

# Method for estimating sperm whale abundance from an acoustic strip transect survey with a two-element towed hydrophone

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## ABSTRACT

A method for estimating sperm whale abundance in an acoustic line-transect survey with a two-element hydrophone is described. The analysis starts from the point where a set of click trains have been identified by an analyst. Using likelihood methods, a description is given of the estimation from each click train of (i) whale positions from the bearing patterns of click trains, (ii) most likely numbers of whales in aggregations and (iii) a radial detection function based on the times of detected clicks and the estimated position. The method uses the complete set of allowable arrangements of these click trains into different numbers of whales. The number of arrangements is potentially very large yet can be computed because many click train combinations are not permissible, e.g. overlapping click trains cannot be from the same whale. It is suggested that the method could work well over perpendicular distances where the detection function is near-certain i.e. a strip transect survey. The method is applied to survey data from the western Mediterranean. Simulations based on the estimated radial detection function support a strip width of 5km. Some shortcomings and areas for further development are discussed.

KEYWORDS: ABUNDANCE ESTIMATE; SURVEY-ACOUSTIC; ACOUSTICS

## INTRODUCTION

Sperm whales (*Physeter macrocephalus*) produce a series of loud regular clicks when diving, and these ‘click trains’ are of similar long duration to the dives themselves. These characteristics make the species unusually amenable to acoustic survey methods.

Acoustic line transect surveys to estimate sperm whale abundance have been successfully carried out where the whales disperse widely and are encountered more-or-less in solitude, e.g. Antarctica (Leaper *et al.*, 2000) and between the Faroe and Shetland Islands (Hastie *et al.*, 2003). However, at most temperate latitudes, adult females and younger animals tend to form aggregations. Counting the number of whales is then more challenging.

In their acoustic/visual line-transect surveys, Barlow and Taylor (2005) used visual methods for estimating aggregation size. This required interrupting the acoustic survey, and making visual counts, which are themselves difficult. Hiby and Lovell (1989) developed a method for point transect acoustic surveys of sperm whales, but it is not clear how it performs as aggregation size becomes large. Some recent acoustic line-transect surveys (e.g. Swift *et al.*, 2009) have used target-motion analysis together with expert manual analysis of click characteristics to identify click trains and count the animals in aggregations, a process that is time-consuming and has some element of subjectivity.

The work presented here attempts to count aggregated sperm whales in uninterrupted (‘passing mode’) acoustic line-transect surveys with an explicit and objective analysis.

In an acoustic survey for sperm whales not all clicks are detected, particularly at greater ranges, and there are periods of prolonged silence (often 10–20 minutes) when the whales do not vocalise much, which correspond more-or-less to the

surfacing of the whales. The long silences between the click trains mean that it is not necessarily clear which trains are produced by which animals, and therefore how many animals are present. Fig. 1 shows the positions of some whales relative to a passing survey vessel, at the times that clicks were made. One problem for the surveyors is that the location of the clicks (and the whales) is not actually known and must be estimated. Another problem is estimating the number of sperm whales present from a set of click trains. Within the strip in Fig. 1 (upper solid grey line), between two and five whales may have been present, depending on which click trains were produced by which animals. In reality the number of animals and click trains could be



Fig. 1. Imaginary example of an unknown number of stationary whales making clicks as a boat (solid rectangle) passes by on a survey trackline (solid black line). Relative to the boat, the whales appear to be moving, and the illustration shows the positions of the whales in the surface plane at the moments they click (dots). Filled dots indicate clicks that are detected by the surveyors and grey dots that were not. Sperm whale clicks are typically produced in trains with longer silences in between. The number of clicks produced has been greatly reduced for the purposes of illustration. As radial distance from the boat increases, the probability of detecting a click is level or falls, and as perpendicular distance from the trackline increases, the probability of detecting a passing whale is level or falls. In this paper, a strip width is inferred within which it is supposed all whales will be detected (solid grey line).

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Table 1  
Main parameters and data.

Data	
$\underline{\tau} = (\tau_1, \tau_2, \dots, \tau_k)$	Detection times of clicks in a train.
$\underline{\delta t} = (\delta t_1, \delta t_2, \dots, \delta t_k)$	Measured time-of-arrival differences at hydrophone pair at detection times.
$\underline{b} = (b_1, b_2, \dots, b_k)$	Estimated bearings at those detection times.
$b(\tau_k)^{(j)}$	The $k$ th bearing $b_k$ detected at the $k$ th time $\tau_k$ for click train $j$ .
$\underline{b}(\underline{\tau})^{(j)}$	The bearings $\underline{b}$ detected at times $\underline{\tau}$ for click train $j$ .
$[\tau]_m$	The $m$ th detection period after resampling at a lower frequency $1/\Delta$ .
$b[\tau]_m$	Average of the bearings detected during the $m$ th detection time.
Constant/known parameters	
$\Delta$	Lower frequency sampling period.
$c$	Click rate of a whale that is in a clicking state.
$\underline{\eta} = (a, b, \rho)$	Vocalisation cycle parameters.
$w_y$	Strip half-width.
$w_r$	Radial detection limit.
$u$	Speed of sound in seawater.
$d$	Separation of hydrophone elements.
$m$	The minimum number of sampling intervals containing click detections required for an animal to be detected
Estimated parameters	
$\underline{X} = (x_0, y_0, v_x, v_y)$	Initial state vector, where $(x_0, y_0)$ = starting position, $(v_x, v_y)$ = velocity of whale relative to survey vessel.
$\underline{X}(t) = (x(t), y(t), v_x(t), v_y(t))$	Dynamical state vector.
$\underline{X}(t)^{(i)}$	The dynamical state vector for the $i$ th click train or combination of click trains.
$n_i$	Number of whales in aggregation $i$ within the strip half-width $w_y$ .
$\sigma_k^2$	Variance of the $k$ th bearing in a sequence of bearings.
$N$	Total abundance of whales in the survey region.

considerably more numerous than in this example. Some animals may be missed altogether if their clicks go undetected, and this must be taken account of in the estimate of abundance. In this paper, a strip width is inferred within which it is supposed all whales are detected, to allow analysis as a strip transect survey. For reference, the data and parameters used in the analysis are summarised in Table 1.

## 1. DATA

In the case of a two-element hydrophone where the axis of the elements is parallel to the survey transect, the basic data are:

times of detections of clicks  $\underline{\tau} = (\tau_1, \tau_2, \dots)$  at one hydrophone element; and

time-of-arrival differences of clicks between the two elements  $\delta t = (\delta t_1, \delta t_2, \dots)$ .

A sequence of bearings can then be estimated  $\underline{b} = (b(\tau_1), b(\tau_2), \dots, b(\tau_k))$  in which  $b(\tau_k)$  is the bearing  $b_k$  detected at time  $\tau_k$  with time-of-arrival difference  $\delta t_k$  using

$$\hat{b}(\tau)_k = \cos^{-1}\left(\frac{\delta t_k \times u}{d}\right) \quad (1)$$

where  $u$  is the speed of sound in water and  $d$  is the distance between the hydrophones.

This estimate is accurate in the 'far field', i.e. accurate at distances much greater than the separation of the hydrophone elements.

The data are ordinarily collected by digital equipment sampling at a 'high' rate, the sampling rate of the digitising equipment (e.g. often 48kHz), and the times of this high-frequency data are treated here as continuous. Because of the resulting high precision, the caret is dropped in the notation for  $b$  from here on.

Later in this paper the data are effectively resampled at a low frequency  $1/\Delta$ , with an average of the bearings taken over each sampling period  $\Delta$ . The reasons for doing so are to:

- (1) approximate normally distributed errors (as discussed in the development of eqn. 9);
- (2) reduce the computational load when forming the allowable combinations of click trains (see section 3).

Using square brackets we can indicate resampled time as

$$[t] = \text{floor}\left(\frac{t}{\Delta}\right) \quad (2)$$

and similarly we can write the  $m$ th resampled detection time as

$$[\tau_m] = \text{floor}\left(\frac{\tau_k}{\Delta}\right) \quad (3)$$

with corresponding average bearing of

$$b[\tau_m] = \overline{b(\tau_k)}, \Delta[\tau_m] \leq \tau_k < \Delta[\tau_m + 1] \quad (4)$$

and we can denote the whole sequence of resampled detection times as  $[\underline{\tau}]$ , and corresponding sequence of average bearings as  $\underline{b}[\underline{\tau}]$ .

