uncertainty. Each sample of source level and detector performance were incorporated to a set of 10 000 randomly simulated clicks, with coordinates  $(r, z)$ , and with off-axis angles calculated from the model of animal position and orientation with respect to the hydrophone. For each simulated click, the SNR at the receiving sensor was calculated, and then the detector characterization was used to estimate the probability of detecting the click. At this stage, if the simulated SNR was lower than the minimum observed in the data, the respective click was considered to have 0 probability of detection. At the other extreme, if the simulated SNR was higher than the maximum observed value, the probability of detection for the respective click was assigned the probability of detection of the highest observed SNR. Simulated SNRs between these extremes were assigned the probability of detection corresponding to the detector characterization shown in Fig. 7. The probability of detection was then averaged over all the  $1000 \times 10\,000$  simulated clicks to arrive at a value of  $\hat{P} = 0.0139$ , with SE of 0.0025 and corresponding CV of 17.89%. Plots of probability of detection as a function of slant range for fixed off-axis angles ( $0^\circ$ ,  $45^\circ$ , and  $90^\circ$ ) are shown in Fig. 8 and may be compared to similar plots of Marques *et al.* (2009, Fig. 3). These results were obtained by



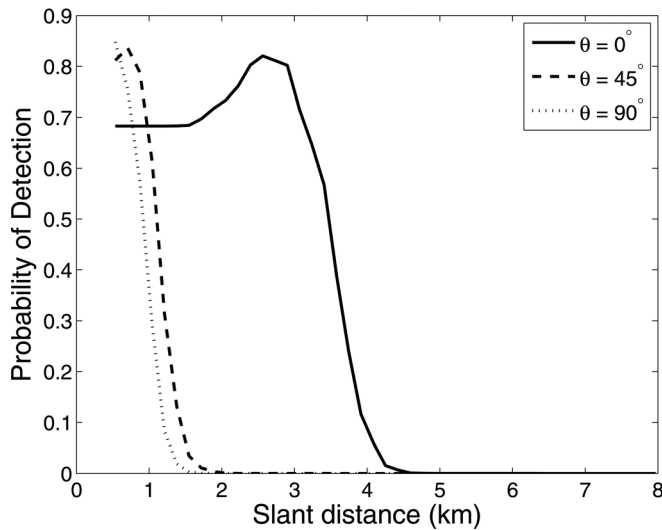


FIG. 8. Estimated detection function as a function of slant distance for three angles measured from the whale's acoustic axis:  $0^\circ$  (solid),  $45^\circ$  (dashed), and  $90^\circ$  (dotted).

using the coherent TL results from Bellhop in the sonar equation [Eq. (2)].

## V. ESTIMATION OF CLICK PRODUCTION RATE

The cue production rate  $\hat{r}$ , or specifically the mean number of times per second that beaked whales produce clicks, is also an essential variable for this density estimation method [Eq. (1)]. In the case study presented by Marques *et al.* (2009), Blainville's beaked whale acoustic tag data from the AUTEK range was used to estimate this quantity. Here, information on animal vocal behavior available in the literature was used to estimate click production rate. It should be noted however, that most of this information is also based on acoustic tags.

The click rate must be averaged over the time period in which density is estimated and should include silent times, that is, times when regular clicks are not observed (Douglas *et al.*, 2005). For beaked whales, periods when no vocalizations are produced include periods at the surface between dives, periods in a foraging dive when clicking pauses during

air recycling, periods when buzz clicks are produced (recall that only regular clicks are used as cues), and periods when whales are not making foraging dives. Table III summarizes data gathered from beaked whale publications that was used to estimate the click production rate.

