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Corresponding Author: Dr. Tiago André Marques,

Corresponding Author's Institution: University of St Andrews

First Author: Tiago André Marques

Order of Authors: Tiago André Marques; Len Thomas; Steve W Martin; David K Mellinger; Susan Jarvis; Ron P Morrissey; Carol-Anne Ciminello; Nancy DiMarzio

Abstract: Estimation of cetacean abundance or density using visual methods can be cost ineffective under many scenarios. Methods based on acoustic data have recently been proposed as an alternative, and could potentially be more effective for visually elusive species that produce loud sounds. Motivated by a data set of minke whale (*Balaenoptera acutorostrata*) being sounds detected at multiple hydrophones at the U.S. Navy's Pacific Missile Range Facility (PMRF), we present an approach to estimate density or abundance based on spatially explicit capture recapture (SECR) methods. We implement the proposed methods in both a likelihood and a Bayesian framework. The point estimates for abundance and detection parameters from both implementation methods are very similar and agree well with current knowledge about the species. The two implementation approaches are compared in a small simulation study. While the Bayesian approach might be easier to generalize, the likelihood approach is faster to implement (at least in simple cases like the one presented here) and more readily amenable to model selection. SECR methods seem to be a strong candidate for estimating density from acoustic data where recaptures of sound at multiple hydrophones/microphones are available, and we anticipate further development of related methodologies in the future.

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1 **Spatially explicit capture recapture methods to estimate**
2 **minke whale density from data collected at bottom**
3 **mounted hydrophones**

4 **Tiago A Marques · Len Thomas · Stephen**
5 **W. Martin · David. K. Mellinger · Susan**
6 **Jarvis · Ronald P. Morrissey · Carroll-Anne**
7 **Ciminello · Nancy DiMarzio**

8 Received: date / Accepted: date

Tiago A Marques · Len Thomas (✉)

Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan
Gardens, University of St Andrews, Fife, KY16 9LZ, Scotland

Tel.: 0044 1334 461801

Fax: 0044 1334 461800

E-mail: len@mcs.st-and.ac.uk

Stephen W. Martin

Space and Naval Warfare Systems Center Pacific, 53560 Hull Street, San Diego, California
92152, U.S.A.

David. K. Mellinger

Cooperative Institute for Marine Resources Studies, Oregon State University, 2030 SE Marine
Science Drive, Newport, Oregon 97365, U.S.A.

Susan Jarvis · Ronald P. Morrissey · Carol-Anne Ciminello · Nancy DiMarzio

Naval Undersea Warfare Center Division, 1176 Howell Street, Newport, Rhode Island 02841,
U.S.A.

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12 elusive species that produce loud sounds. Motivated by a data set of minke whale (*Bal-*
13 *aenoptera acutorostrata*) boing sounds detected at multiple hydrophones at the U.S.
14 Navy’s Pacific Missile Range Facility (PMRF), we present an approach to estimate
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22 amenable to model selection. SECR methods seem to be a strong candidate for es-
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24 sensors are available, and we anticipate further development of related methodologies.

25 **Keywords** minke whale · passive acoustic monitoring · proximity detector · secr ·
26 spatially explicit capture recapture · OpenBUGS

27 1 Introduction

28 The estimation of animal density and abundance is a fundamental requirement for effec-
29 tive management and conservation decisions. However, this is particularly challenging
30 for many cetacean species, which typically occur over very large areas, at low densities,
31 and spend a large proportion of their time submersed. All this makes them especially

32 challenging to survey using standard visual methods. These include distance sampling
33 methods, namely shipboard and aerial surveys in which line transects or cue counting
34 approaches are used (see Buckland et al (2001) for details), as well as capture-recapture
35 methods (e.g. Evans and Hammond, 2004) based on photo-ID or DNA. While working
36 well under certain circumstances, all of these methods have several shortcomings. Low
37 encounter rates create problems in analysis and low precision in the estimates, and
38 surveys are restricted to good weather and daylight conditions. This makes them cost
39 ineffective for many scenarios.

40 In recent years, acoustic data has been proposed as having information about den-
41 sity (Mellinger et al, 2007). Common sense alone suggests that the amount of animal-
42 produced sound (however it is measured) might act as an index of animal abundance.
43 The challenge is to find ways to convert that amount of sound to animal density.
44 Using sound to detect and localize animals from towed hydrophone arrays has been
45 successfully implemented for sperm whales (e.g. Barlow and Taylor, 2005). However,
46 this approach does not really differ from an analysis perspective from conventional
47 line transect distance sampling. On the other hand, Marques et al (2009) presented
48 the first example in which data from fixed hydrophones was used to estimate cetacean
49 density, using an approach akin to cue counting. Unlike for conventional cue counting,
50 the detection function was estimated using a regression based approach using a sample
51 of data for which the animal locations and vocalizations were known from acoustic dive
52 tags.

53 If one has an array of fixed hydrophones, sounds detected at multiple hydrophones
54 can be seen as capture-recapture data. Each sound can be assigned a capture history,
55 say a 1 for each hydrophone where it was detected and a 0 on hydrophones where it
56 was missed. This assumes we can tell when the same sound is received at multiple hy-

drophones, say from timing and/or frequency information, just as we assume we can tell when the same individual is sighted in a photo ID study. Standard capture-recapture analyses could be undertaken, but there are several reasons to focus on the use of spatially explicit capture-recapture (SECR, Borchers and Efford (2008); Borchers (this volume)) methods for estimating density. Firstly, SECR methods explicitly model the dependence of capture probability on distance, thereby reducing the un-modelled heterogeneity that usually hinders capture-recapture analysis. For acoustic data we may expect distance of the sound source to be a major component of capture probability. Secondly, SECR methods estimate density and abundance over an explicitly-defined area, as opposed to traditional methods where the area sampled is not clearly defined and hence converting abundance to density is problematic. SECR has received considerable attention recently, both from classical likelihood (e.g. Efford et al, 2008; Borchers and Efford, 2008; Efford et al, 2009) and Bayesian (e.g. Royle and Young, 2008; Royle, 2009; Royle et al, 2009a) perspectives. In particular Dawson and Efford (2009) have applied likelihood-based methods to acoustic data, estimating bird density from a set of 4 microphones.

