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# Abundance estimates for sperm whales in the Mediterranean Sea from acoustic line-transect surveys

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ABSTRACT

The Mediterranean sub-population of sperm whales is believed to be isolated and is classified as Endangered on the IUCN Red List. Although there is evidence to suggest the population is declining, there is a lack of abundance data. A series of acoustic line-transect surveys were undertaken between 2004 and 2013. In 2004, 3,946km of acoustic effort was conducted in the southern Western Mediterranean basin, resulting in the detection of 159 sperm whales. While in 2007 and 2013, 10,276km of acoustic effort was conducted in the Eastern Mediterranean basin, resulting in the detection of 24 sperm whales. A pooled detection function gave an effective strip half-width of 9.8km. A correction for availability bias was made for each block based on published simulations using data on sperm whale acoustic behaviour: estimates of *g*(0) were 0.95–0.96. Estimated abundances were: Southern Western Mediterranean Block 634 animals [374–1,077] (95% log-normal confidence interval); Hellenic Trench Block 41 [17–100]; Central Aegean Sea Block 33 [5–203]; Herodotus Rise Block 5 [1–28] and Southern Adriatic Sea Block 2 [0–12]. Estimates for all other blocks were zero. The density of sperm whales in the surveyed Southern Western Mediterranean Block was over 17 times higher than for the surveyed Eastern Mediterranean (2.12 and 0.12 whales per 1,000km² respectively). These results, combined with an acoustic survey of the northern Ionian Sea in 2003 and aerial surveys in the northern Western Mediterranean basin in 2010–11, covered approximately 57% of the likely sperm whale habitat in the Western Mediterranean and 75% in the Eastern Mediterranean. Approximate total estimates of sperm whale abundance in the Western and Eastern Mediterranean basins based on extrapolation to the unsurveyed areas are 1,678 and 164 whales respectively. This gives an estimate for the whole Mediterranean Sea of 1,842 animals.

KEYWORDS: SPERM WHALE; MEDITERRANEAN SEA; ABUNDANCE ESTIMATE; DISTRIBUTION; ACOUSTICS; VOCALISATION; CONSERVATION; SURVEY – ACOUSTIC; SURVEY – VESSEL

## INTRODUCTION

The Mediterranean Sea contains extensive areas of abyssal waters, deep basins and trenches bounded by steep slopes; habitats favoured by sperm whales, *Physeter macrocephalus* (Praca and Gannier, 2008; Praca *et al*., 2009). The Mediterranean Sea is semi-enclosed and heavily utilised and the potential impact of human activities on individual sperm whales is therefore significant and of concern (EEA, 1999; Reeves and Notarbartolo di Sciara, 2006).

An assessment of the conservation status of the Mediterranean sperm whales under IUCN Red List Criteria (Notarbartolo di Sciara *et al*., 2012) has classified the sub-population as Endangered and probably declining. Furthermore, genetic studies (Drouot *et al*., 2004a; Engelhaupt, 2009) indicate that the Mediterranean sub-population is likely to be isolated from that of the Atlantic.

Reeves and Notarbartolo di Sciara (2006) and Notarbartolo-di-Sciara (2014) indicate that the most significant threat is from entanglement in fishing gear, e.g. high-seas swordfish driftnets (Northridge, 1991; Tudela *et al*., 2005). Although national and international regulations ban driftnets from the area, Illegal, Unregulated and Unreported (IUU) fisheries persist throughout the Mediterranean (ACCOBAMS, 2006; FAO, 2015). Reeves and Notarbartolo di Sciara (2006) also highlight the impact of shipping on sperm whales and underwater noise (e.g. from seismic exploration, military operations, illegal dynamite fishing) is also cited as a source of concern.

Distribution data for sperm whales in the Mediterranean tend to be localised and large areas, particularly in the south and east, have received minimal effort. One wide-ranging study (Gannier *et al*., 2002) found sperm whales distributed along the Hellenic Trench and the west coast of Greece, around the Balearic Islands of Spain, and along the northwestern Mediterranean from the Gulf of Lyons to the Ligurian Sea. Examples of more localised studies include those of Gordon *et al.* (2000) who determined the distribution of sperm whales using acoustic point surveys in the Ligurian Sea, and Frantzis *et al.* (2014) who carried out extensive acoustic research in the waters of southwestern Greece showing concentrations of sperm whales along the Hellenic Trench and its continuation to the northwest and east.

Abundance estimates from line-transect surveys are available for the northern Ionian Sea, Sicilian and Malta Channels, from an acoustic line-transect survey (Lewis *et al.*, 2007), and from aerial surveys in the northern part of the Western Mediterranean (Laran *et al.,* 2017). Abundance estimates from mark-recapture analysis are available for the Western Mediterranean basin (Rendell *et al*., 2014). They concluded that photo-identification data collected in the period 1990–2008 was inconsistent with a population of greater than 1,000 animals or lower than 200, with their best

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estimate of individuals using their study area being around 400. Frantzis *et al*. (2014) identified 164 individuals and suggested that there may be between 200 and 250 individuals within the Eastern Mediterranean.

Acoustic survey methods for sperm whales are well developed (Gillespie, 1997; Leaper *et al*., 2000), but there have been problems with estimating group size acoustically (Barlow and Taylor, 2005). A pilot survey aimed at refining sperm whale acoustic survey techniques and protocols, analysis methods and determining animal densities required for the planning of a synoptic survey was conducted in the Ionian Sea in 2003. Analysis of the pilot survey particularly focussed on locating individual animals within groups of vocalising individuals, something that had not been an issue for surveys at higher latitudes with animals more widely spaced (Lewis *et al.*, 2007; Whitehead, 2003).

This paper presents density estimates for strata in the Western and Eastern Mediterranean derived from acoustic survey data collected between 2004 and 2013. Options are considered for combining these with previous estimates covering additional areas from acoustic surveys in 2003 (Lewis *et al.*, 2007) and aerial surveys in 2011/12 (Laran *et al.*, 2017), towards a total estimate for sperm whale abundance in the Mediterranean.

## METHODOLOGY

### Survey block and transect design

The study area was divided into 10 survey blocks. Survey block areas and transect distances are summarised in Table 1. The 'Southern Western Mediterranean' (SWM) survey block was designed to cover the whole of the southern part of the Western Mediterranean basin (Fig. 1). The Eastern

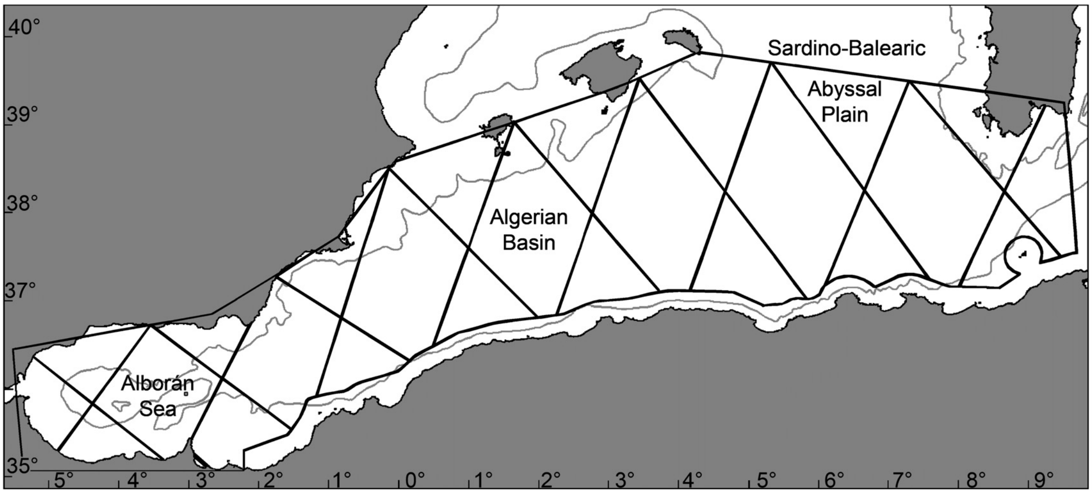

Fig. 1. SWM survey block and transect design. A black line marks the block outline and designed transects and a grey line marks the 1,000m isobath.

Table 1

Survey design data. Information on basin, survey year and survey blocks, transect lengths and survey coverage rate (length of designed transect/area of survey block). Areas of survey blocks were calculated using a cylindrical equal area projection.

| Basin, year and survey block | Area (km$^2$) | Number of designed transects | Length of designed transects (km) | Designed coverage rate (km/1,000km$^2$) |
|---|---|---|---|---|
| **Western Mediterranean Basin** | | | | |
| 2004 | | | | |
| Southern Western Mediterranean (SWM) | 298,904 | 16 | 4,279 | 14.3 |
| **Eastern Mediterranean Basin** | | | | |
| 2003* | | | | |
| Sicilian and Malta Channels | 62,100 | 5 | 940 | 15.1 |
| Northern Ionian Sea | 271,500 | 12 | 4,671 | 17.2 |
| 2007 | | | | |
| Southern Ionian Sea and Gulf of Sirte | 301,748 | 7 | 2,657 | 8.8 |
| Herodotus Rise | 106,623 | 7 | 1,637 | 15.4 |
| Hellenic Trench | 115,680 | 19 | 3,073 | 26.6 |
| Central Levantine Sea | 43,783 | 3 | 589 | 13.5 |
| Cyprus | 157,552 | 5 | 1,304 | 8.3 |
| Kritiko Pelagos | 49,616 | 13 | 1,585 | 31.9 |
| Southern Adriatic Sea | 31,072 | 9 | 908 | 29.2 |
| 2013 | | | | |
| Northern Aegean Sea | 15,356 | 6 | 379 | 24.7 |
| Central Aegean Sea | 65,104 | 5 | 404 | 6.2 |
| Eastern Mediterranean summary | 1,220,134 | 91 | 18,147 | 14.9 |
| **Surveyed Mediterranean summary** | **1,519,038** | **107** | **22,426** | **14.8** |

*2003 survey originally reported in Lewis *et al.* (2007).

