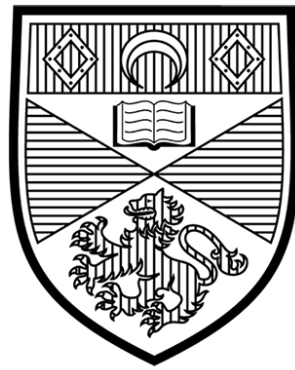


A SIMULATION STUDY ON
THE EFFECTS OF
EVASIVE ANIMAL MOVEMENT
ON
LINE TRANSECT ABUNDANCE ESTIMATES

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Declaration

I hereby certify that this dissertation, which is approximately 9,710 words in length, has been composed by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a degree. This project was conducted by me at the University of St Andrews from May 2023 to August 2023 towards fulfilment of the requirements of the University of St Andrews for the degree of MSc Applied Statistics and Datamining under the supervision of Len Thomas.

Date ...29.8.2023...

Signature of Candidate ...Alexander Ross....

A handwritten signature in black ink, appearing to read 'Alexander Ross', written in a cursive style.

Abstract

A frequently used method in statistical ecology for the estimation of animal populations based on line transect data is that of distance sampling. Since it assumes uniform animal distribution in the area surveyed, however, such estimates are biased when the animals respond to the observer before their detection. In this paper, we present the findings of a simulation study to assess the extent to which the evasive responsive movement behaviour exhibited by marine turtle species influences estimates of their abundance. Distance data showing evasive movement of varying severity were simulated on the basis of the survey design of an ongoing project to study sea turtle-vessel interactions in the Gulf of Mexico. We examined the results from both a single boat observer, to which the conventional distance sampling method was applied, as well as from two configurations of a boat and drone as double observers, for which mark-recapture distance sampling was implemented. Accuracy of the estimates of the primary observer's trackline detection probability $p_1(0)$ and of turtle abundance N in the presence of evasive movement was compared across these three methods. The single observer method showed greatest bias in abundance estimates (-20% bias for uniform distribution and -27% for extreme movement) due to inaccurate $p_1(0)$ estimation. The trial double observer configuration gave the most accurate estimates of abundance (-3% bias for uniform distribution and -14% for extreme movement), as well as of primary trackline detection probability. This study demonstrates how accurate estimates of animal abundance can be made in the presence of evasive movement patterns.

1 Introduction

The study of ecology seeks to learn about the distribution and abundance of living organisms, primarily plants and animals, and the relationship that these organisms have both with each other and with their natural environment (Buckland *et al.*, 2001). Population ecology, with which this paper is concerned, is one of the several branches of this discipline, which also encompasses ecosystem ecology, landscape ecology, as well as others, and is particularly important as investigations in other branches are often underpinned by population data. It distinguishes itself from the other types by its scope, being interested in groups of taxonomically-related organisms and, more particularly, in the fundamental properties such as growth, reproduction, and survival that influence their abundance (Rockwood, 2006). However, obtaining measurements of population abundance and density (abundance per unit area) is not as straightforward as simply observing and recording all individuals of a certain species in question in their associated habitat, as this presents an inordinate and often impossible task, due not only to the size of biological populations but also to the many factors which shape population dynamics and cause abundance to fluctuate spatially as well as in time. Followingly, statistical sampling methods of abundance estimation are necessary to provide accurate quantitative evaluations of populations.

Motivations for population estimation extend beyond academic curiosity, however, because understanding the states and dynamics of populations is essential for informing efforts regarding wildlife conservation and preservation of biodiversity, which may mitigate negative human impact on the natural world and foster the general health of ecosystems around the globe. The motivating case on which our investigation is founded is that of an ongoing project being carried out by the Marine



Figure 1: Map of Florida with the three study sites marked by red points; the St. Petersburg site is in Pinellas County, the Sarasota site is in Sarasota county, and the Destin site is in Okaloosa County. Created with QGIS.

Turtle Research, Ecology and Conservation Group (MTRECG) to assess risk and conduct public outreach to reduce vessel-strikes on the sea turtle population along Florida’s Gulf coastline. The Gulf of Mexico is home to five of the world’s seven marine turtle (*Chelonioidea*) species, harbouring the leatherback (*Dermochelys coriacea*), Kemp’s ridley (*Lepidochelys kempii*), hawksbill (*Eretmochelys imbricata*), green (*Chelonia mydas*), and the loggerhead (*Caretta caretta*), the most abundant in American coastal waters (National Research Council, 2010). According to the U.S. Endangered Species Act, all of these species are either threatened or endangered. Human boating activities in the gulf are known to be an important contributor to the decline of these turtles, with fishing and trawling taking foremost blame for turtles stranded due to injury or death (Chaloupka *et al.*, 2008). For this reason, such efforts to protect these animals are of paramount importance to reducing the risk of extinction for these dwindling populations. This project develops on the exploratory study conducted by Fuentes *et al.* (2021), which investigated responses of conservation and enforcement experts as well as of recreational boaters to potential conservation interventions regarding the same topic.