## 2. ESTIMATE OF POSITION OF WHALE FROM A SINGLE CLICK TRAIN

### 2.1 Maximum Likelihood Estimation

The aim here is to find an estimate of whale position from the sequence of bearings of detected clicks. It is important to stress the assumption that the whales are at the surface. In fact they are often at depth. For example a whale at 1000m depth directly below the hydrophone will be assumed to be at the surface at a perpendicular distance of 1000m.

Following Nardone *et al.* (1984) we can define an initial state vector as:

$$\underline{X} = (x_0, y_0, v_x, v_y) \quad (5)$$

where  $(x_0, y_0)$  is the initial position of the whale relative to the boat, in directions parallel and perpendicular to the trackline respectively

and  $(v_x, v_y)$  is the velocity of the whale relative to the boat, assumed constant.

This determines a dynamical state vector at time  $t$  of

$$\underline{X}(t) = (v_x t + x_0, v_y t + y_0, v_x, v_y) \quad (6)$$

The parameters of  $\underline{X}(t)$  are given by  $\underline{X}$  (eqn. 5).

Given  $\underline{X}$ , we have estimates of the bearing to the whale at time  $t$  of:

$$\beta(t) = \tan^{-1}\left(\frac{v_y t + y_0}{v_x t + x_0}\right) \quad (7)$$

and a range at time  $t$  of:

$$r(t) = \left[ (v_x t + x_0)^2 + (v_y t + y_0)^2 \right]^{1/2} \quad (8)$$

Nardone *et al.* (1984) give the likelihood of the initial state vector  $\underline{X}$  with the observed data (bearings  $\underline{b}$  detected at times  $\underline{\tau}$ ), under the assumption of normally distributed bearing errors. With the present notation this is:

$$L_{b|\underline{\tau}}(\underline{X}) = \frac{1}{((2\pi)^n \det(\underline{W}))^{1/2}} \exp\left(-\frac{1}{2}(\underline{b} - \beta(\underline{\tau}))^T \underline{W}^{-1}(\underline{b} - \beta(\underline{\tau}))\right) \quad (9)$$

where

$$\underline{W} = \text{diag}(\sigma^2), \text{ in which } \sigma^2_k = \text{var}(b_k)$$

The notation for the subscript  $b|\underline{\tau}$  is here intended to indicate that the times of detections  $\underline{\tau}$  are given and there is no information at this stage about the process of signal production and detection which leads to these detection times.

The MLE estimates of  $\underline{X}$  have an estimated covariance matrix given by (Nardone *et al.*, 1984):

$$\hat{S} = [A^T R^{-1} W^{-1} R^{-1} A]^{-1} \quad (10)$$

where

$$A = \begin{bmatrix} \cos \beta(0) & -\sin \beta(0) & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots \\ \cos \beta(\tau_k) & -\sin \beta(\tau_k) & \tau_k \cos \beta(\tau_k) & -\tau_k \sin \beta(\tau_k) \\ \vdots & \vdots & \vdots & \vdots \\ \cos \beta(\tau_K) & -\sin \beta(\tau_K) & \tau_K \cos \beta(\tau_K) & -\tau_K \sin \beta(\tau_K) \end{bmatrix}$$

$R = \text{diag}(r^2)$  in which  $\underline{r}$  is the vector of range estimates,  $K$  is the total number of bearings in the sequence,

and with the time origin set here to the time of the first detection ( $\tau_1$ ).

Having an estimate of the covariance matrix provides information about the error structure of the locations. The two eigenvalues of the covariance matrix estimate the variances of the errors in the directions of its eigenvectors.

Note that if there are insufficient bearings in a sequence, then a positional estimate will be impossible or highly erroneous. If there are sufficient detection data available, and therefore sufficient bearings data, then a sampling period  $\Delta$  can be introduced such that the bearings used in eqn. 9 are *average* bearings over each such period. By the Central Limit Theorem, if there are enough bearings over each  $\Delta$ , then the average bearings will have normally distributed errors irrespective of the original distribution. This is the approach taken in this paper to satisfy the error assumptions of eqn. 9.

In the remainder of this paper a simpler situation is modelled, in which whales are assumed stationary and the vessel speed is constant and known (i.e. only  $x_0$  and  $y_0$  are free parameters in eqn. 5).

*Example*

An example of positional estimates of click trains made from real data using this approach is shown in Fig. 2. In this example the whales are assumed stationary, the boat moving in the x direction (along the transect) at speed  $s_x$ , (i.e. the state vector is  $\underline{X} = [x_0, y_0, -s_x, 0]$ ) and a global estimate (i.e. for all click trains) of the variance of the bearings has been made from the data.

The ellipses around the location estimates (dots) are approximate error regions, using the eigenvalues of the estimated covariance matrix. Intuitively, the shape corresponds well with the crossings of the bearings.

**3. ESTIMATE OF NUMBER OF WHALES IN AN AGGREGATION FROM MANY CLICK TRAINS**

The more general and often realistic case of data from several whales present at once in an aggregation (e.g. Figs 1 and 2) is covered here. The approach used is based on the idea of generating all possible arrangements of click trains, that is, all the different ways click trains might be matched together as different whales. In this respect, it resembles the work by Hiby and Lovell (1998), which generated all possible arrangements of detections from a double-platform survey.

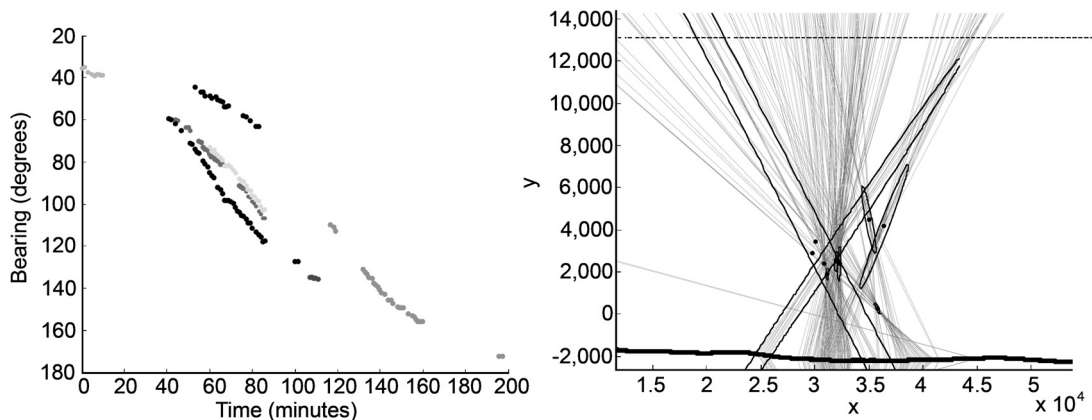


Fig. 2. Left: Bearing-time plot of received click trains. Here an analyst has grouped together clicks into eight different trains, but trains separated by prolonged silence cannot be matched together objectively. Right: Estimated positions of sources of click trains (single dots) with error ellipses. The boat track is shown along the x-axis and the measured bearings as grey lines.

### 3.1 Arrangements of click trains in an aggregation:

Define

$T = \{1, 2, \dots\}$  to be the set of indices of the click trains, of size  $|T|$ .

and

$S = \{S_1, S_2, \dots\}$  to be the set of allowable combinations of the elements of  $T$ , of size  $|S|$ .

$G = \{G_1, G_2, \dots\}$  to be the set of possible arrangements of click trains, of size  $|G|$ . Each element of  $G$  is an arrangement: it is a set containing disjoint combinations of the elements of  $S$ , that is also exhaustive, in the sense that it contains every element of  $T$ .

In the present analysis, the number of possibilities is constrained; for example, simultaneous click trains cannot be from the same whale. The total number of possible subsets of  $T$  is  $2^{|T|} - 1$ , but the total number of allowable click train combinations is less (since some combinations are disallowed), so that:

$$|S| = \mathbf{1}^T (\mathbf{I} - \mathbf{A}_T)^{-1} \mathbf{1} \quad (11)$$

where

$\mathbf{1}$  is a column vector of ones,

$\mathbf{I}$  is the identity matrix, and

$\mathbf{A}_T$  is an adjacency matrix between click trains, that is,  $a_{ij} = 1$  if  $T(i)$  followed by  $T(j)$  is potentially the same whale, and 0 otherwise.