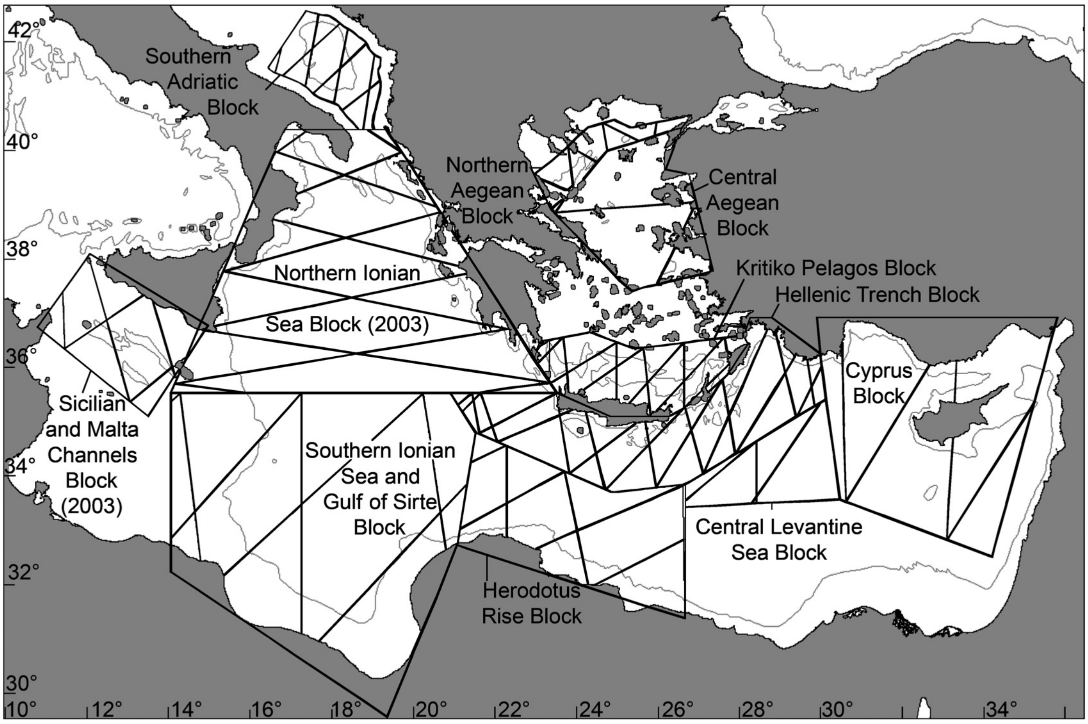

Fig. 2. Eastern Mediterranean survey blocks and designed transects. Line styles as for Fig. 1. The Northern Ionian Sea and Sicilian and Malta Channels blocks were acoustically surveyed in 2003 (Lewis *et al.*, 2007) and are shown for completeness.

Mediterranean Sea was divided into nine survey blocks (Fig. 2). The Northern Ionian Sea and Sicilian and Malta Channels blocks were surveyed in 2003 (Lewis *et al.*, 2007). The Southern Adriatic and Kritiko Pelagos blocks were designed to enclose well-defined basins. The Hellenic Trench Block was defined as a separate stratum based on Frantzis *et al.* (2003) which showed a relatively high density of sperm whales within this area which included the oceanic trench comprising the Hellenic, Pliny and Strabo Trenches and the Rhodes Basin. Within each survey block the transects used were randomly selected from a set of equal-spaced zigzag designs with near even coverage probability (after Strindberg and Buckland, 2004). Where feasible, transects were designed to be approximately perpendicular to the bathymetry and so lie across any potentially depth-related animal-density gradients.

### Survey protocol

The survey vessel used was the 22m auxiliary-powered sailing research vessel *Song of the Whale*. The optimum survey speed selected was 7 knots (13km hr$^{-1}$); this represented a compromise between the need to travel at least two to three times faster than typical sperm whale horizontal swimming speeds but not so fast as to introduce significant hydrophone flow, propeller or engine noise. Sections of transect where vessel speed dropped to less than 4 knots (7.4km hr$^{-1}$) were excluded as being too slow to allow whales to be located accurately using target motion analysis or for reliable line-transect analysis (Hiby, 1986). The acoustic surveys were conducted 24 hours per day and in all prevailing Beaufort sea states, 0 to 5, in all three surveys.

An additional component of the project was to collect supplementary data on individual sperm whales including fluke images for photo-identification. In order to avoid bias the vessel did not break from the transect until it had travelled 6.5km (30 minutes at survey speed) along the survey track after the last vocalising sperm whale had passed abeam. This protocol ensured that all animals in an aggregation within range had the possibility of being detected and maximised the range of bearings to each animal (which were used for positional information). During acoustic encounters with sperm whales the vessel made a series of zigzag turns along the transect in order to determine whether individuals were to the left or right of the transect; such information would be useful should a subsequent close approach be made. Zigzag turns were made at 5° to the transect with the second turn after 1km and subsequent turns every 2km until the end of the encounter. Such small course alterations can resolve the left-right ambiguity in a vocalising animal's location which arise when a linear array is towed in a straight line. The biased coverage introduced by such short-duration zigzags i.e. an increase in distance travelled of 0.4% and a maximum lateral deviation from the transect of less than 100m, was considered negligible.

### Acoustic data acquisition

Acoustic data were collected using a two-element hydrophone array towed 200m behind the vessel. The array consisted of two *Benthos* AQ-4 elements spaced about 3m apart connected to *Magrec* pre-amplifiers with a gain of 29dB. The 'distance' between the two elements, as an acoustic travel time, was required for click bearing determination. This was obtained for each survey (in order to include variations in salinity) by measuring the mean time-of-arrival difference between revved propeller beats using *Rainbow Click*. The overall response of the system was approximately flat from 10Hz to 40kHz. Signals were amplified with a 10dB gain and then digitised using an *M-Audio* Delta 66 sound card in 2004 and 2007 and a *National Instruments*

6251 data acquisition card in 2013. In 2007 a 470Hz high-pass filter was used at the amplification stage to reduce hydrophone cable strum. Continuous recordings were made to 16-bit WAV files at a sample rate of 48k samples per second on each of the two channels. IFAW's *Rainbow Click* software automatically analysed incoming sounds and displayed candidate sperm whale clicks on a time-bearing display (similar to Fig. 3c) providing real-time data to inform decisions on making turns and breaking from the transect.

## Acoustic data analysis

### *Click train identification*

After the survey, recordings were analysed automatically with the *Rainbow Click* software in order to identify candidate sperm whale clicks. The output from this analysis was a set of files containing short waveform clips (typically 2–3ms long) of each candidate click. This process ran fully automatically, but produced a high rate of false detections arising from transient noises. Candidate clicks were examined in more detail by an analyst using a variety of tools