The data collection process for our motivating project consists of a series of surveys conducted either by both boat and drone concurrently or singly by boat at each of three study sites—Blind Pass and Johns Pass, in Pinellas County of the Tampa Bay area, Big Sarasota Pass and New Pass in Sarasota County, and East Pass, located in Okaloosa County on the Emerald Coast of Florida’s panhandle. These sites are shown in Figure 1 above. To avoid areas that are non-surveyable as a result of unfeasible bathymetry, each site was split into strata based on channels in the region. Different strata at each of these sites are surveyed every other month, with surveys having begun in January 2023. The boat surveys are carried out from a vessel travelling along standardised transects with a small team of observers recording information for each turtle sighted. To address the vessel activity part of the project, an independent observer records information on vessels sighted. The drone surveys are conducted at the same time as the shipboard surveys, with the drone

flying at the same speed above the boat. The data collected from these platforms will enable identification of areas of particularly likely turtle-vessel interactions and of the factors that influence the risk of vessel-strike. It seeks to achieve this objective by leveraging the collected data to determine the abundance and temporal distribution of sea turtles in relation to vessel use activity at each of the surveyed sites, allowing the identification of strategies to reduce marine turtle vessel-strike and the assessment of the challenges and opportunities associated with implementing them. It can thus be seen that accurate estimation of sea turtle abundance is a vital component needed for the project to succeed in its aims.

The method of analysis typically used for abundance estimation using the line transect survey approach characterising our project is that of distance sampling. However, the validity of the results produced under this method rely on several assumptions, one of which is that the animals are distributed uniformly in the study area. It may be stated alternatively as assuming that animals are detected at their initial location, before any movement in response to the observer, as described by Buckland *et al.* (2001, p.31), ensuring that animals are located independently of the transect line position (Thomas *et al.*, 2010). This poses an issue in our case due to the mobility of the turtle subjects, which have been seen to respond to the observing vessel's presence by moving away from it. In this way they exhibit evasive responsive movement. Although random animal movement does not cause much problem, the violation of the uniformity assumption can introduce significant bias into estimates of density and abundance, as was observed by Fewster *et al.* (2008) in a population of eastern grey and red kangaroos in Queensland, Australia. To understand how strong the bias is in our context, it is necessary to study the effect that various degrees of evasive movement have on the estimates of abundance which will ultimately be derived from the data gathered during the course of this project.

Since we sought to investigate the manifestations of the practical implications of evasive movement, whose influence on abundance estimates that are made from the real data cannot be readily ascertained, a simulation study presented itself as most appropriate. This follows on from the similar methodology used by Turnock and Quinn (1991), who used simulation to evaluate methods proposed to deal with attractive responsive movement using data from shipboard sightings of Dall's porpoise in the Gulf of Alaska. However, there exist few other studies that have used simulations to examine the implications of responsive movement, and as such we present in this paper a somewhat novel research inquiry. Here we make use of computer-simulated distance data generated according to a realistic framework informed by field observations of sea turtles. Other covariates, for which data is also recorded during the surveys, were not included in order to simplify the analysis and thereby produce more generally applicable results and recommendations. The cases of both single observer, for which we used conventional distance sampling analysis, and double observer, for which we used mark-recapture distance sampling methods, analyses are included. In each case, data showing varying degrees of responsive movement were simulated, as well as uniform distribution data for comparison. We hoped to quantify the effect of responsive movement on sea turtle abundance estimates at the study sites in order to provide a basis for suggestions on how to correct for the phenomenon and allow accurate figures for population size to be obtained in spite of its presence—a key part to guiding protection efforts of sea turtles on Florida's Gulf coast.

2 Background

Pearl and Reed’s 1920 proposal of the logistic curve as a model for animal population growth marked the first example of an experimental, demographic approach to population estimation (Kingsland, 1982). Wide-ranging developments since then have precipitated a range of methods for closed population abundance estimation and their success has led to the growing power of population estimation as a tool for learning about populations of various species. These methods can largely be divided into distance sampling methods and mark-recapture methods, although there exist others such as the N-mixture and Random Encounter models (Iijima, 2020). Distance sampling methods are all extensions of quadrat sampling, whereby quadrats of fixed area are placed at random in a site containing the population of interest. Its density can then be estimated as the average number of individuals observed in the quadrats, and its abundance as the product of this density with the total study area. To make the counting process more convenient and efficient, this method can be modified by replacing quadrats with strips, allowing the observer to traverse each strip along a single line at its centre. Density may be estimated similarly in this case by dividing the total number of observed individuals by the total area of the rectangular strips. This is known as strip transect sampling. In the project on which this investigation is based, the surveys conducted adhere to the line transect method of population sampling, which was first attempted experimentally by R. T. Kings in the 1930s.