In this paper, we compare Bayesian and likelihood based approaches to SECR, using as motivation the estimation of density of sounds produced by common minke whales (*Balaenoptera acutorostrata*) off the coast of Kauai, Hawaii. Minke whales are one of the most abundant baleen whale species worldwide, but they are also one of the smallest and can be very difficult to detect using standard visual survey methods. Although commonly sighted in high latitude waters, they are rarely seen in tropical and sub-tropical areas, despite being heard there during winter and spring. This is particularly true around the Hawaiian Islands, where extensive aerial and shipboard surveys (e.g. Mobley Jr. et al, 1999; Rankin et al, 2007) have produced only a handful

82 of sightings, but the characteristic “boing” sound attributed to minke whales (Barlow
83 and Taylor, 2005) can be detected readily in the right season (e.g. Rankin et al, 2007).
84 Therefore, methods based on acoustic rather than visual detections might prove more
85 effective at estimating their abundance.

86 The data used here come from a set of 16 bottom-mounted hydrophones that are
87 part of the U.S. Navy’s Pacific Missile Range Facility (PMRF), an instrumented testing
88 range located along the western shore of Kauai. The hydrophones are part of the Bark-
89 ing Sands Underwater Range Expansion (BSURE), which extends northwest of the
90 island, covering approximately 2,300km² and having water depths to 4,500m through-
91 out most of its area. While the hydrophones were designed for tracking underwater
92 objects such as submarines and torpedos, they are capable of detecting minke whale
93 boing vocalizations, and are therefore well suited to study this cryptic cetacean.

94 The paper is structured as follows. The next section describes the Bayesian and
95 likelihood based approaches to SECR. These are then applied to the case study data
96 in section 3. Section 4 presents a simulation study evaluating performance of the two
97 approaches in a simple scenario that mimics the case study. Lastly, a discussion section
98 gives the main conclusions and suggests potential avenues for future investigation.

99 It is not our intention in this paper to provide a definitive estimate of minke whale
100 (sound) density in the study area; instead we focus on establishing the utility of the
101 SECR methodology and comparing approaches to analysis. This is (to our knowledge)
102 the first time that: (1) both a Bayesian and likelihood SECR implementation are di-
103 rectly compared, (2) a Bayesian SECR model has been applied to acoustic data, here
104 using proximity detectors (see below for details) and (3) SECR is proposed to estimate
105 density of cetaceans.

106 2 SECR models and inference

107 In this section, we outline the models and estimation approaches. A non-technical
108 introduction to SECR models is given by Borchers (this volume); more details of the
109 likelihood-based methods are in Borchers and Efford (2008) and Efford et al (2009);
110 details of a similar Bayesian method (with different types of detectors) is in Royle and
111 Young (2008) and Royle et al (2009a).

112 As initially conceived, SECR models consider that animals' home range centres
113 are at unobserved locations $\mathbf{X} = (X_1, X_2, \dots, X_N)$, where X_i represents the position
114 of animal i (i.e., its cartesian coordinates in 2-dimensional space). Inference is focused
115 on estimating N , the number of home range centres in a given area A (e.g. Borchers
116 and Efford, 2008; Royle and Young, 2008), as well as density, $D = N/A$. In the current
117 scenario, the equivalent to the home range centres are the actual sound source locations.
118 Hence the focus of our estimate using SECR is the number and density of sound
119 sources within a given area A and time period T . The estimation of the actual animal
120 abundance requires dividing the estimated sound source abundance \hat{N} by T and sound
121 production rate, and we do not deal with this here.

122 The Bayesian and likelihood approaches have several differences (details below),
123 so we deal with them separately in the sections below. However, they both use the
124 same model for sound detection, as follows. Consider an array of K hydrophones, each
125 with known location. A sound produced at location X is detected at hydrophone k
126 ($k = 1, \dots, K$) with probability $p_k(X; \boldsymbol{\theta})$ where $\boldsymbol{\theta}$ is a vector of detection parameters.
127 Hydrophones operate independently, so that the probability a sound is detected on at
128 least one hydrophone is $p(X; \boldsymbol{\theta}) = 1 - \prod_{k=1}^K (1 - p_k(X; \boldsymbol{\theta}))$. Detection probability is
129 assumed to be a non-increasing function of horizontal distance $d_{X,k}$ between sound

130 source at X and hydrophone k : $p_k(X; \boldsymbol{\theta}) = g(d_{X,k}; \boldsymbol{\theta})$. There are many candidate
 131 models for the distance detection function g ; here we use three, all of which have a
 132 long history in the classical distance sampling literature:

- 133 1. half-normal $g(d; \boldsymbol{\theta}) = g_0 \exp(-d^2/(2\sigma^2))$ with $\boldsymbol{\theta} = (g_0, \sigma)$
- 134 2. hazard rate $g(d; \boldsymbol{\theta}) = g_0(1 - \exp(-(d/\sigma)^{-z}))$ with $\boldsymbol{\theta} = (g_0, \sigma, z)$
- 135 3. negative exponential $g(d; \boldsymbol{\theta}) = g_0 \exp(-d/\sigma)$ with $\boldsymbol{\theta} = (g_0, \sigma)$

136 Detectors such as this, where an object (in this case a sound) can be “captured”
 137 on more than one detector and where the detector can capture many objects in one
 138 “trapping session”, are termed “proximity detectors” by Efford et al (2008). Other de-
 139 tectors (not relevant to passive acoustics) are described in that paper. For simplicity in
 140 what follows, we consider only one “trapping session”, although generalization to mul-
 141 tiple sessions (with potentially varying animal densities and/or detection parameters)
 142 is simple.