As seen in Table III, several studies have measured inter-click intervals (ICIs). However, such information can not be inverted into click production rate since it does not account for periods of silence both during deep foraging dives (for example, while emitting buzz clicks) and at or near the surface. Here, click production rate is estimated as

$$\hat{r} = \hat{r}_d \times \hat{d}/86400, \quad (13)$$

where  $\hat{r}_d$  is the average number of clicks per whale per deep foraging dive,  $\hat{d}$  is the average number of deep dives per day, and 86 400 is the number of seconds per day. The former quantity is estimated as

$$\hat{r}_d = (\hat{t}_v - \hat{t}_s)/ICI, \quad (14)$$

where  $\hat{t}_v$  is the average duration between times when a whale starts and stops clicking during a deep dive,  $\hat{t}_s$  is the average total time that a whale is either silent or producing buzz clicks during a deep dive, and ICI is the average inter-click interval during the vocal periods. The first quantity,  $\hat{t}_v$ , is estimated for Blainville's beaked whale in three papers (Table III). In cases where a range is given (Johnson *et al.*, 2006), we approximate it by averaging the low and high ends of the range. DiMarzio *et al.* (2008) give separate estimates for three individuals. Therefore we use seven available estimates for  $\hat{t}_v$ : 23, 33, 26, 36, 34.8, 31.4, and 34.02 min, yielding a mean of 31.17 min with standard error (SE) of 1.83. For average silent period  $\hat{t}_s$ , we assume that buzz clicks are the only cause and ignore small silent periods due to air recycling and other reasons. A mean buzz length of 2.9 s is reported by Johnson *et al.* (2006), and we estimate the number of buzzes per dive to be the average of the three values available in Table III (23, 26, and 38). This yields an estimated  $\hat{t}_s$  of 1.40 min with SE 0.22. For inter-click interval, ICI, six estimates are available from four papers, with a mean of 0.33 s and SE of 0.048. Combining these estimates

TABLE III. Vocal behavior data for beaked whales, *Ziphius cavirostris* (Zc) and *Mesoplodon densirostris* (Md), available in the literature and used for estimating click production rate. The inter-click interval (ICI), mean click duration, duration of deep foraging dives, the amount of time spent clicking during each dive, the IDI (or inter-deep-dive interval), and the number of buzz clicks produced per foraging dive are derived from acoustic tag studies.

Reference	ICI (s)	Click Duration ( $\mu$ s)	Dive Duration (min)	Vocal Time/dive (min)	IDI (min)	Buzzes/dive
Frantzis <i>et al.</i> (2002)	0.4–0.5 (Zc)	–	–	–	–	–
Johnson <i>et al.</i> (2004)	$\sim$ 0.4 (Zc)	175 (Zc)	50 (Zc)	–	–	27 (Zc)
	0.2–0.4 (Md)	250 (Md)	–	–	–	23 (Md)
Madsen <i>et al.</i> (2005)	0.2–0.5 (Md)	–	–	–	–	–
Johnson <i>et al.</i> (2006)	0.37 (Md)	–	–	23–33 (Md)	–	26–38 (Md)
Tyack <i>et al.</i> (2006)	–	–	–	33 (Zc)	121 (Zc)	–
	–	–	–	26 (Md)	139 (Md)	–
Ward <i>et al.</i> (2008)	0.31 (Md)	–	57 (Md)	36 (Md)	–	–
DiMarzio <i>et al.</i> (2008)	–	–	–	34.8 (Md)	–	–
	–	–	–	31.4 (Md)	–	–
	–	–	–	34.02 (Md)	–	–

in Eq. (14) yields  $\hat{r}_d = 5413.203$ . Standard methods can be used to obtain the variance of a combination of independent quantities (Seber, 1982), and these yield an SE of 858.64 or CV of 15.86%.

The quantity  $\hat{d}$  is estimated as the inverse of the inter-dive interval, for which there is only one estimate (Table III) for Blainville's beaked whale of 139 min or 0.096 days. This gives an estimate of number of dives per day of 10.36, with no variance. This is in agreement with a mean value of 10 dives per day given by Tyack *et al.* (2006). Substituting these quantities into Eq. (13) gives an estimate of click production rate  $\hat{r}$  of 0.649 clicks/s, with CV 15.86%. For comparison, the value found by Marques *et al.* (2009) was 0.407 clicks/s, with CV 9.8%.