Define  $Q$  as the  $(|G| \times |S|)$  matrix in which

$$q_{ij} = \begin{cases} 1, & \text{if } S_j \in G_i \\ 0, & \text{otherwise} \end{cases}$$

Each row of  $Q$  represents an arrangement  $G_i$ , as defined above.

The number of whales in each arrangement is given by the  $(|G| \times 1)$  vector:

$$\underline{w} = Q \mathbf{1} \quad (12)$$

where  $\mathbf{1}$  is a column vector of ones.

#### Example

Consider the imaginary case shown schematically in Fig. 3 containing 3 click trains.

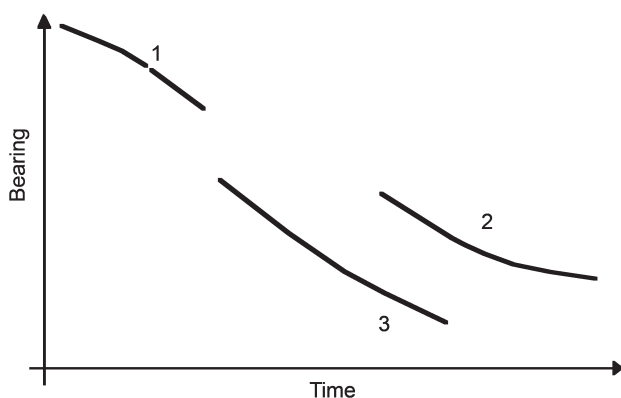


Fig. 3. Bearing-time plot for whale trains in the example. Trains 2 and 3 must be from different whales since they overlap in time.

In this case the various sets defined above are:

$$T = \{1, 2, 3\}$$

$$S = \{\{1, 3\}, \{1, 2\}, 1, 2, 3\}$$

$$G = \{\{\{1, 3\}, 2\}, \{\{1, 2\}, 3\}, \{1, 2, 3\}\}$$

so that  $|T| = 3$ ,  $|S| = 5$ ,  $|G| = 3$

Note that  $S$  does not include the combinations  $\{2,3\}$  or  $\{1,2,3\}$  because click trains 2 and 3 overlapped in time and could not have come from the same whale. So the number of allowable click train combinations ( $|S| = 5$  in this case) is less than the total number of possible subsets of  $T$  ( $2^3 - 1 = 7$ ).

The adjacency matrix in this case is

$$\mathbf{A}_T = \begin{pmatrix} 0 & 1 & 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

The lower triangle in the matrix is all 0 because the trains are sequenced in time (if train  $i$  follows  $j$  then  $j$  cannot follow  $i$ ). The element at row 2 and column 3 is 0 because train 3 overlaps in time with train 2 and so cannot be from the same whale. Eqn. 11 gives  $|S| = 5$  as expected.

The matrix of arrangements is:

$$Q = \begin{bmatrix} 1 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 & 1 \\ 0 & 0 & 1 & 1 & 1 \end{bmatrix}$$

and the number of whales over the arrangements is:

$$\underline{w} = Q \mathbf{1} = \begin{bmatrix} 2 \\ 2 \\ 3 \end{bmatrix}$$

### 3.2 Estimate of numbers of whales based on positional likelihood

Define  $l_j$  to be the likelihood associated with the  $j$ th click train combination  $S_j$  as given by eqn. 9. The vector of data is obtained by combining the data associated with the component click trains, the combined data being  $b[\underline{\tau}]^{(j)} = \bigcup_{i \in S_j} b[\underline{\tau}]^{(i)}$  with the superscripts indicating the  $i$ th click train and the  $j$ th combination of click trains. The likelihood of the combined data is given by eqn. 9. Define  $\underline{l}$  to be the  $(|S| \times 1)$  vector of all these  $l_j$ ,  $j = 1 \dots |S|$ , i.e. a vector of the likelihoods for each click train combination:

$$l_j = L_{b[\underline{\tau}]^{(j)}}(\underline{X}^{(j)}) \quad (13)$$

The likelihood considered as a function of the number of detected whales  $n$  is given by:

$$L(n) = \sum_{w_i=n} \exp(q_i \log \underline{l}) \quad (14)$$

where  $q_i$  denotes the  $i$ th row of the matrix  $Q$ .

The likelihood of any arrangement is from a model with a number of parameters that depends on the number of whales and their associated state vector  $\underline{X}$ . For example, in models in which the relative velocity of the whales is assumed constant and known, there are two free parameters for each whale. For models in which the whales have a constant

but unknown velocity, there are four free parameters for each whale. There may also be additional free parameters relating to the variances of the bearings,  $\sigma_k^2$ , if these are estimated.

When considering all the arrangements to estimate n using eqn. 14, the AIC statistic can be used to incorporate a penalty for the number of free parameters q:

$$AIC = -2 \log L + 2q \tag{15}$$

If there are p free parameters for each whale, then combining eqns. 14 and 15 gives:

$$AIC(n) = -2 \log L(n) + 2np \tag{16}$$

The estimate of the number of observed whales is the value of n corresponding to the minimum AIC.

**4. MODEL OF VOCALISATION CYCLE**

**4.1 Model of alternating clicking/silent states**

Sperm whale vocalisations are quite predictable and closely related to the dive cycle, which is itself quite regular partly because of the requirement that the whales breathe. Regular and fairly constant clicking occurs for most of the time that the whales are submerged and generally ceases when the whales are at the surface. The purpose of a model for what is the whales’ ‘intermittent availability’ for detection (Laake and Borchers, 2004) is to estimate a detection function (see Estimate of a Radial Detection Function, below).

A mathematical model of sperm whale vocal behaviour can therefore be provided by an ‘alternating renewal process’ (Cox 1962). The whales alternate between a clicking state of duration  $T_c$  during dives and a silent state of duration  $T_s$  while at the surface. This gives the sequence  $T_{c_1}, T_{s_1}, T_{c_2}, T_{s_2}, \dots$  where the alternating silent or clicking periods  $T_s$  or  $T_c$  are independently and identically distributed.

The probability  $\pi_c(t)$  that a whale is in a clicking state at time  $t$ , given that it was in a clicking state at time 0, can be derived analytically using Laplace transforms (Cox, 1962). If it is assumed that the statistical process started a long time ago (long before time 0), then this is termed an ‘equilibrium’ alternating renewal process. In the equilibrium renewal process, the observer is effectively starting to observe at a random moment during the clicking state. Alternatively, the ‘ordinary’ alternating renewal process gives the probability that the whale is in a clicking state given that it *entered* a clicking state at time 0.

Using  $\Gamma$ -distributions for the two probability density functions (pdfs) with positive integer shape parameter considerably simplifies the analysis. This restriction gives an Erlang distribution. The duration of the clicking state then has pdf given by

$$f(t, a, \rho) = \frac{\rho(\rho t)^{(a-1)} \exp(-\rho t)}{(a-1)!} \tag{17}$$

where  $a$  is the shape parameter (a positive integer), and  $\rho$  is the scale parameter. The duration of the silent state has a similar distribution, with positive integer shape parameter  $b$ . A further assumption made here is that the two Erlang distributions share the scale parameter  $\rho$ . Restricting the shape parameter to integer values still gives a wide family of distributions.

The parameters of both distributions can be collected together in a vector  $\eta = (a, b, \rho)$ . In the analysis described in this paper, it is assumed that this parameter vector is fixed and homogenous throughout the population of whales being surveyed.

Assume that detection of a whale click is immediate and certain when it is made within some range (not yet specified). Suppose the whale passes abeam at time  $t_0$ , its closest approach to the survey vessel, and when detection is most certain. Then either the whale is already in a clicking state at time  $t_0$ ; or it is in a silent state at time  $t_0$  and enters a clicking state straightaway or more likely some time later.

In the first case, the clicking state is joined at a random moment in time (assuming the whale’s vocalisations are unrelated to position of the survey vessel), and the first detected click is (nearly) immediate ( $\tau_1 \approx t_0$ ). The probability of being in a clicking state from then is described by an ‘equilibrium’ renewal equation, with the Laplace transform (Cox, 1962) of:

$$\mathcal{L}\{\pi_c(t - \tau_1)\} = \frac{a}{a+b} + \frac{\rho}{a} \left\{ \frac{ab}{\rho(a+b)s} - \frac{\{(\rho+s)^a - \rho^a\}\{(\rho+s)^b - \rho^b\}}{s^2\{(\rho+s)^{a+b} - \rho^{a+b}\}} \right\} \tag{18}$$

In the second case, the whale is detected when it later enters a clicking state, so the first click detection is at  $\tau_1 \geq t_0$ . The probability of being in a clicking state after the first click is described by an ‘ordinary’ renewal equation with the Laplace transform:

$$\mathcal{L}\{\pi_c(t - \tau_1)\} = \frac{1 - \rho^a / (\rho + s)^a}{s\{1 - \rho^{a+b} / (\rho + s)^{a+b}\}} \tag{19}$$

These models are plotted in Fig. 4 using the empirical parameter values  $\eta$  estimated in the next section.