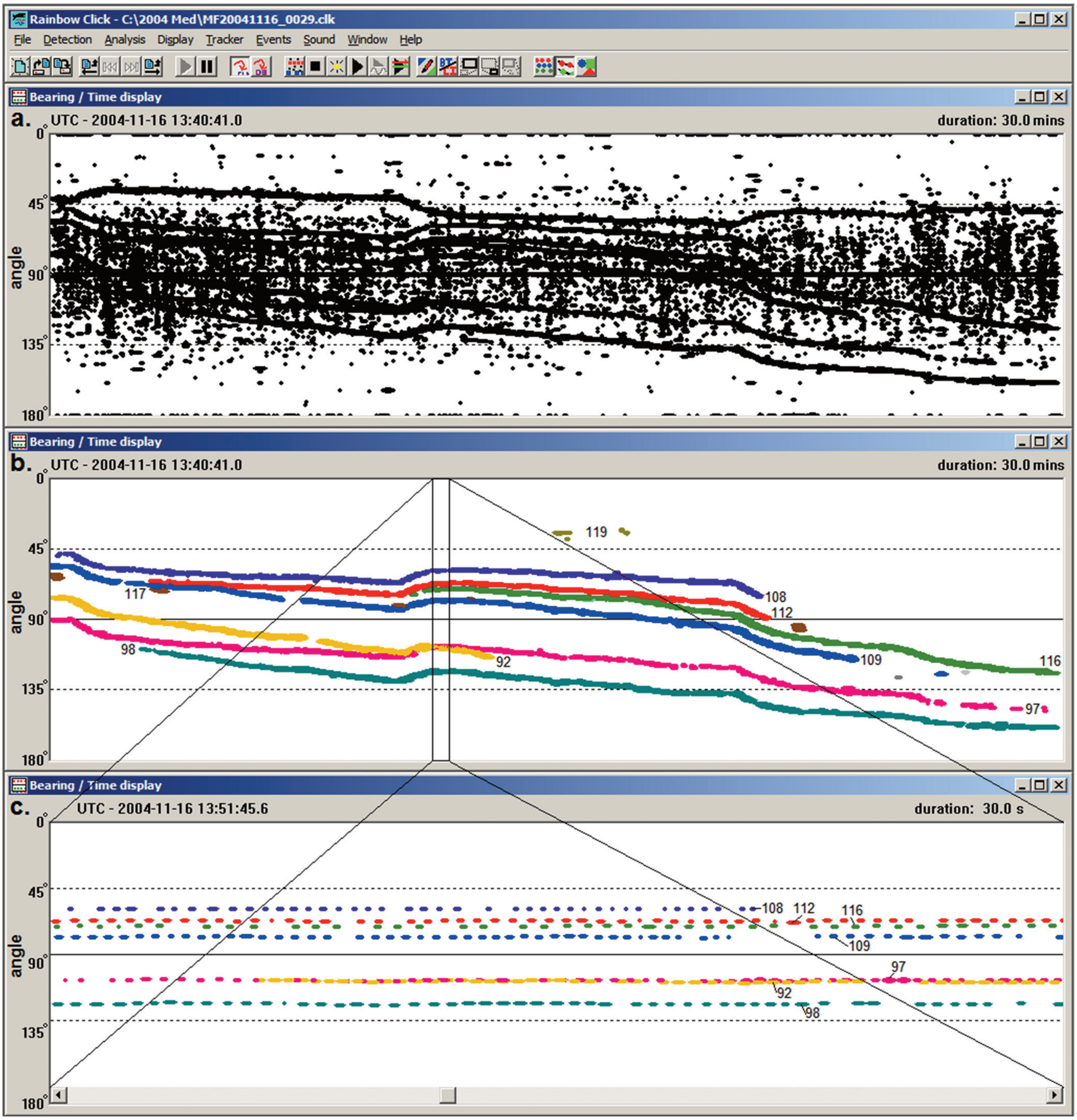

Fig. 3(a–c). Screen images from *Rainbow Click*. Candidate sperm whale clicks are plotted on time versus angle axes. Clicks plotting at 0˚ are directly ahead of the hydrophones; those plotting at 90˚ are perpendicular to the hydrophones, while those plotting at 180˚ are directly behind the hydrophones. (a) Plot of candidate sperm whale clicks for a 30 minute period. (b) Plot of analysed clicks for same period: click properties (click bearings, spectral characteristics, ICIs and sound) have been used to remove non-sperm whale clicks (including those from a ship at ≈45°), to remove echoes of sperm whale clicks and to assign the remaining clicks to click trains and these to individual whales. There are distinct click sequences for seven whales; kinks in the trajectories of these sequences are a consequence of the vessel being turned through ±10° every 2km while passing the aggregation. (c) Zoomed-in view of a 30s section, note that clicks from whales 92 and 97 have been separated even though clicks are on similar bearings, using ICIs.

and display types in *Rainbow Click* in order to identify sperm whale clicks, which were then assigned to click trains. Assignment of click sequences to click trains was based on the bearing information, spectral characteristics, inter-click intervals (ICIs) and audible sound. The term 'click train' is used here to denote a virtually unbroken sequence of clicks on a consistent time-bearing trajectory produced by an individual whale (equivalent to the 'block' of Wahlberg, 2002 and the 'click series' of Møhl *et al.*, 2003). Sequences of click trains were assigned to individual whales by manually linking click trains across time-gaps. This produced a chain of click trains for each whale (the 'track' of Møhl *et al.*, 2003). Generally, the longer the time-gap between successive click trains the more uncertain such links are likely to be. Time gaps between click trains can arise when an animal stops clicking following feeding creaks (typically 2–10s; Gordon, 1987; Jaquet *et al.*, 2001; Miller *et al.*, 2004), when an animal stops regular clicking mid-dive for short periods to recycle air for sound production (typically 6 to 117s; Madsen *et al.*, 2002; Wahlberg, 2002), when an animal stops clicking between successive dives (on average for 17.6 minutes with a maximum of 32–34 minutes; Teloni, 2005) or when the received levels of clicks fall temporarily below the system's acoustic detection threshold. The latter may occur when an animal changes its orientation while diving (Miller *et al.*, 2004), reduces its output level, moves between layers with differing propagation properties or if background noise levels increase.

Individual animals are most easily separated using click-bearing differences, however where two or more animals produce clicks on consistently similar bearings, a situation more likely at greater distances as angular differences between animals decrease, then ICIs, and to a lesser extent spectral characteristics can be used to distinguish animals (e.g. whales 92 and 97 in Fig. 3c). When animals are on the limits of the acoustic detection range some clicks will lie below the detection threshold and click sequences will become broken and intermittent. At this point the assignment of short click trains to individual whales becomes difficult and therefore such click trains remain unlinked and as such provide insufficient click bearings for localisation (see following section).

### *Determination of perpendicular distances*

With a two-element array, the time-of-arrival differences of clicks at the elements can be used to calculate an angle between the click and the array axis (Leaper *et al.*, 1992). If whale dive depth is ignored, target motion analysis can be used to determine perpendicular distances of animals from the survey track by intersecting bearings to clicks as described in Leaper *et al.* (2000). However, the perpendicular distances to whales measured are absolute distances in three dimensions from the hydrophone array axis. Since sperm whales usually vocalise at depth these distances will be greater than the true perpendicular distance from the trackline. The difference between these two distances will increase towards the survey track. The effect on the histogram of detections is to displace detections made close to the line to a greater distance. Leaper *et al.* (1992) showed that this effect will cause minimal bias when ESHW is considerably greater than maximum dive depth, and further examples in the Appendix support this. Small deviations in course allow the left-right ambiguity from this method to be resolved (Fig. 4) by taking the side which gave the most precise location.

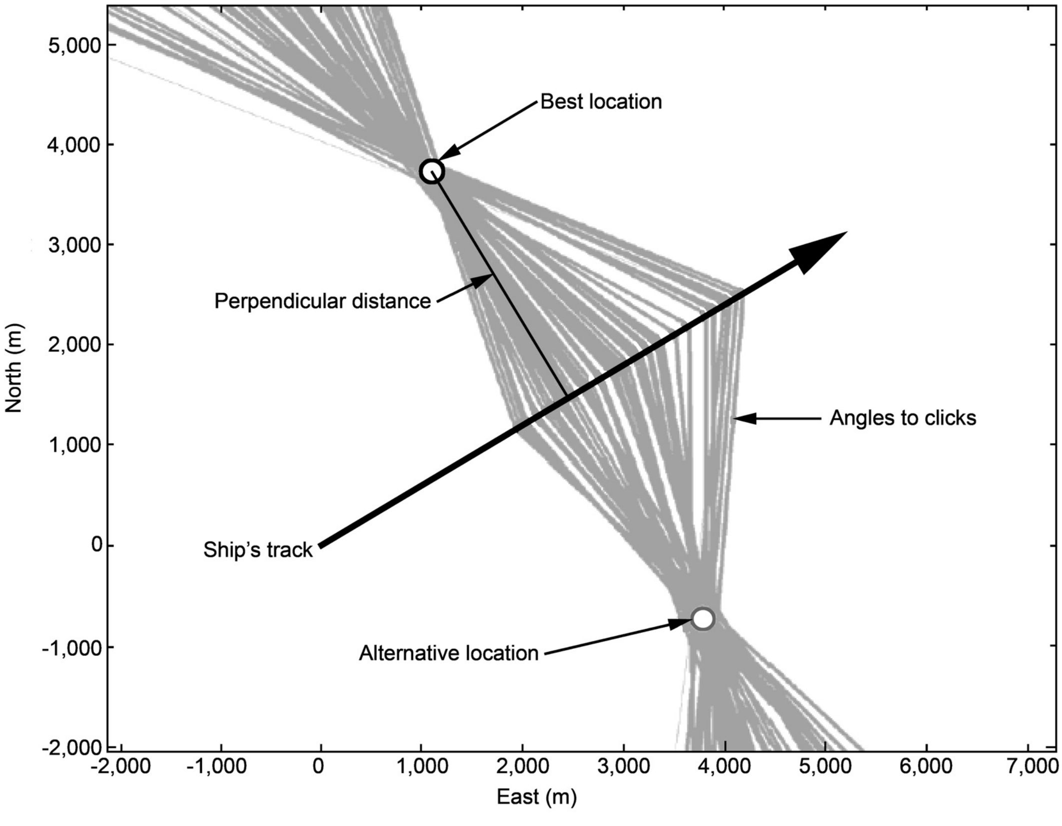

Fig. 4. Crossing of bearings to clicks at the sea surface in order to estimate the whale's position and perpendicular distance from the survey track.

A maximum-likelihood estimation routine was used to select the best position (Matthews, 2014). The routine also calculated and displayed an error ellipse for each position with the two axes of the ellipse showing the 95% confidence limits of the position in those directions. Animals with too few clicks for the estimation of locations were excluded from the entire analysis (detection function and total count).

Program *Distance* (Buckland *et al.*, 2001; version 6, release 2, Thomas *et al.*, 2009) was then used to estimate a detection function based on the acoustically derived perpendicular distances.