143 Assume n sounds in the period of interest were detected on one or more hy-
 144 drophones. Let ω_{ik} represent the detection of the i th sound at the k th hydrophone,
 145 such that $\omega_{ik} = 1$ if the sound was detected, 0 otherwise. $\boldsymbol{\omega}_i$ is the capture history of
 146 the i th sound, and $\boldsymbol{\omega}$ is all the recorded capture histories.

147 2.1 Likelihood-based methods

148 For simplicity, we assume that sound source locations are distributed in space according
 149 to a homogeneous Poisson process with intensity D . Extension to an inhomogeneous
 150 process is conceptually straightforward, and is given by Borchers and Efford (2008).
 151 The joint likelihood for D and the detection parameters $\boldsymbol{\theta}$ given the capture histories

152 ω can be written

$$L(D, \theta | n, \omega) = Pr(n|D, \theta) Pr(\omega | n, \theta) \quad (1)$$

153 where $Pr(n|D, \theta)$ is the marginal distribution of the number of sound sources detected,
 154 n , and $Pr(\omega | n, \theta)$ is the conditional distribution of the capture histories given n . (In
 155 the inhomogeneous Poisson case the latter distribution will also depend on the spatial
 156 intensity parameters.)

157 Given the assumption that sound source locations follow a Poisson process, then
 158 n is the outcome of a thinned Poisson process, which has a Poisson distribution with
 159 parameter $Da(\theta)$, where $a(\theta) = \int_{X \in A} p(X; \theta) dX$ has an intuitive interpretation as
 160 the “effective sample area” (see Borchers, this volume, for details). The area A needs
 161 to be large enough that no detections can occur from outside of it; in practice Efford
 162 (2009) suggests it is sufficient to define A as a rectangle with limits formed by buffering
 163 the hydrophones at a distance w such that $g(w) < 0.01$. The first term in (1) is thus

$$Pr(n|D, \theta) = n!^{-1} Da(\theta)^n \exp(-Da(\theta)). \quad (2)$$

164 Assuming independence between detections, the second term in (1) can be written

$$Pr(\omega | n, \theta) = \binom{n}{n_1, \dots, n_C} a(\theta)^{-n} \int_{X \in A} \prod_{i=1}^n Pr(\omega_i | X, \theta) dX \quad (3)$$

165 where the first part is the multinomial coefficient (with n_1, \dots, n_C representing the
 166 frequency of each of the C unique capture histories), the second part ($a(\theta)^{-n}$) is there
 167 because we condition on the number of observed capture histories, and the remain-
 168 der is the probability of obtaining capture history ω_i given sound source location X ,
 169 integrated over all possible locations. Since hydrophones operate independently,

$$Pr(\omega_i | X, \theta) = \prod_{k=1}^K p_k(X; \theta)^{\omega_{ik}} (1 - p_k(X; \theta))^{(1 - \omega_{ik})}. \quad (4)$$

170 Note that, because the sound source locations are not known, they are integrated
 171 out of the likelihood. In practice, to reduce computational effort during maximiza-
 172 tion, the likelihood is evaluated over a discrete grid of points, and the integrations
 173 become sums (Efford et al, 2009). The choice of the grid size is a compromise between
 174 computational efficiency and no influence on the results.

175 One approach to estimation of D , which we call the “full likelihood” approach, is
 176 joint maximization of the parameters D and θ in (1). Variances on parameters can
 177 be estimated from the inverse of the information matrix and profile likelihoods can be
 178 used to obtain confidence intervals.

179 An alternative (e.g. Borchers and Efford, 2008) when D is homogeneous is to max-
 180 imize the conditional likelihood

$$L(\theta|n, \omega) \propto a(\theta)^{-n} \int_{X \in A} \prod_{i=1}^n Pr(\omega_i|X, \theta) dX \quad (5)$$

181 to obtain estimates of θ and hence $\hat{a} = a(\hat{\theta})$. From this, D can be estimated using
 182 the Horvitz-Thompson-like estimator $\hat{D} = n/\hat{a}$. While the estimates derived from both
 183 full and conditional likelihoods are equivalent, the Horvitz-Thompson-like formulation
 184 permits different variance estimators for \hat{D} than the full likelihood. Borchers and Ef-
 185 ford (2008) suggest two in their supplementary materials, one assuming fixed N in the
 186 study area, and the other random N . Both have design-based and model-based compo-
 187 nents (see Discussion), and can be expected to be more robust than the full likelihood
 188 estimator to departures from a Poisson animal distribution. (We note in passing that
 189 these two estimators are sometimes referred to as “binomial” and “Poisson”, e.g., in
 190 Efford (2009), but we prefer to use the terms fixed- N and random- N as neither as-
 191 sumes animals follow binomial or Poisson distributions.) Confidence intervals can be
 192 obtained by assuming D follows a normal or log-normal distribution.

193 All of the above inference can be carried out using the `secr` package (Efford, 2009)
 194 in R (R Development Core Team, 2009).