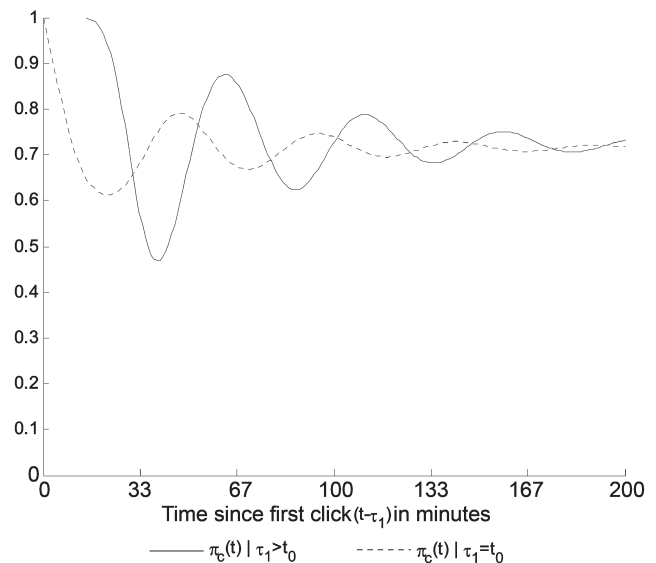


Fig. 4. Probability that a whale is clicking as a function of time since the first detected click at  $\tau_1$ . It is assumed here that detection is certain and immediate if a whale is in a clicking state. If as the whale passes abeam at time  $t_0$ , the time of the first detection  $\tau_1 = t_0$ , then the observer has joined a clicking state at a random moment and an ‘equilibrium’ model is used. If  $\tau_1 > t_0$ , the observer has joined the beginning of a clicking state and an ‘ordinary’ model is used. See text and Fig. 5 for further details.

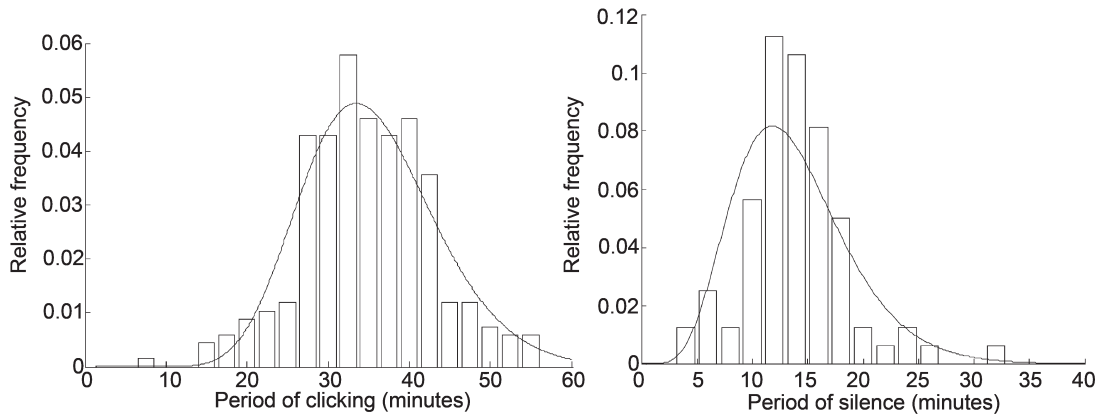


Fig. 5. Clicking and silent periods in minutes (data from Teloni, 2005) with fitted distributions.

#### 4.2 Estimate of parameters from real data on durations of vocal and silent states

The results of fitting to empirical data from Teloni (2005) are shown in Fig. 5. These results were obtained by fitting gamma distributions and rounding the shape parameters, giving  $\eta = (17, 7, 0.5)$ . The two distributions have means of 14 minutes (silent state) and 34 minutes (clicking state).

The fit of the model to these data is not particularly good; for example the data for the clicking periods seems more peaked than the model. However the data itself may be somewhat problematic, as it is not clear how click trains were matched in the original analysis, especially when intervals of silence were long. Under the circumstances the model seems a reasonable first approximation.

#### 5. ESTIMATE OF A RADIAL DETECTION FUNCTION

Using the vocalisation cycle model of the previous section, we can go on to estimate the probability of detecting a clicking whale over a short time interval  $\Delta$ .

Let  $h(r; \underline{\phi})$  be a radial detection function for an individual sperm whale *click* produced at range  $r$ , with parameter vector  $\underline{\phi}$ . Assume that  $h(0) = 1$ , i.e. a click at radial distance 0 will definitely be detected.

Let  $c$  be the click rate, assumed constant, of a whale that is in a clicking state. The expected number of clicks in a sampling interval is then  $c\Delta$ .

Let  $f(r; c, \underline{\phi}, \Delta)$  be the probability of detecting *at least one* click from a clicking whale at range  $r$  over a sampling period  $\Delta$ . If there are negligible changes in  $h(r)$  over a sampling period, then  $f$  will be:

$$f(r; \underline{\phi}, c, \Delta) = 1 - (1 - h(r; \underline{\phi}))^{c\Delta} \quad (20)$$

The constant parameters  $\Delta$  and  $c$  are omitted as arguments from this point on.

To estimate the parameters  $\underline{\phi}$  in eqn. 20, recall that:

- (i) the estimated range to a whale as a function of time, given its position vector, is  $r(\underline{X}(t))$  (eqn. 8); and
- (ii) the probability  $\pi_c(t)$  that a whale is in a clicking state at time  $t$  given that it was in a clicking state initially, was given in eqns 18 and 19.

For the observed detection times  $[\underline{\tau}]$  in the click train of an *individual* animal passing by given  $\underline{X}$  and whose vocalisation cycle vector  $\underline{\eta}$  is also known, the likelihood of the detection parameters  $\underline{\phi}$  is then:

$$L_{[\underline{\tau}]}(\underline{\phi} | \underline{X}) = \prod_{[t]=\varepsilon_1}^{\varepsilon_2} \{f(r[t])\pi_c[t]\}^{\delta[t]} \{1 - f(r[t])\pi_c[t]\}^{(1-\delta[t])} \quad (21)$$

$$\text{where } \delta[t] = \begin{cases} 1 & \text{if } [t] \in [\underline{\tau}] \\ 0 & \text{if } [t] \notin [\underline{\tau}] \end{cases},$$

i.e. a binary variable indicating whether or not time  $[t]$  was one of the detection times  $[\underline{\tau}]$ , and

$\varepsilon_1, \varepsilon_2$  are the times at which the whale is first and last within radial detection limit  $w_r$ .

When there is more than one whale, the likelihoods (eqn. 21) for each can be multiplied together.

#### 6. ESTIMATE OF ABUNDANCE

This paper uses a strip transect approach to estimate abundance, i.e. where detection of whales is assumed to be certain within the strip (and detections beyond it are excluded). The smaller survey strip compared to that which might be used in distance sampling means a potential loss of precision in the analysis, but could allow:

- (1) more objective identification of the click trains and the size of each aggregation, using a statistical rather than heuristic approach;
- (2) more detailed justification of the detection function used; and
- (3) a less labour intensive analysis.

The radial detection function from section 5 can be used to identify or test the strip size within which detection of a whale is certain. In section 7.5, simulations with some estimated (radial detection function,  $\underline{\phi}$ ) and assumed (vocalisation cycle,  $\underline{\eta}$ ) parameter values are carried out to support the strip half-width used.

If detection is certain, the total number of whales  $\hat{n}$  within the survey strip of half-width  $w_y$  is the sum of  $\hat{n}_i$  over all aggregations  $i$ . With appropriately random transects and

equal coverage probability, the estimate of the number of whales  $\hat{N}$  in the entire survey area  $A$  is:

$$\hat{N} = \frac{A\hat{n}}{2Lw_y} \quad (22)$$

where  $L$  is the total survey line length. If the strip transect approach is valid (i.e.  $w_y$  is known) then the only uncertain element is  $\hat{n}$ . Lognormal-based confidence limits on  $\hat{N}$  can be obtained using the survey transects as sampling units to estimate variance (Buckland *et al.*, 2001; Borchers *et al.*, 2002).