If sperm whales remain silent for sufficiently long periods then they will not be detected. A stationary sperm whale close to the trackline will be within detection range for a period of about 2× detection range/survey speed. For a detection range of 8km and mean survey speed of 12km $hr^{-1}$ such an animal should be within detection range for about 80 minutes. However, the period for which reliable locations can be obtained will be shorter than this. A typical sperm whale dive-cycle involves a dive lasting 30–45 minutes, followed by a period of recovery at the surface, typically averaging 7–10 minutes (Whitehead, 2003; Watwood *et al.*, 2006), with no instances greater than 34 minutes (Teloni, 2005), before the cycle is repeated. Animals usually stop clicking while ascending from a dive, produce no 'usual' clicks during the recovery period at the surface and resume clicking while descending on the subsequent dive. Teloni (2005) reported a mean for this quiet ('interclicking time') period of 17.6 minutes with a maximum of 32–34 minutes, with a mean of 35.1 minutes for the period with clicks ('clicking time'). Watwood *et al.* (2006) found that tagged whales in the Ligurian Sea (within the Western Mediterranean basin) spent 97% of their time in normal foraging dive cycles.

Earlier acoustic surveys for sperm whales (e.g. Leaper *et al.*, 2000; Hastie *et al.*, 2003; Barlow and Taylor, 2005; Lewis *et al.*, 2007; Swift *et al.*, 2009) have assumed that the probability of detecting a whale directly on the trackline, $g(0)$, is 1. This assumption is supported by data from joint visual and acoustic surveys where sperm whales were never detected visually without being detected acoustically (e.g. Leaper *et al.*, 1992; Gillespie, 1997; Leaper *et al.*, 2000; Barlow and Taylor, 2005). However, there are cases where animals, particularly those in social groups, have been observed in shallow, acoustically inactive, near-surface drift-dives (Miller *et al.*, 2008) or close to the surface for several hours either silent or infrequently producing click sequences such as codas (e.g. Fais *et al.,* 2016). Codas are rarely picked up on towed hydrophone surveys and may not propagate as far as regular clicks (e.g. Whitehead, 2003; Barlow and Taylor, 2005). During the extended non-vocalising periods these animals may not be detected by a towed hydrophone survey.

To estimate $g(0)$ allowing for such silent periods, Fais *et al*. (2016) used a simulation approach based on (DTag) data from adult sperm whales in the Azores. The Azores are at similar latitudes to the Mediterranean with an apparently similar mix of female and sub-adult groups. Hence, it is reasonable to assume similar vocal behaviour to the Azores within the Mediterranean. Their simulation generated estimates of $g(0)$ and its variance across a range of effective strip half-widths (ESHWs) and vessel speeds. Estimates of $g(0)$ for this study used the results of Fais *et al*. (2016) applied to the ESHW and mean vessel speed for each block. Corrected densities for each block were calculated by dividing by these estimates of $g(0)$.

## RESULTS

Acoustic surveys were carried out in the SWM Block from 19 October to 24 November 2004, and in the Eastern Mediterranean from 13 May to 30 October 2007 and from 26 to 30 July 2013 (Northern and Central Aegean blocks). The lengths of acoustically surveyed transects for each survey block are given in Table 3.

### Distribution of detected whales

The positions of detected whales in the Western and Eastern Mediterranean basins are shown in Figs 5 and 6 respectively. The numbers of distinct whales detected in each aggregation in these figures are minimum aggregation sizes since some animals within the aggregations may have been further from the track than the acoustic detection range. The largest aggregation was found in the SWM Block comprising over 23 whales. Whales within this aggregation were distributed

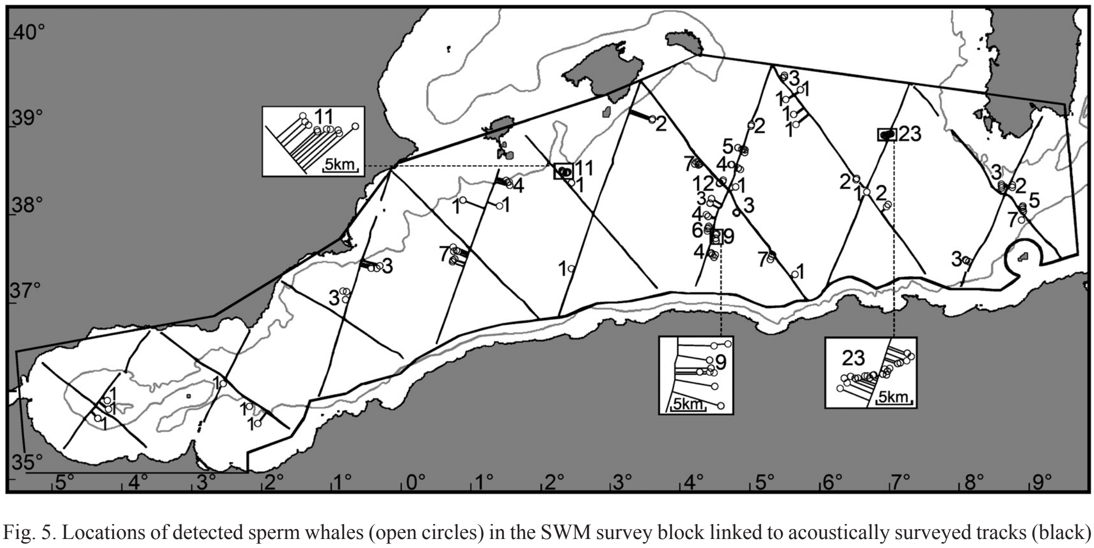

Fig. 5. Locations of detected sperm whales (open circles) in the SWM survey block linked to acoustically surveyed tracks (black) by perpendicular black lines. The number of detected sperm whales is given at each location. Examples of aggregations are shown in the inset boxes. The 1,000m isobath is shown in grey and the survey block outline in black.

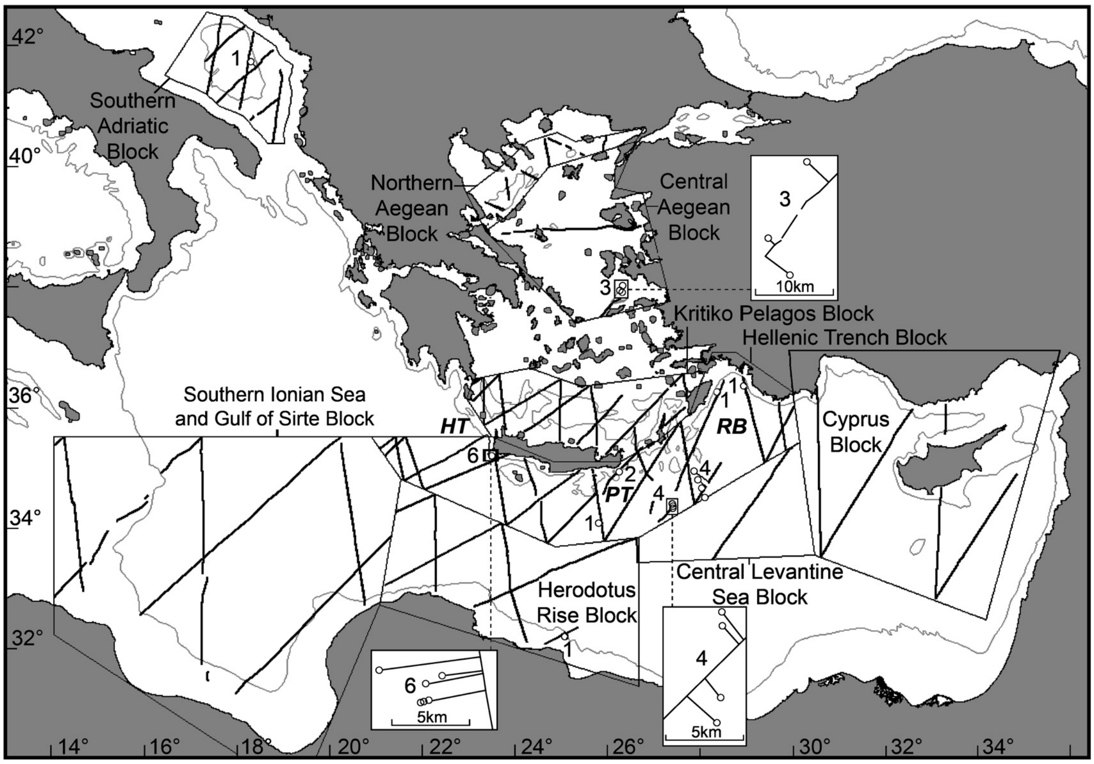

Fig. 6. Locations of detected sperm whales (open circles) in the Eastern Mediterranean, details as for Fig. 5. Abbreviations mark the following bathymetric features: *HT*: Hellenic Trench, *PT*: Pliny Trench and *RB*: Rhodes Basin.

in a band measuring approximately 2km by 11km (see Fig. 6 inset).

Within the Eastern Mediterranean there were 19 detections in the Hellenic Trench Block, 3 in the Central Aegean Block and 1 detection in each of the Herodotus Rise and Southern Adriatic blocks. The largest aggregation detected comprised of a minimum of six animals at the southeastern end of the Hellenic Trench.

### Detection function determination and abundance estimation

For both the SWM Block ($n = 159$) and for detections pooled across all the Eastern Mediterranean blocks ($n = 24$) a truncation distance of 28km was selected resulting in the exclusion of 4 (2.5%) and 1 (4.2%) obvious outlying animals respectively, leaving 155 and 23 animals available for detection function estimation. Selection of the truncation distance was based on recommendations in Thomas *et al.* (2010). Histograms of truncated detection distances are shown in Fig. 7.

To improve precision of the estimated ESHW, detections from the SWM Block were pooled with those of the Eastern Mediterranean blocks (Fig. 7c). Such pooling was appropriate given all surveys used the same vessel, field protocols and predominantly the same acoustic equipment.