195 2.2 Bayesian methods

196 There are several differences between the model described in the previous section and
 197 that used here. Firstly, the Bayesian model is parameterised in terms of abundance N
 198 within an area A , rather than density D , and this N is assumed to be a fixed quantity.
 199 This leads to a binomial likelihood for n given N , rather than the Poisson likelihood for
 200 n given D in the previous section.. Secondly, data augmentation is used to deal with
 201 the un-observed capture histories and sound source locations. Thirdly, being Bayesian,
 202 prior distributions are used on all unknown parameters, although since uniform priors
 203 with widely spaced limits are used, the posterior and likelihood surfaces will have the
 204 same shape within the truncation bounds.

205 Let $\tilde{\omega}$ be the capture histories of the N sound sources in the study area A . n of
 206 these are observed, and therefore have one or more non-zero elements; the remaining
 207 ($N - n$) contain only zeros. The equivalent of (3), conditioning on the sound source
 208 locations, is then

$$Pr(\tilde{\omega}|N, \mathbf{X}, \boldsymbol{\theta}) = \binom{N}{n_0, \dots, n_C} \prod_{i=1}^N Pr(\tilde{\omega}_i|X_i, \boldsymbol{\theta}). \quad (6)$$

209 Inference is based on the joint posterior distribution

$$\begin{aligned} Pr(N, \mathbf{X}, \boldsymbol{\theta}|\boldsymbol{\omega}) &\propto Pr(N, \mathbf{X}, \boldsymbol{\theta})Pr(\tilde{\omega}|\boldsymbol{\omega}, N)L(N, \mathbf{X}, \boldsymbol{\theta}|\tilde{\omega}) \\ &= Pr(N)Pr(\mathbf{X}|N)Pr(\boldsymbol{\theta})L(N, \mathbf{X}, \boldsymbol{\theta}|\tilde{\omega}) \end{aligned} \quad (7)$$

210 where a discrete uniform prior distribution is used for $Pr(N)$, with lower bound 0
 211 and an (arbitrarily high) upper bound M , and uniform prior distributions are used

212 for $Pr(\mathbf{X}|N)$ and $Pr(\boldsymbol{\theta})$. Note that $Pr(\tilde{\boldsymbol{\omega}}|\boldsymbol{\omega}, N) = 1$, which is why it disappears from
 213 the second line, and $L(N, \mathbf{X}, \boldsymbol{\theta}|\tilde{\boldsymbol{\omega}})$ has the same form as (6) except that $\tilde{\boldsymbol{\omega}}$ is the fixed
 214 variable.

215 In practice, the fact that the dimension of both $\tilde{\boldsymbol{\omega}}$ and \mathbf{X} depend on N raises
 216 computational issues. These are sidestepped by a further data augmentation, where
 217 $(M-N)$ additional all-zero capture histories and sound source locations are added (see
 218 Royle et al (2007) for the general framework, and Royle et al (2009b) and Royle and
 219 Young (2008) for applications). Let M be the fixed size of a superpopulation of sound
 220 sources, with capture histories $\tilde{\boldsymbol{\omega}}^*$ and locations \mathbf{X}^* . n of the capture histories are
 221 observed; the remaining $(M - n)$ contain only zeros. Let $\mathbf{z} = (z_1, \dots, z_M)$ be a vector
 222 of indicator variables, such that $z_i = 1$ if sound source i is part of the population N , 0
 223 otherwise. This means N is now a derived parameter in the model: $N = \sum_{i=1}^M z_i$. Let
 224 the z_i for each sound source follow a Bernoulli distribution with parameter ψ . Inference
 225 is then based on the joint posterior

$$\begin{aligned} Pr(\mathbf{z}, \mathbf{X}^*, \boldsymbol{\theta}, \psi|\boldsymbol{\omega}, M) &\propto Pr(\mathbf{z}, \mathbf{X}^*, \boldsymbol{\theta}, \psi)Pr(\tilde{\boldsymbol{\omega}}^*|\boldsymbol{\omega}, M)L(\mathbf{z}, \mathbf{X}^*, \boldsymbol{\theta}, \psi|\tilde{\boldsymbol{\omega}}^*) \\ &= Pr(\mathbf{X}^*)Pr(\boldsymbol{\theta})Pr(\psi)Pr(\mathbf{z}|\psi)L(\mathbf{z}, \mathbf{X}^*, \boldsymbol{\theta}|\tilde{\boldsymbol{\omega}}^*) \end{aligned} \quad (8)$$

226 where uniform prior distributions are used for $Pr(\mathbf{X}^*)$ and $Pr(\boldsymbol{\theta})$, a uniform (0,1) prior
 227 is used for $Pr(\psi)$, $Pr(\tilde{\boldsymbol{\omega}}^*|\boldsymbol{\omega}, M) = 1$, and

$$L(\mathbf{z}, \mathbf{X}^*, \boldsymbol{\theta}|\tilde{\boldsymbol{\omega}}^*) = \binom{M}{n_0, \dots, n_C} \prod_{i=1}^M z_i Pr(\tilde{\boldsymbol{\omega}}_i^*|X_i^*, \boldsymbol{\theta}). \quad (9)$$

228 The marginal posterior distributions of N , $\boldsymbol{\theta}$ and \mathbf{X} from (8) are then same as (7), but
 229 implementation is greatly simplified.

230 The most convenient route to fitting the Bayesian models to data is via short
 231 programs written in OpenBUGS (Thomas et al, 2006). An example program is provided
 232 as an appendix.

Table 1 Summary of case study data.