**7. SOME SIMULATION RESULTS**

A set of simulations were carried out to test various aspects of the method. These were not intended to provide comprehensive results and further investigations are needed. Some important common assumptions, also shared with the Mediterranean analysis in section 8, were:

- (1) the whales are stationary;
- (2) the boat motion is constant and known ( $v_x = 3 \text{ ms}^{-1}$  and  $v_y = 0 \text{ ms}^{-1}$ );
- (3) the ‘far-field’ approximation (eqn. 1) for the bearing from a hydrophone pair is adequate;
- (4) whales click at a constant rate when in a clicking state ( $1.2 \text{ s}^{-1}$ );

- (5) the bearings have the same errors,  $\sigma_j^2 = \sigma^2$  for all  $j$  (in reality, errors increase as angles approach the hydrophone’s axis); and
- (6) the whale is at the surface (i.e. not diving)

**7.1 Error structure of position estimates**

Simulations were carried out in which the individual bearing errors were assumed to be independently and identically normally distributed with a known variance  $\sigma^2$ , which was then estimated in the simulations. In terms of the timing of the detected bearings, three example scenarios were examined, where the whale’s clicks were detected (a) for 10 minutes abeam of the boat, (b) for 10 minutes ahead of the boat and (c) for periods given by the alternating model for the vocalisation cycle.

Examples of bearings and detection times from the latter two cases are illustrated in Fig. 6, along with some examples of the estimated positions and errors. (The results for case (a) are qualitatively similar to case (c) and are not shown). The true initial positions of the whale in cases (b) and (c) were  $(x_0, y_0) = (8,000, 5,000)$ , and  $(x_0, y_0) = (900, 5,000)$  in case (a). The error structure (ellipses), as determined from the estimated covariance matrix are in agreement.

The results of the simulations are shown in Table 2. In these examples where bearing errors are constant, estimation

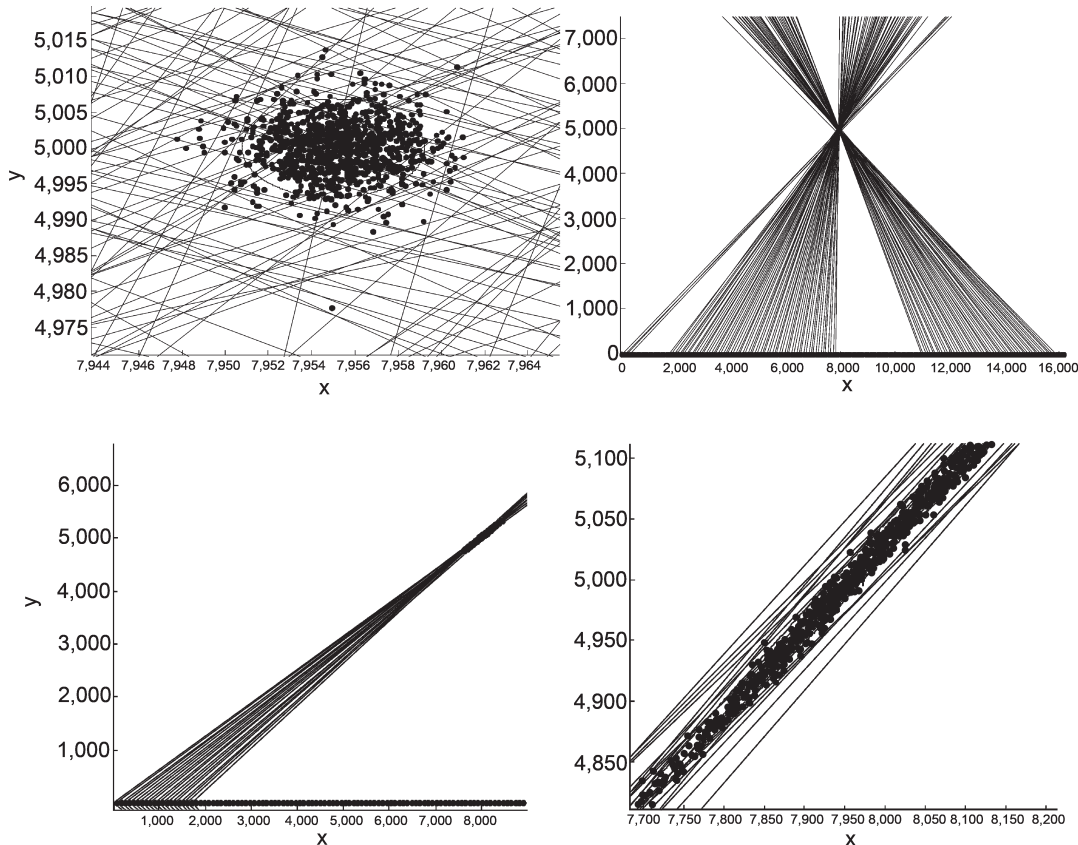


Fig. 6. Illustration of simulations of the estimation of a stationary whale’s position from the detected bearings, as a boat passes by on a transect left-to-right along the x-axis at known speed. For clarity, the bearings from a single simulation run only are shown (grey lines). Position estimates of each simulation are shown as black dots. Ellipses are error regions based on the average of the estimated covariance matrices.

Top figures: A sequence of bearings made according to the vocalisation cycle model, and a close-up of the estimated positions.

Bottom figures: A 10 minute sequence of bearings detected when the whale is at some distance ahead of the boat.

Table 2

Results of simulations to estimate the position of a whale at known fixed position (see Fig. 6 for illustrations of these scenarios). 1,000 trials each.  $b(\ )$  is the bias and  $sd(\ )$  the standard deviation. For the burst scenarios (10-minute sequences) the total number of clicks detected 720 and number of bearings per sampling period  $n=36$ .

Position scenario	$\sigma^2$	Clicking	$\hat{b}(\sigma^2)$	$\hat{sd}(\sigma^2)$	$\hat{b}(x_0)$	$\hat{b}(y_0)$	$\hat{sd}(x_0)$	$\hat{sd}(y_0)$
Ahead	1	Burst	-0.04	0.31	36.4	146.8	24.2	103.6
Ahead	10	Burst	-0.54	3.2	53.0	449.1	36.6	317.6
Ahead	1	Model	0.14	0.27	0.16	2.20	0.03	3.7
Ahead	10	Model	1.09	2.57	-0.13	6.8	-1.0	10.79
Abeam	1	Burst	0.03	0.37	2.38	18.7	3.32	32.7
Abeam	10	Burst	-0.54	3.11	2.08	10.6	16.1	108.0

Table 3

Results of simulations to estimate number of whales  $n$ .  $|G|$  is the number of (valid) arrangements and  $|S|$  is the total number of (valid) train combinations. See text for further details. There were 50 simulations in each set.

$n$	Simulation set	Goodness-of-fit processing?	$\bar{ G }$	$sd( G )$	$\max( G )$	$\bar{ S }$	$sd( S )$	$\max( S )$	$\bar{n}$	$sd(n)$
6	1	n	21.8	57.9	281	10.9	4.8	25	6.08	0.34
8	2	n	1,288.0	451.2	2756	15.76	7.3	44	8.02	0.55
10	3	n	936.2	4,266.6	27,720	22.1	11.6	65	10.1	0.53
6	4	y	4.0	4.2	19	8.6	2.3	13	6.0	0.35
8	5	y	17.2	41.6	227	12.6	4.0	25	8.04	0.53
10	6	y	28.6	47.7	232	16.7	4.3	26	10.1	0.52

of  $\sigma^2$  seems to be fairly accurate. There is a fairly low bias in the estimation of the (along-axis) position  $x_0$ . The bias in estimates of  $y_0$  (perpendicular to axis) is higher than for  $x_0$ , but still quite accurate, except in the case of a burst of a click train ahead of the boat (b).

In summary, the estimates of position are accurate (low bias) and precise (low variance) when bearings are obtained at widely different angles, i.e. when whales go past the beam during a click sequence (a), or when a series of click sequences are obtained over a long period of time (c). However, when whales are only detected a long way ahead (or behind), bearings are nearly parallel and the errors are relatively large in the direction of the bearings.