## VI. RESULTS AND DISCUSSION

Table IV presents a summary of the values for each component of Eq. (1) derived in the previous sections. Combining these results in Eq. (1) then yields an overall population density  $\hat{D} = 69.60$  animals/1000 km<sup>2</sup> (CV 24.64%, 95% CI 50.86–95.25). The estimated average probability of detection  $\hat{P}$  was calculated by using the coherent TL results from the Bellhop propagation model. For comparison,  $\hat{P}$  and the corresponding CV obtained by using the incoherent TL and spherical spreading law were 0.0158 and 18.54%, and 0.0201 and 16.08%, respectively.

The results obtained by this study can be compared to those of Marques *et al.* (2009). The estimated cue rate  $\hat{r}$ , 0.649 clicks/s, is a factor of 1.595 higher than the rate reported by Marques *et al.* (2009) from direct DTAG data analysis (0.407 clicks/s). The estimate here was based on sparse literature for this species, including little information from this geographic area (most of it was from the Mediterranean Sea). The simulated average probability of detection  $\hat{P}$  was 0.0139, while that estimated analytically by Marques *et al.* (2009) was 0.032, or 2.30 times higher than the current study. The mean density estimate  $\hat{D}$  of 69.60 animals/1000 km<sup>2</sup>, compared to that of Marques *et al.* (2009) (25.3–22.5 animals/1000 km<sup>2</sup>), differs by a factor of 2.75–3.09. The estimate of Marques *et al.* (2009) was derived from the whole range, using clicks detected on a total of 82 hydrophones, to obtain values of  $n_c$  and  $\hat{c}$ . Re-analyzing the Marques *et al.* (2009) estimate using the  $n_c$  and  $\hat{c}$  for only hydrophone 57, but values of  $\hat{P}$  (0.032) and  $\hat{r}$

TABLE IV. Summary of the values derived for each parameter needed to estimate density of Blainville's beaked whale at AUTECH using Eq. (1), and their associated CVs.

Parameter	Value	CV %
# Detected clicks $n_c$	53403	0.43
True positive rate $(1 - \hat{c})$	0.703	5.95
Max. detection distance $w$	8 km	–
Estimated prob. detection $\hat{P}$	0.0139	17.89
Time period $T$	4961 min	–
Average cue rate $\hat{r}$	0.649 clicks/s	15.86
# Hydrophones $K$	1	–

(0.407) from their paper, yields an estimate of 48.164 animals/1000 km<sup>2</sup> (CV 35.08%), differing from the current study's result by a factor of 1.44.

A detection function for Blainville's beaked whales was estimated from the Monte Carlo model and is plotted as a function of slant range for fixed off-axis angles (0°, 45°, and 90°) in Fig. 8. The plateau observed in the first 1.5 km for on-axis clicks is due to the assumption that simulated SNRs that are higher than the maximum observed value have probability of detection equal to that of the highest observed SNR. This assumption is an oversimplification and ideally a better characterization of the probability of detection for higher SNRs could be derived from manual analysis of more data. Another option would be to extrapolate the GAM results (Fig. 7), continuing the trend for decreasing detection probability with higher SNR. However, GAM extrapolation is usually unreliable. The results shown in Fig. 8 indicate that off-axis clicks are most likely to be detected within 1 km of the hydrophone, with a rapid decrease in the probability of detection out to 2 km. For on-axis angles, the highest probability of detection occurs at approximately 3 km away from the hydrophone. This peak occurs because of the peak in the curve characterizing detection probability as a function of SNR (Fig. 7). The probability of detection then decreases rapidly with increasing distance, reaching almost zero probability at approximately 5 km. The estimated detection functions from Marques *et al.* (2009) (Fig. 3, upper right corner) show overall higher probabilities of detection at shorter slant distances as compared to this study. It should be noted that in this study the off-axis angle was calculated by implementing a piston model to approximate the beam pattern of Blainville's beaked whale, and such an approach does not discriminate the components of the off-axis angle into vertical and horizontal.