Date	Start time (GMT)	# detections	# unique boings (n)	Capture frequency					
				1	2	3	4	5-9	10-14
5 Mar 06	22:15:55	63	14	2	2	4	2	2	2
13 Mar 06	23:05:28	75	12	1	3	0	0	6	2
19 Apr 06	02:59:40	6	5	4	1	0	0	0	0
19 Apr 06	04:29:40	12	10	8	2	0	0	0	0
16 Apr 07	03:52:20	41	9	2	2	0	1	3	1
21 Apr 07	02:49:43	36	7	1	0	1	1	3	1
Total		233	57	18	10	5	4	14	6

233 3 Case study

234 3.1 Case study methods

235 The data come from six 10-minutes sample periods, taken from March and April 2006
 236 and 2007 (Table 1). For this simple analysis, we collapsed data over sampling occasions
 237 and treated them as a single 1 hour period. Sounds were recorded at 16 bottom-mounted
 238 hydrophones in BSURE, spaced from 8km to 18km apart and arranged in two lines
 239 (Figure 1). A custom-developed detector and classifier (Mellinger et al., unpublished)
 240 was utilized to detect minke whale boing vocalizations on the multiple hydrophones.
 241 The boing detector outputs included detailed timing and frequency content informa-
 242 tion. This information was utilized to make initial manual associations (i.e., determine
 243 whether detections at different hydrophones were of the same sound). The association
 244 outputs served as inputs to the SECR analysis.

245 Likelihood-based models were fit using the `secr` package (version 1.2.10) in R (ver-
 246 sion 2.9.2). As mentioned in section 2.1, it is necessary to define a buffer distance w

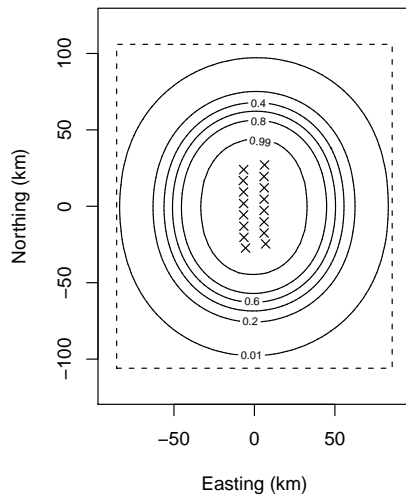


Fig. 1 Layout of BSURE case study hydrophones (crosses), solid contour lines showing probability of detecting a sound from that location with one or more hydrophones (denoted $p.(X; \theta)$ in the text) estimated from a likelihood-based analysis with the half-normal detection function model, and the dashed rectangle showing the 80km buffer used in that analysis.

247 for integration, and Efford (2009) advises setting it such that $g(w) < 0.01$. We took an
 248 iterative approach: fitting detection function models with increasing values for w and
 249 determining when values of log-likelihood, σ and D stabilized. We found that, for the
 250 half-normal, hazard rate, and negative exponential models, $g(w) = 0.01$ corresponded
 251 to $w \approx 80, 110, \text{ and } 150\text{km}$ respectively, and at these distances the log-likelihood and
 252 parameter estimates were stable to three significant figures. In our case this was good
 253 enough for model selection, because there were large differences among models; however
 254 had the models been closer, more accuracy and hence large buffer distances would have
 255 been required. Given the above buffer distances, we fit the models by maximizing the
 256 conditional likelihood (5) and selected the best model on the basis of minimum Akaike

257 information criterion for small sample sizes (AICc). Minke whale boings are readily
258 detectable on the bottom-mounted hydrophones, and it is highly plausible that all bo-
259 ings produced at zero distance are detected with certainty. Initial analyses, where g_0
260 was estimated, gave values of $\hat{g}_0 > 0.99$. We therefore fixed this parameter at 1.0. After
261 obtaining maximum likelihood estimates of the remaining detection function parame-
262 ters, density was estimated using the Horvitz-Thompson-like formulation described in
263 section 2.1, with conditional (fixed-N) variance estimate.

264 Bayesian models were fit in OpenBUGS version 3.0.3 using the Appendix code.
265 Since model selection is not straightforward in OpenBUGS (Deviance information
266 criterion is not available for discrete nodes) only the half-normal detection function
267 model was fit (the best fitting model using likelihood based methods), using a buffer
268 of $w = 80\text{km}$ and fixing $g_0 = 1$. The superpopulation size, M was chosen in a similar
269 manner to the buffer: increasing values were tried until further changes had no affect
270 on inference. A useful shortcut diagnostic was to check that the posterior upper 97.5th
271 quantile for ψ was well away from its upper bound of 1. We found that a value of
272 $M \approx 2\hat{N}$ worked well; this amounted to adding 350 artificial all-zero capture histories
273 to the dataset (to give $M=407$). We set a uniform prior on σ with lower bound 0
274 and upper bound again large enough that it did not affect posterior estimates – for
275 these data a value of 50 km was used (this value was obtained by trial and error, mak-
276 ing sure the posterior results were not constrained by this choice). Starting values for
277 the MCMC chain were set by choosing values for all quantities at random from their
278 priors. Convergence was checked informally, by starting multiple chains from random
279 start points, examining trace plots, and checking that resulting parameter estimates
280 from different chains were indistinguishable except for Monte-Carlo error. Initial in-
281 vestigations showed that 3000 samples was a sufficient burn-in to ensure convergence

282 to the target posterior distribution and that keeping 100,000 samples after that was
283 sufficient for 3 significant figure accuracy in parameter estimates.