The fitted detection functions are shown in Fig. 7. These show a peak in the 2–4km bin. This could be explained by whale diving behaviour resulting in the overestimation of small perpendicular distances due to whales at depth (this effect is examined in the Appendix). The best model, based on the lowest Akaike's Information Criterion (AIC), of detection probability with perpendicular distance was a hazard-rate model with no adjustment terms.

Detection function results are summarised in Table 2, survey effort and survey block coverage are summarised in Table 3, while density and abundance estimates are summarised in Tables 4 and 5.

The abundance and density estimate results show there was a higher density of sperm whales in the SWM Block, with 2.12 whales per 1,000km² than in the Eastern Mediterranean where the density across all surveyed blocks, including those surveyed in 2003, was only 0.12 whales per 1,000km². In the Eastern Mediterranean the Central Aegean, Hellenic Trench and Northern Ionian Sea blocks had the higher densities with estimated densities of 0.51, 0.36 and 0.24 whales per 1,000km² respectively. Outside of these three blocks the density of sperm whales in the Eastern Mediterranean was extremely low. While the SWM Block comprised less than 20% of the total area of the acoustically surveyed Mediterranean (including the 2003 survey), it contained over 81% of the total estimated number of whales within the surveyed blocks.

## DISCUSSION

### Distribution and abundance

The density of sperm whales in the surveyed SWM Block was over 17 times higher than for the surveyed blocks of the Eastern Mediterranean (2.12 and 0.12 whales per 1,000km² respectively). The survey showed that within the SWM Block whales tended to be concentrated in the abyssal waters between Menorca and Algeria. In the Eastern Mediterranean whales were concentrated in the Hellenic oceanic trench and its easterly extension, in the North Ikaría Basin of the Aegean Sea and in the northern Ionian Sea. It is notable that much of the remainder of the Eastern Mediterranean had very low numbers of sperm whales.

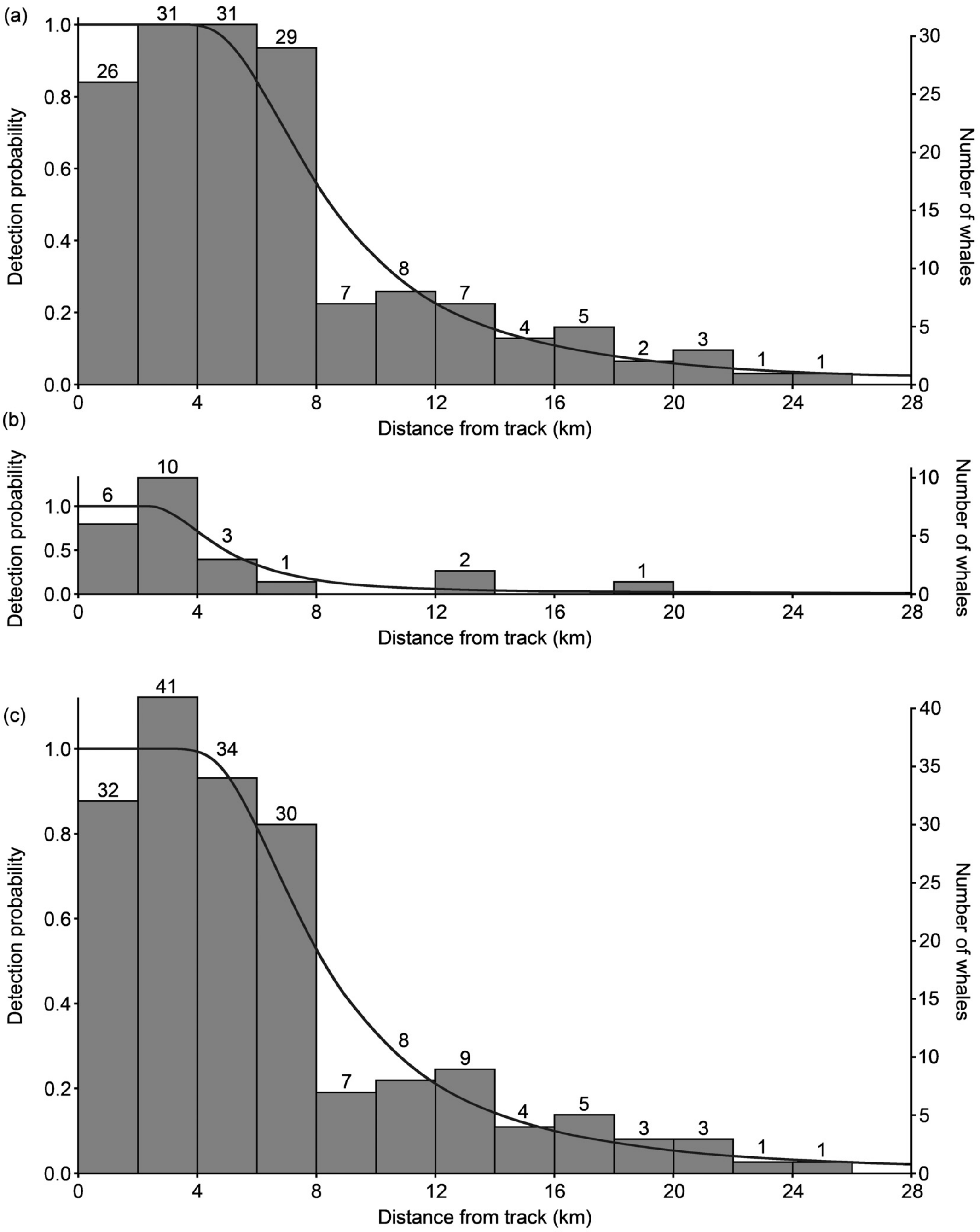

Fig. 7(a–c). Histograms of perpendicular distances to sperm whales with fitted hazard-rate detection functions for: (a) SWM survey block; (b) pooled Eastern Mediterranean survey blocks and (c) pooled SWM and Eastern Mediterranean survey blocks. Eastern Mediterranean blocks do not include the Northern Ionian Sea and Sicilian and Malta Channels blocks, surveyed in 2003, as these used different acoustic equipment and vessel (14m auxiliary powered sailing yacht *RV Song of the Whale I*). Distances are truncated at 28km.

In this analysis, the determination of each whale's distance from the trackline for distance sampling relies on an experienced analyst assigning unbroken sequences of clicks to click-trains, linking these click-trains together and then assigning these linked click-trains to distinct whales. Target-motion analysis can then be carried out on these linked click-trains to obtain distances from the trackline. A probabilistic approach to this process is described in Matthews (2014). This involves generating the sample space of all allowable combinations of click trains, and using information about which combinations are more probable, to find the most likely number of whales present within a strip transect. The approach uses a model of sperm whale click behaviour during normal dive cycles. Matthews (2014) used this approach to calculate an abundance estimate for the SWM Block using the same data as are used in this paper. The abundance estimate obtained in Matthews (2014) was 652 [336, 1,265]. This estimate is very similar to the equivalent estimate ($\hat{N}$ = 602 animals [342, 1,058]) from this study, i.e. prior to applying a correction for $g(0)$.

The distribution of perpendicular distances in this study drops off very quickly at distances greater than 8km but then has a long tail up to the truncation distance of 28km. There are a number of possible explanations for this. It could be that few mature male sperm whales were encountered, but

Table 2

Detection function parameters.

| Region | Blocks pooled to determine detection function | Selected truncation distance (km) | Number of whales (after truncation) used to determine detection function | ESHW (effective strip half-width) (km) | ESHW coefficient of variation | ESHW 95% log-normal confidence interval (km) | Model with lowest AIC |
|---|---|---|---|---|---|---|---|
| Southern Western Mediterranean (SWM) | No pooling | 28.0 | 155 | 10.0 | 8.5% | 8.5–11.8 | Hazard-rate with no adjustment terms |
| Eastern Mediterranean | 2007 and 2013 Eastern Mediterranean blocks | 28.0 | 23 | 6.0 | 24.9% | 3.6–10.0 | Hazard-rate with no adjustment terms (weakly monotonically non-increasing constraint required) |
| Southern Western and Eastern Mediterranean | All detections (2004 SWM, 2007 and 2013 Eastern Mediterranean blocks) | 28.0 | 178 | 9.8 | 7.9% | 8.4–11.4 | Hazard-rate with no adjustment terms |
| Ionian Sea (2004)* | Ionian Sea block and supplementary tracks | 20.0 | 40 | 10.0 | 12.1% | 7.9–12.7 | Uniform with a cosine adjustment term |

*From Lewis *et al.* (2007).