Results of our calculations show that the higher the energy flux density (or source level) used (from the defined normal distribution), the higher the average probability of detection for the 10 000 simulated clicks (Fig. 9). This

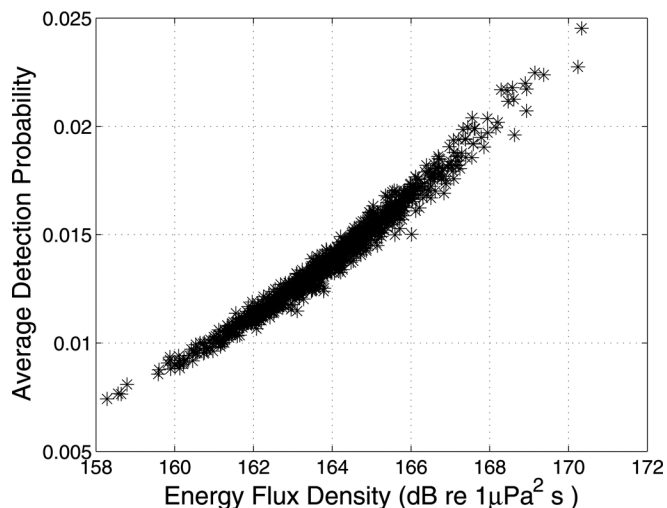


FIG. 9. Average probability of detection from the 10 000 simulated clicks for each realization of energy flux density taken from a Gaussian distribution.

suggests that uncertainty in source levels contributes heavily to variance in calculated density, as compared to uncertainty due to detector characterization. At the same time, Fig. 7 also shows considerable uncertainty about the probability of detection at high SNR values. It is stressed here that the detector-and-classifier characterization performed in this study relied on only a single, small, randomly chosen time period. Detection characterization for future density estimates should be more systematic and extensive. We also note that the use of this density estimation method requires a detector that is well characterized rather than optimal. Uncertainty associated with the detector performance was measured by the residual variance of the generalized additive model (GAM) fit to the detector characterization data. This uncertainty is then used in the final density estimate uncertainty by the Monte Carlo procedure: each iteration of the simulation used a random detector characterization curve, sampled from a list of possible curves derived from the GAM. So uncertainty in density is not dependent on how good or bad the detector is, it depends on how well the detector is characterized, and hence what the residual error on the GAM curve is. However, a poor detector will give a lower number of detections to work with, and this will contribute to a higher variance in density (as the encounter rate CV will be higher). Hence, even if it can be accurately characterized, having a poor detector is not without cost. To obtain accurate density estimates in future acoustic monitoring studies, accurate estimation of cue (click) rates is also required. For sperm whales, for example, it is known that group size (Whitehead and Weilgart, 1990) and time of day (Weilgart, 1991) affect click rates, and differences are also observed between males and females (Goold and Jones, 1995). However, insufficient information is available in the literature for Blainville's beaked whales to accurately model diurnal variations in vocal behavior, and variations with group size and sex. Therefore, click production rate was assumed to be the same for all age/sex classes and for all group sizes.

The density estimation method from whale vocalizations recorded at a single sensor developed in this paper is intended to be applied to any species and to data recorded from any isolated acoustic sensor, including fixed acoustic sensors deployed at or close to the surface, sonobuoys, or deep autonomous hydrophones. The necessary input parameters for the model which are related to environmental properties and animal vocal behavior often vary with geographic location and target species. Previous density estimates of Blainville's beaked whales at AUTECH have relied on different analyses to arrive at estimated densities. Moretti *et al.* (2006) and Marques *et al.* (2009) both relied on DTAG data collected at AUTECH simultaneously with their sound recordings to arrive at their density estimates. Here only information found in the literature was used to estimate density. Note that the information found in the literature for beaked whales comes mostly from DTAG data, although none of the data used are from the geographic area of this study. By only using information available in the literature we hope to point the way toward density estimates that may be made with minimal, or even no use of acoustic tag data at all. The idea is that such data are sufficiently difficult and expensive to

collect that they cannot be used for every species, and in every area, where density estimates are desired.