284 3.2 Case study results

285 There were 233 detections of 57 individual boing sounds in the test dataset (Table 1).

286 For the likelihood-based implementation, the half-normal detection function model
287 was strongly favoured, with the next best model, the hazard rate, having a ΔAICc of
288 > 13 , and the negative exponential model trailing a distant third (Table 2). Estimated
289 probability of detecting a sound for locations within A from the half-normal model is
290 shown in Figure 1. The estimated detection functions (illustrated in Figure 2), and
291 hence densities, were quite different among the three models, with the hazard rate
292 giving a density estimate about 40% lower than the half-normal, with the negative
293 exponential being about 50% lower again. Estimated density from the half normal
294 model was 47.88 sounds per hour per 10,000km² (SE 10.60). This corresponds to 179
295 sounds per hour within the 80km buffer area used for that model ($A = 37,283 \text{ km}^2$).

296 The Bayesian implementation of the half-normal model gave very similar results to
297 the likelihood-based implementation. The posterior mean estimate of ψ was 0.46 with
298 95% central posterior interval of 0.28-0.69. The upper value was well away from 1.0,
299 providing reassurance that a large enough number of artificial zero capture histories
300 had been used.

Table 2 Results from analysis of case study data. Values in brackets after estimates are standard errors. Density (\hat{D}) units are sounds per hour per 10,000km². σ represents the scale parameter of the 3 models considered, z represents the shape parameter of the Hazard-Rate model.

Model	ΔAICc	Param. estimates	\hat{D}	CI(\hat{D})
Likelihood-based method				
Half-normal	0	$\sigma = 21.37(2.27)$	47.88 (10.60)	40.23-72.10
Hazard rate	13.11	$\sigma = 27.36(3.84)$, $z = 3.60(0.41)$	28.45 (7.48)	13.80-43.10
Negative exponential	46.71	$\sigma = 32.56(11.87)$	13.62 (8.13)	3.25-62.98
Bayesian method				
Half-normal	-	$\sigma = 21.72(2.50)$	48.46 (10.26)	30.04-70.54

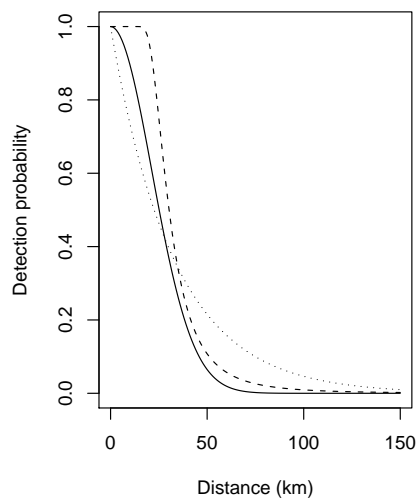


Fig. 2 Estimated half-normal (solid line), hazard rate (dashed line) and negative exponential (dotted line) detection functions fit by maximum likelihood to the case study data.

301 4 Simulation study

302 4.1 Simulation study methods

303 To check the performance of the different approaches under known conditions, we
304 undertook a small simulation study. We simulated 100 replicate populations of $N =$
305 175 objects located at random within a rectangular study area defined by an 80km
306 buffer around the hydrophones. This corresponds to a true density of $D = 46.94$ per
307 10,000km². Hydrophones were located at the same positions as previously, and we
308 simulated detection of each object at each hydrophone according to a half-normal
309 detection function with $\sigma = 20$. The simulated data were analyzed in the same way
310 as the real data, except for the following. For the likelihood-based analysis, we fit only
311 a half-normal detection function. We were interested in comparing variance estimates
312 from both the unconditional likelihood, and the conditional likelihood with assumed
313 random and fixed N , so we recorded all three. For the Bayesian analysis, we used only
314 10,000 samples after burn-in, to save computer time. No thinning was used. Informal
315 checks for convergence consisted in, for some of the simulated data sets, starting the
316 Monte Carlo chains at different points and checking they converged on similar values.

317 4.2 Simulation study results

318 The simulated data comprised a mean of 187.23 detections (SD 30.57) of 49.78 detected
319 objects (SD 6.23), slightly lower than the numbers in the case study (because a slightly
320 lower D and σ was used).

321 Both likelihood and Bayesian methods gave very similar estimates on average,
322 with negligible bias in estimates of both σ and D (Table 3). The standard deviation

Table 3 Summary of results from simulation study. For the mean estimated SD of the density estimate (\hat{D}) and corresponding confidence interval (CI) coverage, the three values represent respectively the full likelihood, binomial and Poisson based estimates. σ represents the scale parameter of the Half-Normal model.

Statistic	Likelihood-based	Bayesian
	method	method
Mean $\hat{\sigma}$ (true value 20)	20.11	20.34
SD $\hat{\sigma}$	1.84	1.89
Mean estimated SD $\hat{\sigma}$	1.95	2.00
95% CI coverage $\hat{\sigma}$	0.96	0.96
Mean \hat{D} (true value 46.94)	47.28	48.00
SD \hat{D}	8.87	9.13
Mean estimated SD \hat{D}	10.00; 9.27; 9.29	9.29
95% CI coverage \hat{D}	0.99; 0.95; 0.94	0.95

323 of the estimates (i.e., the actual standard deviation of the 100 replicate estimates
324 of σ and D for each method) was also very similar between methods. The Bayesian
325 method also did a good job of estimating the standard deviation: the mean of the
326 estimated standard deviation on \hat{D} was 9.29, while the actual standard deviation was
327 9.13. There was a suggestion that the full likelihood method slightly over-estimated
328 the standard deviation: the mean estimate was 10.00 while the true value was 8.87.
329 This led to slightly high 95% confidence interval coverage for the full likelihood method
330 (0.99); by contrast the coverage of the 95% posterior credibility interval was exactly
331 at the expected 0.95. The standard deviations of the derived estimates of D from the
332 conditional likelihood formulation were very similar, and closer to truth (9.27 for the
333 binomial and 9.29 for the Poisson), and the corresponding confidence interval coverage
334 was better.