Table 3

Acoustic survey effort and survey block coverage.

| Basin, year and survey block | Months surveyed | Number of transects surveyed | Total length of surveyed transects (km) | Mean survey speed (knots) | (km/h) | % of planned transect length surveyed | Survey coverage rate (km/1,000km$^2$) | Effective strip half-width (ESHW) (km) | Effective area surveyed (km$^2$) | % of survey block surveyed |
|---|---|---|---|---|---|---|---|---|---|---|
| **Western Mediterranean Basin** | | | | | | | | | | |
| 2004 | | | | | | | | | | |
| Southern Western Mediterranean (SWM) | | | | | | | | | | |
| Not pooled | 10–11 | 16 | 3,946 | 6.8 | 12.6 | 92% | 13.2 | 10.0 | 79,034 | 26% |
| Pooled[1] | 10–11 | 16 | 3,946 | 6.8 | 12.6 | 92% | 13.2 | 9.8 | 76,977 | 26% |
| **Eastern Mediterranean Basin** | | | | | | | | | | |
| 2003* | | | | | | | | | | |
| Sicilian and Malta Channels | 8–9 | 4 | 892 | 6.1 | 11.2 | 95% | 14.4 | 10.0 | 17,840 | 29% |
| Northern Ionian Sea | 8–9 | 8 | 3,486 | 6.0 | 11.1 | 75% | 12.8 | 10.0 | 69,720 | 26% |
| 2007 | | | | | | | | | | |
| Southern Ionian Sea/Gulf of Sirte | 5–7, 9 | 7 | 2,339 | 6.6 | 12.3 | 88% | 7.8 | 9.8 | 45,638 | 15% |
| Herodotus Rise | 7, 9 | 7 | 1,214 | 6.5 | 12.0 | 74% | 11.4 | 9.8 | 23,676 | 22% |
| Hellenic Trench | 5–7 | 18 | 2,703 | 6.5 | 12.0 | 88% | 23.4 | 9.8 | 52,724 | 46% |
| Central Levantine Sea | 9 | 3 | 258 | 7.1 | 13.1 | 44% | 5.9 | 9.8 | 5,037 | 12% |
| Cyprus | 6 | 5 | 1,175 | 6.8 | 12.7 | 90% | 7.5 | 9.8 | 22,923 | 15% |
| Kritiko Pelagos | 9 | 13 | 1,305 | 6.7 | 12.5 | 82% | 26.3 | 9.8 | 25,449 | 51% |
| Southern Adriatic Sea | 10 | 6 | 724 | 6.8 | 12.6 | 80% | 23.3 | 9.8 | 14,114 | 45% |
| 2013 | | | | | | | | | | |
| Northern Aegean Sea | 7 | 6 | 240 | 6.3 | 11.8 | 63% | 15.6 | 9.8 | 4,678 | 30% |
| Central Aegean Sea | 7 | 4 | 318 | 6.5 | 12.1 | 79% | 4.9 | 9.8 | 6,202 | 10% |
| Eastern Mediterranean summary | 5–10 | 81 | 14,654 | 6.4 | 11.9 | 81% | 12.0 | – | 288,001 | 24% |
| **Surveyed Mediterranean[1]** | **5–11** | **97** | **18,600** | **6.5** | **12.0** | **83%** | **12.2** | **–** | **364,978** | **24%** |

*2003 survey originally reported in Lewis *et al.* (2007). [1]For the total surveyed Mediterranean the effective area surveyed and percent of survey block surveyed were calculated using the values of ESHW for the SWM block derived using the pooled detection function.

that male vocalisations tend to have higher source levels and therefore can be detected at substantially greater distances than females and immature males. It could also be that there are occasional conditions when stratification in the water column leads to extended propagation. Whatever the factors affecting the probability of being detected at greater distances, whales at perpendicular distances of < 8km have an almost uniform probability of being detected. By treating the survey as a strip transect with a half-width of 8km and truncating all animals at greater distances, a density of 1.95 individuals per 1,000km$^2$ for the SWM Block is obtained (compared to 1.96 for the non-pooled detection function in Table 4), showing that the estimated density is not sensitive to the choice of truncation distance.

Combined estimates for multiple strata include surveys conducted in different years and different months. There is insufficient data on seasonal movements of sperm whales in the Mediterranean to indicate whether this could cause a bias in the total estimates. However, there will inevitably be additional variance for any combined estimates due to whale movements between strata, that is not captured in the variances presented in Tables 4 and 5.

Table 4

Sperm whale density and absolute abundance estimates.

| Basin, year and survey block | Number of whales before truncation | Number of whales after truncation | Density estimate (whales/ 1,000km$^2$) | Estimate of number of whales in block | 95% log-normal confidence interval (whales) | Coefficient of variation |
|---|---|---|---|---|---|---|
| **Western Mediterranean Basin** | | | | | | |
| 2004 | | | | | | |
| Southern Western Mediterranean (SWM) | | | | | | |
| Not pooled | 159 | 155 | 1.96 | 586 | 333–1,033 | 27.5% |
| Pooled[1] | 159 | 155 | 2.01 | 602 | 342–1,058 | 27.3% |
| **Eastern Mediterranean Basin** | | | | | | |
| 2003* | | | | | | |
| Sicilian and Malta Channels | 0 | 0 | 0.00 | 0 | | |
| Northern Ionian Sea | 17 | 16 | 0.23 | 62 | 24–165 | 44.2% |
| 2007 | | | | | | |
| Southern Ionian Sea and Gulf of Sirte | 0 | 0 | 0.00 | 0 | | |
| Herodotus Rise | 1 | 1 | 0.04 | 5 | 0–41 | 112.5% |
| Hellenic Trench | 19 | 18 | 0.34 | 39 | 15–101 | 47.3% |
| Central Levantine Sea | 0 | 0 | 0.00 | 0 | | |
| Cyprus | 0 | 0 | 0.00 | 0 | | |
| Kritiko Pelagos | 0 | 0 | 0.00 | 0 | | |
| Southern Adriatic Sea | 1 | 1 | 0.07 | 2 | 0–18 | 97.7% |
| 2013 | | | | | | |
| Northern Aegean Sea | 0 | 0 | 0.00 | 0 | | |
| Central Aegean Sea | 3 | 3 | 0.48 | 31 | 2–591 | 116.5% |
| Eastern Mediterranean summary | 41 | 39 | 0.11[+] | 139 | 71–273 | 35.5% |
| **Surveyed Mediterranean[1]** | **200** | **194** | **0.49[+]** | **741** | **473–1,160** | **23.2%** |

*The results from the 2003 survey (Lewis *et al.*, 2007) were derived using a different detection function to the results from 2007 and 2013. [1]For the estimate for the total surveyed Mediterranean the contribution from the SWM block is the estimate that was derived using the pooled detection function. [+]Density subtotal and total are calculated as the sum of the estimates of the number of whales divided by the total area of each region. Confidence limits are from program *Distance* except for 2003 data for the Northern Ionian Sea block from Lewis *et al.* (2007).

Table 5

Sperm whale density and absolute abundance estimates after adjustment for $g(0)$. Values of $g(0)$ and associated standard error are from Fais *et al.* (2016), these values depend on ESHW and mean survey speed for each survey block. In all cases standard error was 0.03. Footnotes as for Table 4.

| Basin, year and survey block | $\hat{g}(0)$ | Density estimate (whales/1,000km$^2$) | Abundance estimate (whales) | Abundance estimate 95% log-normal confidence intervals (whales) | Coefficient of variation |
|---|---|---|---|---|---|
| **Western Mediterranean Basin** | | | | | |
| 2004 | | | | | |
| Southern Western Mediterranean (SWM) | | | | | |
| Not pooled | 0.95 | 2.06 | 617 | 362–1,051 | 27.7% |
| Pooled[1] | 0.95 | 2.12 | 634 | 374–1,077 | 27.5% |
| **Eastern Mediterranean Basin** | | | | | |
| 2003* | | | | | |
| Sicilian and Malta Channels | 0.96 | | | | |
| Northern Ionian Sea | 0.96 | 0.24 | 65 | 28–149 | 44.3% |
| 2007 | | | | | |
| Southern Ionian Sea and Gulf of Sirte | 0.95 | | | | |
| Herodotus Rise | 0.95 | 0.04 | 5 | 1–28 | 112.5% |
| Hellenic Trench | 0.95 | 0.36 | 41 | 17–100 | 47.4% |
| Central Levantine Sea | 0.95 | | | | |
| Cyprus | 0.95 | | | | |
| Kritiko Pelagos | 0.95 | | | | |
| Southern Adriatic Sea | 0.95 | 0.07 | 2 | 0–12 | 97.7% |
| 2013 | | | | | |
| Northern Aegean Sea | 0.95 | | | | |
| Central Aegean Sea | 0.95 | 0.51 | 33 | 5–203 | 116.5% |
| Eastern Mediterranean summary | – | 0.12[+] | 147 | 74–289 | 35.7% |
| **Surveyed Mediterranean[1]** | **–** | **0.51[+]** | **781** | **497–1,226** | **23.3%** |

**Abundance estimate for the Mediterranean Sea**

The surveys presented here, together with the survey in the northern Ionian Sea and the Sicilian and Malta Channels in 2003 (Lewis *et al*., 2007) covered over 75% of potential sperm whale habitat in the Eastern Mediterranean and over 35% in the Western Mediterranean. Potential sperm whale habitat (blue and pink areas in Fig. 8) was considered to include the whole Mediterranean except the Tunisian and Libyan shelf, the Northern Adriatic Sea and the northernmost Aegean Sea, which all have water depths less than 500m. Aerial surveys in four blocks in the northern Western Mediterranean (Laran *et al*., 2017), covered an additional 22% of the Western Mediterranean (see Fig 8.). Thus, within the Western Mediterranean the combined acoustic and aerial surveys have covered 57% of the basin. Laran *et al*. (2017) estimated abundance for four aerial survey blocks (Gulf of Lions, Tyrrhenian Sea, Slope and Oceanic Blocks), which averaged across winter and summer surveys gave 0, 0, 167 and 300 animals per block respectively, resulting in density estimates of 0.00, 0.00, 3.15 and 3.65 whales per 1,000km² respectively.