## 7.2 Estimation of number of detected whales in an aggregation

Aggregations of whales of known size were simulated passing a survey vessel and the numbers of whales in the aggregations were estimated. The whales vocalised according to the model outlined in section 4 and the radial detection function had parameter values estimated from the Mediterranean survey (section 8). Various parameter values

Table 4

Parameter values used in simulations to estimate whale numbers (section 7.2) and the Med. survey data (section 8). See text for further details.

Click rate when in a clicking state (c)	1.2 per sec.
Strip half-width ( $w_y$ )	5km
Radial detection limit ( $w_r$ )	15km
Vocalisation cycle parameters ( $\eta$ )	(17, 7, 0.5)
Speed of sound in water (u)	1,500 m/s
Hydrophone separation (d)	3m
Minimum number of detections in a train (m)	10
Sampling period ( $\Delta$ )	30 secs
Vessel velocity ( $v_x, v_y$ )	(3, 0) m/s
Whale velocity ( $s_x, s_y$ )	(0,0) m/s
Condition limit	1e8
Significance level for goodness-of-fit comparison ( $\alpha$ )	1/1,000

are shown in Table 4. As in the Mediterranean analysis, the variance of the bearings was estimated separately for each aggregation.

## 7.3 Elimination of click train combinations

Trains or combinations of trains were eliminated (i.e. treated as undetected) if any of the following conditions applied:

- (1) the number of detections in the train (i.e. number of sampling intervals containing detections) was less than the minimum number allowed;
- (2) the lower limit of  $y$  was beyond  $w_y$ ;
- (3) the position-fitting routine failed to converge;

There were further criteria for combinations of trains only:

- (4) A nearly-singular estimated covariance matrix (eqn. 10) was obtained, where the condition number of the matrix was larger than threshold. This removes unreliable location estimates.

To reduce the computational burden, before further processing a goodness-of-fit test compared the log-likelihood of a particular click train combination with the sum of the log-likelihoods of its  $s$  component click trains. Denoting these as  $\log L_s$  and  $\log L_T$  respectively, a statistic is calculated as  $2(\log L_T - \log L_s)$ . Since in these simulations the relative velocity of the boat is assumed known, there are only three free parameters for any click train combination (the position of the whale  $x_0$  and  $y_0$ , and an estimate of the variance of bearings, assumed the same for all trains in the aggregation).  $L_T$  and  $L_s$  are associated with  $2s + 1$  and 3 degrees of freedom respectively. The statistic was compared with a critical value of  $\chi^2_{\alpha, 2s-2}$ , and click train combinations rejected if necessary;  $\alpha$  was chosen to keep the rate of rejected combinations fairly low.



**7.4 Simulation steps**

Data were simulated in steps (1)–(4):

- (1) generate  $j = 1, \dots, n$  whales with  $\underline{X}^{(j)} = (x_0, y_0, v_x, v_y)$ ,  
 where  $y_0 \sim \text{UNIF}(0, w_y)$   
 $x_0 = \sqrt{(w_x^2 - y^2)}$   
 $v_x, v_y$  are known
- (2) generate observed detection times  $\tau_i$  for each click train using  $\eta, \phi, \underline{X}^{(j)}$ ;
- (3) generate observed bearings  $\underline{b}$  for each click train using  $\tau_i, \underline{X}^{(j)}, \sigma^2$ . Homogeneous bearing errors,  $\sigma_i^2 = 1$  were assumed;
- (4) click trains are separated into different whales when not meeting a joining criterion (details below). An example of some simulated data is shown in Fig. 7.

Estimates were simulated in the remaining steps:

- (5) estimate  $\underline{X}^{(i)}$  ( $i = 1 \dots |T|$ ) for each train using eqn. 9;
- (6) eliminate trains in the set  $T$  that are invalid;
- (7) form the adjacency matrix representing valid train combination pairs (some pairs are invalid e.g. if simultaneous);
- (8) form the set  $S$  representing the allowable train combinations;
- (9) eliminate train combinations in the set  $S$  that are invalid;
- (10) estimate  $\underline{X}^{(j)}$  ( $j = 1 \dots |S|$ ) for each combination of trains using eqn. 9;

(11) form the set  $G$  representing all the possible arrangements; and

(12) estimate  $n|\{\underline{X}^{(j)}\}$  using eqn. 16

The results of the simulations are given in Table 3, and show that removing train combinations based on goodness-of-fit clearly reduces  $|S| |G|$  and therefore the computational load. There is a small positive bias in estimates of  $n$ .

**7.5 Simulated distribution of perpendicular distances of detected whales**

Simulation steps (1)–(4) of 7.4 were used to simulate click trains for single whales (other steps relating to combining ambiguous trains were omitted since these relate to aggregations of whales). Various parameter values used are shown in Table 4. The parameters  $\phi = (2171, 5.01)$  were those estimated in section 8. Trains were rejected if they satisfied any of the conditions outlined in section 7.2, i.e. they were treated as nondetections. In a trial with 1,000 runs, 999 were detected. The simulations appear to support the assumption of certain or near-certain detection of whales within the strip, i.e.  $g(y) = 1$  from  $y = 0$  to 5km.

**8. APPLICATION TO A REAL SURVEY**

The methods described here were applied to data acquired on a real survey of the southwestern Mediterranean. in 2004, described in Lewis *et al.* (In prep.). Click trains from the survey were identified and joined together by an analyst. In Lewis *et al.* (In prep.), the positions of the whales were estimated by the method described in this paper, and those positions were used to carry out a conventional distance sampling analysis. The alternative analysis given here avoids

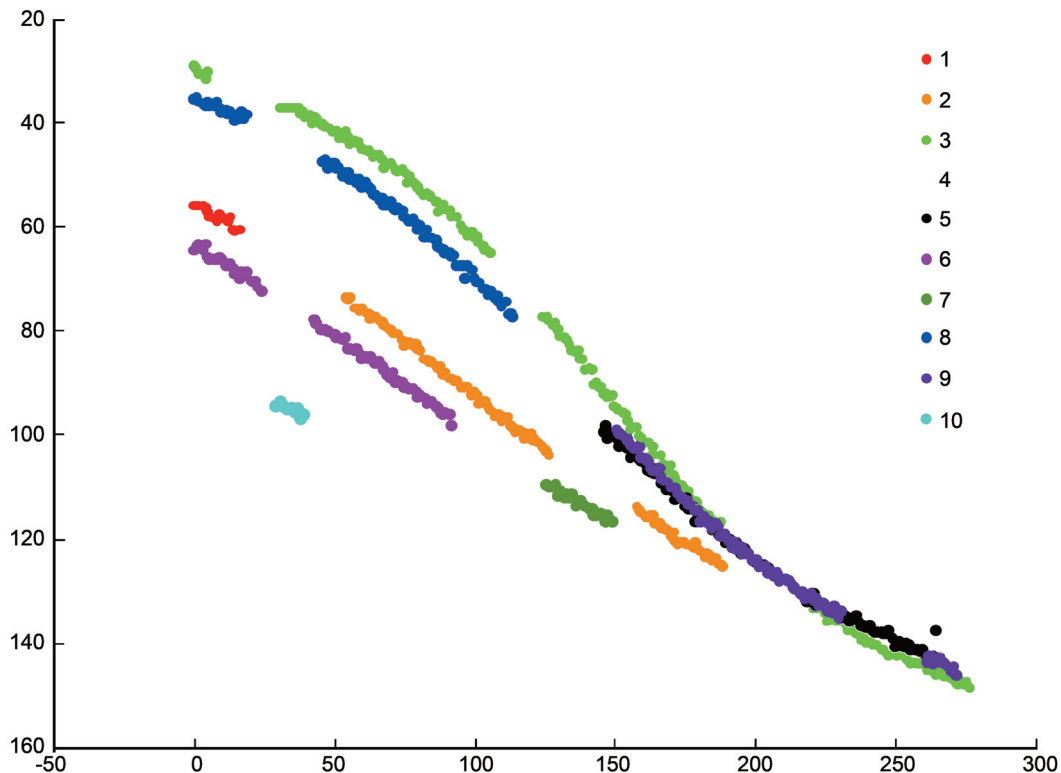


Fig. 7. Example bearing-time plot of simulated data. The simulated click trains, in this case from six vocalising whales, were broken apart if there was an interval of silence of more than the average period of silence, 14 minutes. This gave 10 click trains that required matching in order to estimate the number of whales present.