335 5 Discussion

336 Although there is no ground truth with which to compare the case study estimates, the
337 results appear reasonable given what is known about minke whale acoustic behaviour.
338 We expect certain detection at zero horizontal distance, and that was backed up by pre-
339 liminary SECR analyses. The fitted half-normal detection function parameter estimate
340 of 21.4 (likelihood-based) or 21.7 (Bayesian) is reasonable, corresponding to a detec-
341 tion probability of about 0.95 at 10km, 0.5 at 25km and 0.1 at 45km (Figure 2). Calls
342 produced at constant source level and homogeneous propagation and background noise
343 conditions will all be detectable to a certain distance, beyond which the received level
344 falls below the threshold set for the detector and they are no longer detectable. The
345 resulting “step” detection function would be best fit by the hazard rate model, with
346 large (> 5) values of the z parameter. However, variation in source levels, propagation
347 and noise all contribute to a “rounding off” of the detection shoulder, leading to an
348 average detection function that is closer to the half-normal form (see, e.g. Burnham
349 et al, 2004, figure 11.2). It is possible that more flexible models, such as finite mixtures
350 or the semiparametric families used in conventional distance sampling, may provide a
351 better fit. Future work on the case study will focus on applying more complex models
352 of the detection process (such as time-varying detection) to a larger sample of data;
353 parallel field work is also in progress that, if successful, will provide an estimate of
354 animal call rate and potentially allow estimation of animal, rather than call, density.

355 We assume in this work that the manual association of sounds was done without
356 error, i.e. that no detected sounds were incorrectly associated as having the same sound
357 source, and that all detected sounds from a given source were identified and associated.
358 This seems a reasonable assumption given the amount of human effort put into this

359 task. We envisage that applications of these methods in the future might be based
360 on an automated association procedure. If one can characterize the association phase
361 and an eventual association error process, it should be possible to include this directly
362 in the estimation procedure. Therefore the precision in the estimates would include a
363 component due to mis-association.

364 We also considered sound and hydrophone locations to exist in two-dimensional
365 (horizontal) space, which is clearly a simplification for hydrophones located at around
366 4.5km depth and whales diving in the top few hundred meters of water. If the main
367 determinant of detection probability is direct distance, rather than horizontal distance,
368 then variation in whale and hydrophone depth represent un-modelled sources of het-
369 erogeneity. However, in our case, compared with other sources of variation (such as in
370 source level and propagation conditions) this seems quite minor. In other cases (with
371 deeper diving whales and shallower hydrophones, or smaller σ) it may be more impor-
372 tant, in which case the methods could be extended to three dimensions, with additional
373 assumptions about the depth distribution of sound sources being required.

374 Another simplification was that our analysis assumed a homogeneous density, even
375 failing to account for the islands of Kauai and Niihau, both of which occur within the
376 study area. This is acceptable given the preliminary nature of the test case analysis;
377 however, in future work, we hope to explore the relationship between biologically rele-
378 vant covariates such as depth and density. We will also need to account for the masking
379 effect of islands on sound propagation.

380 Our simple simulation study showed that both likelihood and Bayesian methods
381 yield unbiased estimates and standard deviations when their assumptions are met (or
382 nearly met in the case of the likelihood method, which assumes random N when it was
383 fixed in the simulations). Our estimates were based on likelihood modes in the former

384 method and posterior means in the latter, but as with many analyses, this did not
385 seem to generate a significant difference in estimates. Under small sample sizes, where
386 likelihoods might be severely skewed, the posterior mode might be a better candidate
387 than posterior mean in the Bayesian method.

388 Mean estimated standard deviation of D in the full likelihood method was high
389 compared with the actual value (the standard deviation of the estimated D 's), but this
390 is understandable given that the method assumes population size in the study area is
391 a Poisson random variable when it was actually fixed in the simulation. The two con-
392 ditional likelihood variance estimators produced estimates of standard deviation that
393 were smaller on average than the full likelihood estimates, and closer both to the actual
394 standard deviation of the likelihood estimator and to the estimate from the Bayesian
395 method. To understand these differences requires some discussion of the form of the
396 conditional likelihood variance estimators. The fixed- N estimator has two components:
397 the first is design-derived and reflects the uncertainty in D arising from sampling only
398 a proportion a of the study area A , assuming each animal is sampled independently;
399 the second is model-derived and reflects the additional uncertainty due to estimating
400 the parameters of a . The random- N estimator also has two components, with the first
401 arising from an assumption that the variance of n is equal to its mean (i.e., that animal
402 locations are independent of one another), and the second component being the same
403 as the second component of the fixed- N estimator. It turns out that the first component
404 of the fixed- N estimator is just $(1 - \hat{a}/A)$ times the first component of the random- N
405 estimator – this term can be thought of as a finite population correction factor that
406 will cause the first component of the fixed- N estimator to go to zero when all of A is
407 sampled. Hence, it is inevitable that the fixed- N estimator produces smaller estimates
408 of variance than the random- N estimator, as we found. Because our simulations used

409 a fixed N , all assumptions of the fixed- N estimator were met, and hence it was not
410 surprising that it produced estimates of standard deviation in D that were close, on
411 average, to the actual value. It was more surprising that the random- N estimator also
412 performed well and this estimator deserves further investigation.