When counting cues or estimating the rate of false positive detections, multipath arrivals can be a source of error and must be accounted for during data analysis. In the case of beaked whale clicks at AUTECH, recordings of vocalizations rarely have detectable multipath arrivals, perhaps due to the highly directional nature of the clicks. However, it is possible to separate direct and indirect arrivals using the different signal characteristics of the two arrivals (Bagenstoss, 2008). For sperm whales and dolphins, which more commonly have multipath arrivals, grouping clicks into trains (Starkhammar *et al.*, 2011; Bagenstoss, 2011) can also help in identifying direct and reflected-path arrivals. Another alternative is to use manual validation by a trained analyst to determine the average number of times clicks are received, and then incorporate this information in the estimation of the false positive rate. Although difficult, this is feasible under certain circumstances, as, for example, when few animals are present or when vocalizations are relatively uncommon.

Estimates of variance and confidence limits are just as important as the estimate of the mean. Our estimates of uncertainty for several relevant parameters were based on poorly supported assumptions about real-world uncertainty in the input quantities. For example, for click rate, we used the variance from an unweighted average of reported estimates, which probably underestimates true uncertainty. For source level and animal beam pattern, rough approximations were made from assumptions of those parameters found in the literature. Here a single sensor was considered, a conscious decision given the proof-of-concept goal of this work. But the use of a single sensor implied that the variance in the number of cue counts had to be obtained based on a distributional assumption. While a Poisson distribution was assumed, in other similar settings an over-dispersed Poisson has been suggested (e.g., Buckland *et al.*, 2001), and so there is not a definite answer regarding the variance estimation under this setting. However, more robust estimates would be based on a design that considers an array of hydrophones even if, for practical purposes, they are all operating independently. This will allow variance on counts over space to be obtained using an empirical variance estimator. Note that this is the recommended procedure in closely related distance sampling surveys (Buckland *et al.*, 2001), and the one we recommend to obtain reliable estimates of density. Additionally, an array of sensors means that, averaged across space, the assumption of uniform distribution in space, used here to obtain the estimated average probability of detection, is much more likely to hold.

Population density estimation based on passive acoustics is in its infancy. However, the approach looks promising. We anticipate considerable research in this area: developing dedicated hardware, refining detection and classification algorithms, further developing estimation methods, and improving our knowledge of species' acoustic behavior. As an example, cue rate estimates are needed in general to convert detected cues to a measure of abundance, but such rates are currently unknown for most species. In general, directly measuring the variables required for density estimation is far



preferable to deriving their values based on assumptions and modeling. For example, estimation of a detection function based on *in situ* data measurements (e.g., Marques *et al.*, 2009) or dense arrays of linked sensors (e.g., Marques *et al.*, 2010) automatically integrates all species/site specific characteristics, and avoids the need for assumptions made in this paper about source levels, directionality, and sound propagation. However, *in situ* measurements and dense linked sensor arrays can be prohibitively expensive. Our results show that it is possible to use a model-based approach to produce density estimates in reasonable agreement with those from other methods, by making careful use of information available in the literature.

Extensive passive acoustic recordings exist of marine mammal vocalizations from single fixed sensors or sonobuoys. The method described in this paper opens up the opportunity for estimating animal density by analyzing such previously recorded datasets, contributing to the understanding of cetacean population distribution and behavior. We hope that such methods are found to be useful in the common situation where unlinked sensors are deployed, and information from tagged animals is not available for the time and place where acoustic monitoring took place.

## ACKNOWLEDGMENTS

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