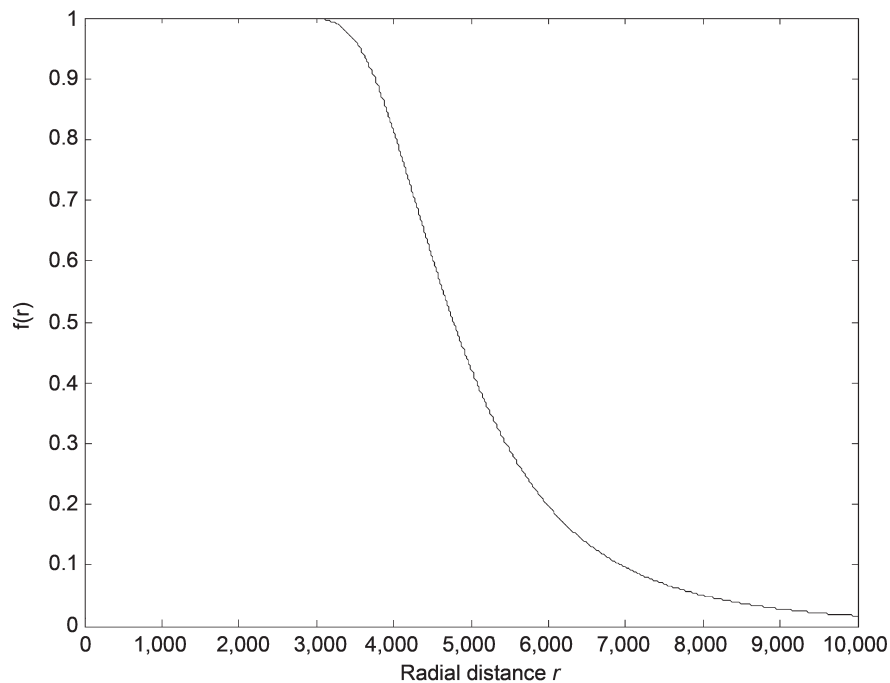


Fig. 8. Curve showing the estimated probability of detecting a whale at radial distance  $r$  (metres), clicking at rate  $c = 1.2$  per sec, over a time period  $\Delta = 30$  seconds, using estimates for the Mediterranean. (See section 8).

subjective joining of click trains when separated by more than a certain interval (see below) and treats the survey as a strip transect.

The parameter values shared with the simulations in section 7.2 are shown in Table 4. Eliminations of click trains or click train combinations were as described in section 7.3. The click trains for the analysis were created by breaking up the click trains originally matched by the analyst. The criterion used was that any of the original trains separated by more than 2 minutes were treated as different trains. A further step in processing the data was a decision to choose the most likely side for any click train, based on eqn. 9.

After estimating the number of whales, only the arrangements corresponding to that number of whales are retained before estimating  $\hat{\phi}$  as described in section 5. For this, the equilibrium vocalisation model (section 4) was used. This is justified by choosing a click randomly from a click train. For this, the click train made closest to the vessel, with the highest detection probability, is chosen. This is to minimise any consequences of missed detections.

The resulting abundance estimate for the entire survey region with 95% lognormal confidence limits was  $\hat{N} = 652$  (336, 1265). The estimated parameter  $\hat{\phi} = (2171, 5.01)$  and the corresponding function  $f(r; \hat{\phi}, \Delta, c)$  is shown in Fig. 8.

## DISCUSSION

The analysis approach outlined here is intended to allow line-transect surveys of aggregated sperm whales to be carried out without the need for visual estimates of the number of whales in aggregations, nor for analysts to make the more subjective links between click trains during analysis. By incorporating all (allowable) arrangements of click trains into the analysis the method attempts to draw more objective conclusions than would be obtained by a visual count of whales or a manual assessment of the number of whales in

the acoustic data. Analysis still begins from a dataset made by an analyst grouping clicks together into trains. This prior process is labour-intensive, and would benefit from automation.

Stopping for visual estimation of whale numbers during an acoustic line-transect survey is worth avoiding where possible: it is time-consuming and can disrupt the survey and disturb the whales. It is also potentially inaccurate: for example, it is difficult to count dispersed whales visually, many of which will be asynchronously submerged for long periods; and when stopping there is a risk of counting whales that would otherwise have been located beyond the survey strip, or not counting whales that would otherwise have been within the survey strip.

Hiby and Lovell (1989) developed a method ('Cartwheels') for acoustic point transect surveys of sperm whales. One immediate advantage is that it is a much more concise analysis than that presented here. In addition, although based on a point transect approach, it is not necessary to interrupt the line transect survey in order to carry out point counts as long as the distance travelled by the vessel during the counts is small relative to the detection range (Gillespie, 1997). Using point transects at intervals means that some information from the survey is not used, but this may be acceptable in many contexts. Hiby and Lovell (1989) showed that the method is quite insensitive to clustering of the whales. The main drawback of the method, if any, is that it uses counts of whales within sectors (octants) of a circle, and it may be problematic to estimate these numbers reliably within large aggregations. Whitehead (2009) provided a more general discussion of this sort of approach.

## Localisation

Given the large number of bearings expected from a passing sperm whale well within detection range, the accuracy of the

location estimate is potentially quite high, and the errors are quite well-defined (unlike the estimates of location made during conventional visual surveys). Nevertheless some disadvantages of the bearings-only solution remain, as identified below:

- (1) The model still assumes that whales either are stationary or at least do not accelerate. The latter assumption is the more realistic but still a simplification. Movement of the whales is therefore a source of further error.
- (2) Position estimates are produced in two dimensions (at the surface) that will be somewhat biased, as in reality the whales are often diving. One consequence of this is that some diving animals within the strip width might be treated as if they are beyond it, and not counted. This is unlikely to be problematic if the strip width is large enough (see Lewis *et al.*, In prep., for further discussion). Another is that the estimate of the number of whales, which is based on positional information, could be biased. This difficulty has not been explored in this paper.
- (3) There is left-right ambiguity: two surface solutions are produced, one on each side. The ambiguity can be resolved if there are known accelerations of the receiving hydrophones, with measurements taken from, for example, boat GPS or heading sensors on the hydrophones. The Mediterranean survey (Lewis *et al.*, In prep.) used deliberate zigzagging of the survey vessel.

A general source of error for towed localisation systems is uncertainty about the position of the receivers (hydrophones) in the system, especially as the hydrophone cable weaves about in the water, or the vessel wanders from its course. These uncertainties could be reduced with improved accuracy of GPS systems in the survey vessel, ‘inertial navigation’ systems in the receivers, or sound sources of known location.

More elaborate acoustic detection systems with more (>2) hydrophone elements have been applied to sperm whales (e.g. Thode, 2005; Teloni, 2005) and can provide better, even instantaneous, estimates of location. If available, this kind of information would allow a simpler and more robust analysis of location than that used here. On the other hand, this hardware is harder to build and deploy, and is more expensive. Because there are typically long intervals of relative silence between trains, matching trains across these intervals would remain a problem, even if acoustically-derived locations were very accurate.

### Vocalisation cycle modelling

The analysis described here assumes that a sperm whale clicks continuously when in a vocalising state, which is somewhat simplistic. Whales are not always completely silent when at the surface either (e.g. Wahlberg *et al.*, 2005), but it is assumed here that surface vocalisations are relatively rare. Further examination of the consequences of a failure to meet these assumptions is required.

In this paper, the model for the time-dependent vocalisation state probabilities (section 4) does not further consider the consequences of false negatives in this element of the analysis, i.e. where clicks are missed because detection

is uncertain. Using a more limited strip half-width and, for any particular whale, using the closest click train to the survey boat to determine the vocalisation state clearly moderates any problem this may cause, but this is an area needing further investigation.

It is assumed here that the vocalisation parameter values  $\underline{\eta}$  are known, corresponding to models fitted to data from the northwest Mediterranean from Teloni (2005). Three problems with this approach are that:

- (1) the empirical data and/or the fit of the model to it could be improved (see section 4);
- (2) the data used are (possibly) from a different population and a different behavioural context; and
- (3) the parameter values are assumed homogenous throughout the population, whereas it is quite likely that there will be, for example, gender and age differences in diving and clicking behaviour.

### Short click trains

Short click trains (trains with few bearings) are problematic in several ways:

- (1) it may not be possible to localise them (maximisation of the likelihood fails);
- (2) solutions may have large errors (if the bearings are nearing parallel);
- (3) they quickly multiply the number of possible arrangements and the required computations; and
- (4) it can be difficult to resolve the side-to-side ambiguity.