413 Given this initial investigation, there appears to be little difference between likeli-
414 hood and Bayesian approaches. One major drawback of the Bayesian implementation
415 in OpenBUGS is that there is no ready method of selecting among different candidate
416 detection function models (or alternative models for spatial density distribution if a
417 non-homogeneous distribution is assumed). In addition, the model formulation used
418 here, with augmentation of the observed capture histories with a large number of ar-
419 tificial all-zero histories, results in rather long computation times (although still short
420 when compared with the time required to collect and process the acoustic data). It is
421 important to check that enough augmentation is used, that wide enough priors are set
422 on detection parameters, and that the burn-in time and number of samples are suffi-
423 cient to yield reliable estimates. By contrast, the likelihood-based methods are rather
424 easier to implement, thanks to the `secr` R package. Model selection via AICc (or other
425 criteria) is straightforward, convergence appeared reliable in the examples we used,
426 and fitting was much faster than in OpenBUGS. For both methods one must check
427 that an appropriately large buffer is used around the sample locations, and for the
428 likelihood-based method one can also vary the number of grid points used in numerical
429 integration. Our suspicion is that the Bayesian approach will make it easier to handle
430 complex scenarios such as random effects in the detection process or mis-association
431 of sounds – both are examples where data augmentation can potentially provide an
432 elegant solution, enabling inference to proceed by integrating out the complicating fac-

433 tors with relative ease. However, for simpler applications it appears at present that the
434 likelihood-based approach is more convenient.

435 We checked the performance of the methods under ideal conditions, where the
436 model assumptions were met and sample sizes were reasonably large. It would be
437 useful to determine how well they perform under more challenging situations, such as
438 alternative detection models, mis-association of calls, inhomogeneity in spatial density
439 and small sample sizes. Previous simulation studies of other varieties of SECR methods
440 have shown them to be reasonably robust to various challenges (e.g. Efford et al, 2008).

441 For these methods to work, the optimal spacing between the acoustic sensors is a
442 function of the scale of the detection process because the information about the de-
443 tection process lies essentially in the “recaptures”. Provided the acoustic data from
444 multiple hydrophones can be seen as capture histories, the SECR approach becomes
445 a natural one to estimate density. We predict in the future that statistical methods,
446 sound processing, survey design and even hydrophone hardware might be developed
447 and optimized with this goal in mind. The sound processing algorithms used here
448 should be easily adapted to other scenarios. The hardware technology required to im-
449 plement similar approaches still needs some development, and therefore the application
450 of these methods outside a setting like a navy range is still not straightforward. The
451 development of cheap and easily deployable sensors is desirable.

452 When a sound is detected at three or more hydrophones with appropriate geom-
453 etry, then given precise information about arrival time and assumptions about sound
454 propagation, it becomes possible to estimate the sound source location (in 2 dimen-
455 sions; more detections are required for 3-d localization). Detection of echoes at a single
456 hydrophone can also potentially be used to provide additional information about loca-
457 tion. In the current study, we make no use of this information, but the SECR methods

458 could be extended to utilize such information when available, potentially yielding more
459 precise inferences. Dawson and Efford (2009) have shown how information about sound
460 source distance that is contained in the relative received amplitude can be used to im-
461 prove inference. Information on bearing from vector-sensing hydrophones could also
462 potentially be used.

463 Passive acoustic methods have enormous potential to provide estimates of density
464 and abundance in situations not readily amenable to surveys by other modalities. In
465 many cases, however, we are limited by our knowledge of the vocal behaviour of the
466 animals, e.g., call rates. Nevertheless, there is a great deal of research interest in the
467 area and many ongoing studies aimed at increasing our knowledge. We anticipate that
468 passive acoustic density estimation will be increasingly applied in future years.

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531 **Appendix: Example OpenBUGS code**

532 This is the code used to run the application example in the Bayesian framework,
 533 a passive acoustic SECR with half-normal (HN) detection function. The user must
 534 input as data the following objects (object names in the code given inside brackets):
 535 (1) the number of detected animals (n), (2) the boundaries of the region over which
 536 integration takes place (Xl , Xu and Yl , Yu), (3) the upper bound on the prior for
 537 sigma ($maxSigma$), (4) the number of added all 0's capture histories required for data
 538 augmentation ($nzeroes$), (5) the traps locations ($traps$, the trap x and y coordinates
 539 need to be respectively in columns 1 and 2), (6) the area over which abundance is
 540 estimated ($Area$) and (7) the capture histories (Y , a matrix in which position i, k is 1
 541 if animal i was detected on trap k , and 0 otherwise). The random variables involved for
 542 which priors are required are (1) the inclusion probability (psi), (2) the HN detection
 543 function parameter ($sigma$), (3) a vector of latent indicator variables associated with
 544 each of M ($=n+nzeroes$) animals (z) and (4) the M animals location (respectively x
 545 and y coordinates ($x1$ and $x2$)).

546 The model specification is:

```
547 model {
548     #prior for inclusion parameter
549     psi~dunif(0,1)
550     #prior for HN detection function;
551     sigma~dunif(1,maxSigma)
552     #for each sound in the augmented capture history
553     for(i in 1:(n+nzeroes)){
554         z[i]~dbern(psi) #inclusion indicator
```

```
555     #draw a sound location
556     x1[i]~dunif(Xl,Xu)
557     x2[i]~dunif(Yl,Yu)
558     #for each trap
559     for(k in 1:K){
560         #calculate distance from trap to sound location
561         dist2[i,k]<-(pow(x1[i]-traps[k,1],2)+pow(x2[i]-traps[k,2],2))
562         #work out prob of detection given location
563         pdet[i,k]<- exp(-dist2[i,k]/(2*sigma*sigma))*z[i]
564         #connect to observed detections
565         Y[i,k]~dbern(pdet[i,k])}]
566     #estimate sound abundance and density
567     N<-sum(z[1:(n+nzeroes)])
568     D<-N/Area}
```

Here is the revised version of our manuscript. We addressed the two minor points raised by the session chairs.