This leaves five unsurveyed areas in the Mediterranean: three in the Western and two in the Eastern Mediterranean. Following Whitehead (2002, p.296), it was assumed that 'sperm whale densities are similar in areas that have and have not been surveyed' and numbers of whales in the five unsurveyed areas were estimated by using the average of the densities from all adjacent surveyed blocks (see Fig 8.).

Within the Western Mediterranean an estimate of 361 whales was made for the unsurveyed central Western Mediterranean (121,276km²) using the average density (2.98 whales per 1,000km²) from the Slope and Oceanic aerial survey blocks in the northern Western Mediterranean and from the SWM Block. For the Tyrrhenian Sea (210,109km²) an estimate of 149 whales was made using the average density (0.71 whales per 1,000km²) from the Tyrrhenian aerial survey block, the SWM Block and from the Sicilian and Malta Channels Block. For the Algerian coastal margin (31,748km²) an estimate of 67 whales was made using the density (2.12 whales per 1,000km²) from the SWM Block alone. This gave an abundance estimate of 1,678 animals and density of 1.99 whales per 1,000km² for the Western Mediterranean.

For the Eastern Mediterranean an abundance estimate of 12 animals was made for the unsurveyed southern Aegean Sea (49,162km²) based on the average density (0.25 whales per 1,000km²) from the Central Aegean Sea and Kritiko Pelagos Blocks and from the southeastern Levantine Sea (354,041km²). Finally, an estimate of five whales was made using the average density (0.01 whales per 1,000km²) from the Herodotus Rise, Central Levantine and Cyprus Blocks. This gave an abundance estimate of 164 animals and density of 0.10 whales per 1,000km² for the Eastern Mediterranean.

With the exception of the Tyrrhenian Sea, the bathymetry within the unsurveyed areas is similar to that in the neighbouring surveyed blocks. The Tyrrhenian Sea, however, is fairly isolated from the adjacent surveyed areas and the bathymetry varies from the adjacent SWM and northern Western Mediterranean aerial survey blocks in a number of aspects, including having a more complex bottom topography. Thus, the extrapolated density in this area is probably the least reliable of all the five unsurveyed areas, but also makes the second largest contribution to the total. There is considerable evidence of sperm whale presence within the Tyrrhenian Sea (e.g. Gannier *et al*., 2002; Drouot *et al*., 2004b; Carpinelli *et al*., 2014 and Mussi *et al*., 2014); additionally, aerial surveys were conducted between 2009–11 (Lauriano *et al*., 2011) in the north and east of the Western Mediterranean, including the Tyrrhenian Sea and the southern Adriatic and Ionian Seas. Eleven sperm whales were sighted; however due to the low number of sightings, no abundance estimate was successfully determined.

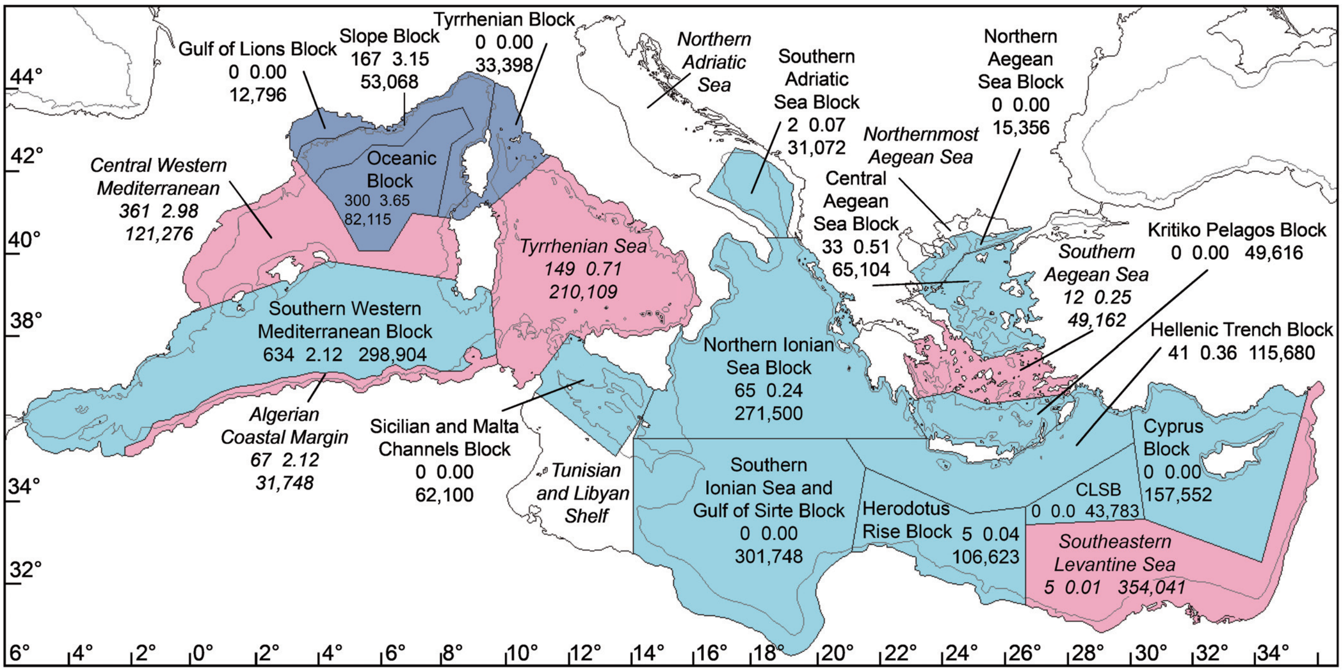

Fig. 8. Summary of surveyed and unsurveyed areas. Acoustically surveyed blocks in light blue, aerial survey block (Laran *et al*., 2017) in dark blue, unsurveyed areas of potential sperm whale habitat in pink and unsurveyed areas not considered potential sperm whale habitat in white. Numbers are: abundance estimate, density (whales per 1,000km²) and area of survey block (km²). Key to blocks: CLSB: Central Levantine Sea Block. The 500m isobath is shown in grey.

The estimate for the Eastern Mediterranean of 164 animals is consistent with that of Frantzis *et al*. (2014) who reported that following 12 years of photo-identification, 164 whales had been identified (excluding ones known to have died) and that the slope on their discovery curve indicated that most animals were known (though a formal mark-recapture analysis is underway). However, our abundance estimate for the Western Mediterranean of 1,678 animals is considerably larger than the upper confidence limit of about 1,000 estimated by Rendell *et al*. (2014). This may indicate a lack of mixing between areas in the Western Mediterranean resulting in a negative bias in the mark-recapture estimate.

The densities of sperm whales reported from other acoustic surveys carried out in broadly similar latitudes to the SWM survey block, which lies between latitudes 35° to 40°N, are two to three times the density of this block (2.12 whales per 1,000km$^2$). Swift *et al*. (2009) reported densities of 4.6 and 3.6 animals per 1,000km$^2$ off northwest Spain (42° to 45°N) and Bay of Biscay (44° to 48°N) respectively, Barlow and Taylor (2005) reported a density of 4.25 animals per 1,000km$^2$ for the eastern temperate North Pacific (21° to 48°N), Leaper *et al*. (1992) reported a density of 5.9 animals per 1,000km$^2$ for the Azores (38° to 39°N) while Fais *et al*. (2016) reported a density of 4.24 animals per 1,000km$^2$ for the Canary Islands (27° to 31°N). These comparisons do suggest that current sperm whale densities for the Mediterranean as a whole are considerably lower than at comparable latitudes elsewhere.

An extrapolated abundance estimate for the whole Mediterranean would be 1,842 animals. As it is not possible to reliably incorporate the uncertainties involved in extrapolating densities to the unsurveyed areas no attempt has been made to estimate the variance associated with this estimate. Although approximate and subject to caveats associated with extrapolation into unsurveyed areas, this estimate provides context for future sperm whale surveys and conservation efforts in the Mediterranean including the basin-wide ACCOBAMS Survey Initiative, and is consistent with the abundance assumed in the IUCN assessment that resulted in sperm whales in the Mediterranean being classified as Endangered (Notarbartolo di Sciara *et al*., 2012). The Tyrrhenian Sea is also highlighted as a priority area where future survey work could contribute most to better estimates of sperm whale abundance in the Mediterranean.

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## APPENDIX: EXAMINATION OF PERPENDICULAR DISTANCES AND BIAS UNDER THE SURFACE ASSUMPTION

The target-motion analysis using bearings assumes a two-dimensional environment, with whales at the surface. Any whales that are diving are effectively rotated onto the surface, i.e. the distance $r$ to the animal found by target-motion analysis is mapped to the surface as a perpendicular distance $y' = r$. As a result the true perpendicular distance of a diving whale is overestimated. The following examines the consequences of this for the survey.

The variables can be transformed between polar ($r$, $\theta$) and Cartesian ($y$, $h$) co-ordinates as shown in Fig. A1.

The variables in the coordinate systems are related by

$$y = r.\cos(\theta)$$
$$h = r.\sin(\theta)$$

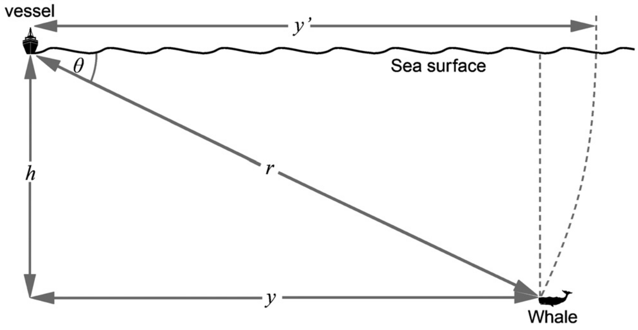

Fig. A1. Co-ordinates (polar and Cartesian) of a whale at depth and its rotation to the surface. A whale at depth $h$ and perpendicular distance $y$ is treated as if it is at perpendicular distance $y'$ at the surface.