These issues have not been investigated in detail in this paper. Instead, short click trains and/or those with these characteristics were removed near the beginning of processing. Removing short trains should have relatively little effect on estimations of group size if, as seems likely, the remaining clicks from a whale enable a good location estimate.

A particular problem, if they are not removed, is that short click trains may not be correctly assigned to the correct side, and if this happens is likely to cause an upward bias in the estimates of aggregation size. Some potential technological solutions to side-to-side ambiguity have been mentioned above.

### Assumption of certain detection

Part of the method outlined attempts to identify a perpendicular truncation distance  $w_y$  within which detection of whales is certain within the survey strip. Some supporting evidence for the value of  $w_y$  chosen in analysis of the Mediterranean survey (5km) has been given. Some estimates of the perpendicular detection function  $g(y)$  from other surveys seem to be broadly consistent with this value (e.g. Lewis *et al.*, In prep.; Leaper *et al.*, 2000) and some are not (e.g. Hastie *et al.*, 2003, Barlow and Taylor, 2005), and background noise is likely to account for much of this variation. Acoustical considerations by Mellinger *et al.* (2003) with their particular setup support the idea of more-or-less certain instantaneous detection  $h(r)$  of a clicking (diving) sperm whale to a range of about 5km. Ward *et al.*

(2012) state ‘all vocalizing sperm whales within a 3.8km radius of a hydrophone are assumed to be detected’, this being the average spacing of their static hydrophones, but they do not discuss the detection limits beyond there.

The strip transect approach does not utilise the extended detection functions used in distance sampling, which offer increased survey coverage and sample sizes, and have a lot of theoretical and applied support (Borchers *et al.*, 2002, Buckland *et al.*, 2001). An advantage of the strip transect is that it is not necessary to simultaneously estimate numbers of whales and detection functions, since if the strip width used is justifiable, only the former task need be carried out. To put it another way, estimating the numbers of whales from the observed click trains when detection is also uncertain seems difficult and can be avoided with strip transects. A practical advantage is that it reduces the number of detected whales in aggregations that need to be counted, so making the required computations more feasible.

The estimated radial detection function  $f(r)$  and simulated perpendicular detection function  $g(y)$  given here have some empirical grounding, though aspects of it such as the constant click rate are certainly very simplistic. It seems likely that further information on the instantaneous radial click detection function  $h(r)$  for sperm whales will be obtained in the future using multi-hydrophone systems and DTAGs.

## CONCLUSION

A method is outlined for acoustically surveying sperm whales with a two-element hydrophone system even when animals are aggregated. The method attempts to identify a perpendicular truncation distance within which acoustic detection of animals is certain, and count the whales within it using the detected clicks. Topics for further examination or development include: automated formation of the initial click trains; removal of short click trains; the effect of violation of the surface assumption, and more detailed modelling of click rates.

## ACKNOWLEDGEMENTS

This work was partly funded by the International Fund for Animal Welfare. The author is funded by the National Institute for Health Research (NIHR) Collaboration for Leadership in Applied Health Research and Care (CLAHRC) for the South West Peninsula at the Royal Devon and Exeter NHS Foundation Trust. The views expressed in this publication are those of the author and not necessarily those of the NHS, the NIHR or the Department of Health in England. Thanks to Tim Lewis for discussion and for many helpful comments. This work benefited greatly from early discussions with David Borchers, who also carefully reviewed an early submitted manuscript, leading to many important corrections and clarifications. Any remaining errors are mine. Further thanks to three anonymous reviewers for their comments and advice.

## REFERENCES

- Barlow, J. and Taylor, B. 2005. Estimates of sperm whale abundance in the northeast temperate Pacific from a combined acoustic and visual survey. *Mar. Mammal Sci.* 21:429–45.
- Borchers, D., Buckland, S. and Zucchini, W. 2002. *Estimating Animal Abundance*. Springer-Verlag, London. i–viii+314pp.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. and Laake, J.L. 1993. *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London. 446pp.
- Cox, D. 1962. *Renewal Theory*. Methuen, London. i–ix+142pp.
- Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean Sanctuary conducted from the RSV *Aurora Australis*. *Rep. Int. Whal. Commn.* 47: 897–907.
- Hastie, G.D., Swift, R.J., Gordon, J.C.D., Slessor, G. and Turrell, W.R. 2003. Sperm whale distribution and seasonal density in the Faroe Shetland Channel. *J. Cetacean Res. Manage.* 5(3): 247–52.
- Hiby, A. and Lovell, P. 1989. Acoustic survey techniques for sperm whales. Paper SC/41/Sp3 presented to the IWC Scientific Committee, May 1989 (unpublished). 60pp. [Paper available from the Office of this Journal]
- Hiby, L. and Lovell, P. 1998. Using aircraft in tandem formation to estimate abundance of harbour porpoise. *Biometrics* 54:1,280–9.
- Laake, J. and Borchers, D. 2004. Methods for incomplete detection at distance zero. pp.108–89. *In: Buckland, S.T., Anderson, K.P., Burnham, K.P., Laake, J., Borchers, D. and Thomas, L. (eds). Advanced Distance Sampling*. Oxford University Press, Oxford. 595pp.
- Leeper, R., Chappell, O., and Gordon, J. 1992. The development of practical techniques for surveying sperm whale populations acoustically. *Rep. int. Whal. Commn.* 42: 549–60.
- Leeper, R., Gillespie, D. and Papastavrou, V. 2000. Results of passive acoustic surveys for odontocetes in the Southern Ocean. *J. Cetacean Res. Manage.* 2:187–196.
- Lewis, T., Gillespie, D., Lacey, C., Matthews, J., Danbolt, M., Leaper, R., McLanaghan, R. and Moscrop, A. 2007. Sperm whale abundance estimates from acoustic surveys of the Ionian Sea and Straits of Sicily in 2003. *J. Mar. Biol. Assoc. UK.* 87: 353–7.
- Lewis, T., Matthews, J., Boisseau, O., Danbolt, M., Gillespie, D., Lacey, C., Leaper, R., McLanaghan, R. and Moscrop, A. *In prep.* Abundance estimates for sperm whales in the south western and eastern Mediterranean Sea from acoustic line-transect surveys. [Available from the author].
- Mellinger, D.K., Thode, A., and Martinez, A. 2003. Passive acoustic monitoring of sperm whales in the Gulf of Mexico, with a model of acoustic detection distance. pp.493–501. *In: Proceedings of the Twenty-first Annual Gulf of Mexico Information Transfer Meeting, January 2002, US Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans.*
- Nardone, S., Lindgren, A. and Gong, K. 1984. Fundamental properties and performance of conventional bearings-only target motion analysis. *IEEE Trans. Automatic Control.* 29(9):775–787.
- Swift, R.J., Gillespie, D., Vázquez, J.A., MacLeod, K. and Hammond, P.S. 2009. Appendix IV, Abundance of sperm whales (*Physeter macrocephalus*) estimated from acoustic data for Blocks 2, 3 and 4 (French and Spanish sectors). *In: Cetacean Offshore Distribution and Abundance in the European Atlantic (CODA)*. Report available from SMRU, Gatty Marine Laboratory, University of St. Andrews, St. Andrews, Fife KY16 8LB, UK.
- Teloni, V. 2005. Patterns of sound production in diving sperm whales in the northwestern Mediterranean. *Mar. Mammal Sci.* 21: 446–457.
- Thode, A. 2005. Three-dimensional passive acoustic tracking of sperm whales (*Physeter macrocephalus*) in ray-refracting environments. *J. Acoust. Soc. Am.* 118: 3,575–84.
- Wahlberg, M., Frantzis, A., Alexiadou, P., Madsen, P. and Möhl, B. 2005. Click production during breathing in a sperm whale (*Physeter macrocephalus*) (L). *J. Acoust. Soc. Am.* 118 (6): 3,404–7.
- Ward, J., Thomas, L., Jarvis, S., DiMarzio, N., Moretti, D., Marques, T., Dunn, C. Claridge, D., Hartvig, E. and Tyack, P. 2012. Passive acoustic density estimation of sperm whales in the Tongue of the Ocean, Bahamas. *Mar. Mammal Sci.* 28(4): E444–E455.
- Whitehead, H. 2009. Estimating abundance from one-dimensional passive acoustic surveys. *J. Wildlife Manage.* 73(6): 1,000–9.