The differentials between these two coordinate systems are given by

$$dh.dy = r.dr.d\theta$$

Therefore, the joint probability density functions (pdf) between the coordinate systems are related by

$$\pi(r;\theta) = \pi_h(r.\sin(\theta)).\pi_y(r.\cos(\theta)).r$$

The marginal of this equation over $\theta$ gives the probability density of the surface distance $y$

$$\pi_r(y) = \int_0^{n/2} \pi_h(r.\sin(\theta)).\pi_y(r.\cos(\theta)).r.d\theta \qquad \text{(A1)}$$

Since $\pi_y(y)$ is uniformly distributed over $(0,w)$, by random placement of the transect lines, we have

$$\pi_y(y) = \begin{array}{l} 1/w, y \le w \\ 0, y < w \end{array}$$

Models for dive depth used here, with depth $h$ and truncation depth $h_{\max}$, are:

(A) a truncated exponential, with pdf

$$\pi_h(h) = \begin{array}{l} \dfrac{\exp(-h/\lambda)}{\lambda(1-\exp(-h_{\max}/\lambda))}, h \le h_{\max} \\ 0, h > h_{\max} \end{array}$$

(B) a nonstandard distribution with pdf

$$\pi_h(h) = \begin{array}{l} \dfrac{2.83}{h_{\max}}, 0 \le h \le \dfrac{h_{\max}}{10} \\ \dfrac{0.25}{h_{\max}}, \dfrac{h_{\max}}{10} < h \le \dfrac{h_{\max}}{2} \\ \dfrac{1.23}{h_{\max}}, \dfrac{h_{\max}}{2} < h \le h_{\max} \end{array}$$

Examples of these two models are shown in Fig. A2 with $h_{\max}$ = 1,000m and, for model A, $\lambda = 300$.

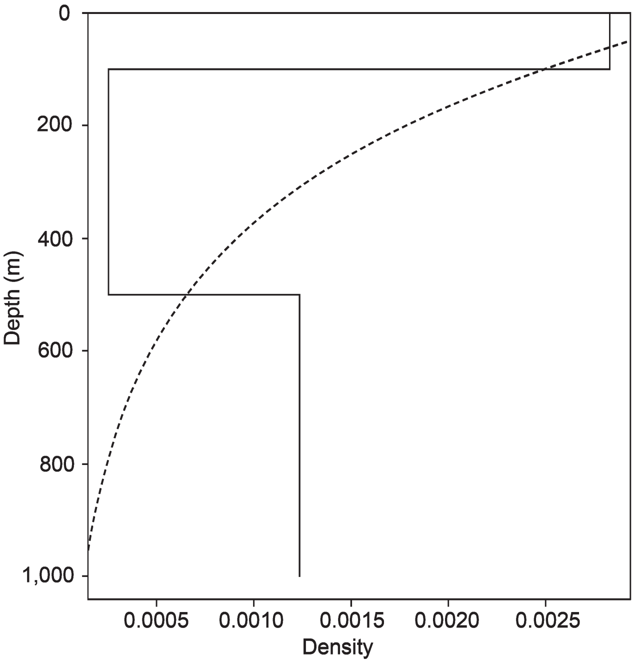

Fig. A2. Dive distributions used: a truncated exponential (dashed, model A) and a nonstandard distribution (solid, model B).

Some pdf curves for surface distances $\pi_r(y)$ for these dive distributions are shown in Fig. A3. Two curves are shown for model A (truncated exponential) and one for model B (nonstandard). It can be seen that there is a heap or spike at around 1,000m (the maximum dive depth) and a probability density diminishing to zero below that. Part of the explanation for the complexity of the function near the survey track is that here the difference is greatest between the radial distance to a diving whale and the perpendicular distance to a surface whale.

The surface assumption of the analysis affects the survey analysis in two ways: a failure to include some animals that are incorrectly estimated as being beyond the truncation distance, and errors it may introduce to the estimate of detection probability.

**Detection probability**

The CDS approach assumes a uniformly distributed perpendicular distribution of animals so that the probability of detecting an animal is:

$$P = \int_0^w g(y)\frac{1}{w}dy \qquad \text{(A2)}$$

In the survey described here, with whales diving according to one of the models A or B and rotation to the surface under the 2D assumption of the target-motion analysis, the distribution of perpendicular distances to animals is no longer uniform (see Fig. A3). The probability of detection is:

$$P' = \int_0^w g(y)\pi_r(y)dy \qquad \text{(A3)}$$

where $\pi_r(y)$ is given in Eqn. A1.

Though in principle A3 can be solved as necessary, A2 is the more convenient (estimated by program *Distance*) and better understood. To investigate bias in using the conventional assumption we calculated the ratio $P/P'$ using dive model A and a hazard-rate detection function, and

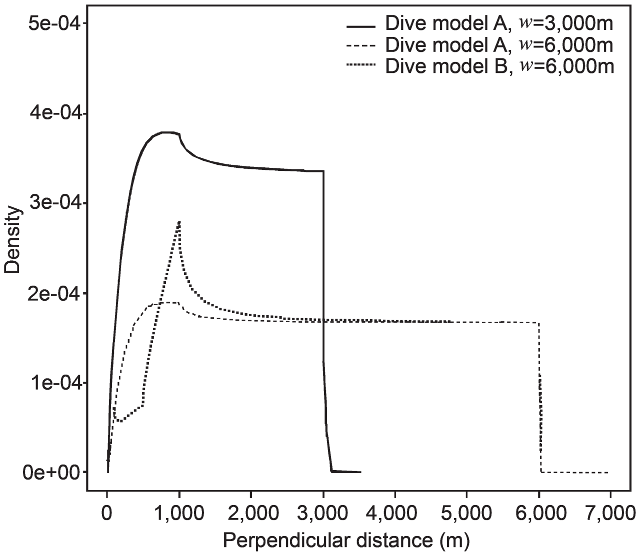

Fig. A3. Distribution of distances for uniformly distributed whales after distortion by the 2D system, using diving models A and B for the depths of the whales. See text for distribution details. Maximum dive depth $h_{\max}$ is set to 1,000m in both models.

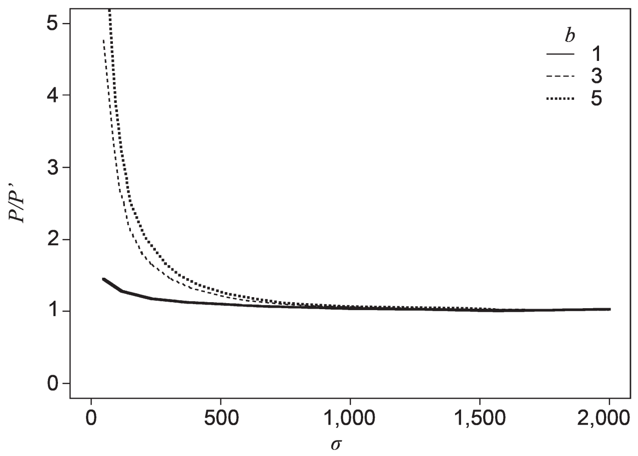

Fig. A4. The ratio *P*/*P'* over a range of the parameter values *b* and $\sigma$ of the hazard-rate detection function, when the parameter values are known. The probabilities *P* and *P'* of detecting animals are explained further in the text.

taking the detection function parameters to be known or unknown.

### *Detection function and parameters known*

The values of *P*/*P'* are shown in Fig. A4 for $w$ = 5,000m. The bias arising from the use of Eqn. A2 is negligible with a hazard-rate detection function and $1 < b < 5$ and $\sigma > 1{,}000$: under these circumstances the hazard-rate function does not respond to the distortion of perpendicular distances close to the survey track (Fig. A3) and performs well. Problems of bias arise when $\sigma < 1{,}000$.

### *Detection function with unknown parameters, and small sample size*

We examined the bias (*P*/*P'*) that arises when the hazard-rate detection function parameters are unknown and estimated by CDS (Eqn. A2). Estimation was carried out using program *Distance* driven by R, using the survey sample size (180) for each run. Each average was based on 100 runs. Results are shown in Table A1. There is strong bias under certain circumstances e.g. when $b$ = 1.

Table A1

Mean of the ratio *P/P'* by simulation, where *P* is obtained by CDS estimation.

| | | *w*/$\sigma$ | | |
|---|---|---|---|---|
| *b* | *w* | 8 | 4 | 2 |
| 1 | 2,000 | 0.42 | 0.56 | 0.73 |
| | 5,000 | 0.43 | 0.68 | 0.74 |
| | 15,000 | 0.81 | 0.92 | – |
| 3 | 2,000 | 0.96 | 0.92 | 0.93 |
| | 5,000 | 0.92 | 1.02 | 0.96 |
| | 15,000 | 1 | 1.02 | – |
| 5 | 2,000 | 1.3 | 1.1 | 1 |
| | 5,000 | 1 | 1 | 1 |
| | 15,000 | 1 | 1 | – |