Line transect sampling is only slightly different from the foregoing description of strip transect sampling in that, rather than counting the number of all individuals seen within the transect, the observer records the distance of each detected individual from the line, thus resulting in a sample of distances. In addition, a wider transect area can be surveyed with this method due to the departure of the assumption that detection of subject animals in the study area is certain. On these grounds, an advantage of this method is that it is typically more efficient than strip transect sampling for sparsely distributed objects, as the size of the obtained sample is larger for a given amount of observation effort (Buckland *et al.*, 2001). If a truncation distance $y = w$ from the line is specified in the survey design, beyond which detected objects are not recorded and added to the sample, the width of the transect is $2w$, giving a searched area of $2wL$, where L is the transect’s length. This truncation is useful as it allows discarding of outliers, whose extreme values make modelling of the relationship between the probability of the observer detecting an animal and its distance from the observer more difficult. Owing to the imperfection of the detection process, however, some of the individuals will not be observed despite being present in the transect. Furthermore, the further an animal is from the observer, and therefore from the transect line, the less likely it is that this animal is detected simply by virtue of the fact that it is harder to spot objects that are further away than those that are closer. The proportion P of animals present at a given distance y from the observer that are detected will thus decrease with increasing distance. An estimate of density may be formulated as

$$D = \frac{n}{2wLP_a}, \quad (1)$$

where P_a denotes the average proportion of animals at a given distance that are detected, or alternatively, the proportion of all animals located within the surveyed area that are detected. This proportion cannot be known with certainty, however,

and so the sample of distances \underline{y} provides a way to estimate it as \hat{P}_a according to

$$\hat{P}_a = \frac{\int_0^w \hat{g}(y) dy}{w}, \quad (2)$$

which is in turn dependent on the conventional distance sampling (CDS) component of the maximum likelihood estimator:

$$\mathcal{L}_y(\underline{\theta}) = \prod_{i=1}^n \frac{g(y_i)\pi(y_i)}{P_a}, \quad (3)$$

where $\underline{\theta}$ is the vector of parameters defining $g(y)$, and $\pi(y_i) = \frac{1}{w}$ is the PDF of distances evaluated at y_i . In these equations we introduce a crucial concept in distance sampling theory—the detection function $g(y)$.

$g(y)$ represents the probability of the observer detecting an object given its location at a perpendicular distance y from the transect line being traversed. (In cases where radial distance and angle from the observer are recorded, as in the surveys conducted for this project, the objects' perpendicular distances from the transect line may be derived as $y_i = r_i \sin \theta_i$.) The distance sampling data allow an estimation of this detection function by fitting a curve to the histogram of collected detection distances. This curve may take a variety of model forms that ensure the function can vary according to the distance data. Buckland *et al.* (2001, p.42) describe how suitable models for modelling $g(y)$ are seen to satisfy three properties: robustness, shape and efficiency. The robustness criterion refers to the function's flexibility, allowing it to fit a wide variety of detection function shapes. The shape criterion refers to the function's possession of a 'shoulder', meaning detection probability near the transect line, *i.e.* of animal at small perpendicular distances, is close to 1; the detection function should be flat at zero distance, that is $g'(0) = 0$, preventing a spike in detection probability from being fitted at $y = 0$. Finally, the efficiency criterion refers to the desired property of the detection function model in giving precise estimates with small variance. The fit of a detection function may be assessed using the χ^2 goodness of fit test, which is the only simple test available for this purpose. Although this statistic can be of use in assessing how closely distance data is reflected by the fitted detection function, a poor fit is not necessarily a cause for great concern and model selection based on AIC (Aikake, 1973) may be preferred.

The detection function is also of particular importance as the successful application of distance sampling rests on three assumptions, the most pivotal of which necessitates that its value be unity at zero distance, or $g(0) = 1$, *i.e.* that detection of an animal that lies on the line itself is certain. This is required because the distance data can only provide information on the relative, rather than absolute, detectability at various distances due to the fact that the true number of animals present at any given distance y is most often not determinable. Violation of the assumption can lead to biased estimates of abundance (Rosa *et al.*, 2022) and this is of concern to our motivating project because the detections from the boat have been evaluated as being subject to marked imperfection even on the transect line. This may be seen as a result of 'visibility bias', which Marsh and Sinclair (1989) first decomposed as being a combination of two separate factors—availability bias and perception bias. Availability bias refers to the observer's failure to detect animals because these animals are unavailable for observation for reasons such as being too far underwater. This source of bias has provided the subject for such studies as

Heide-Jørgensen and Lage (2022), who examined its effects on Narwhal abundance estimates in Greenland. On the other hand, perception bias describes failure to detect available animals as a result of environmental conditions or observer error. The delineation of these bias sources becomes particularly relevant when evaluating the effectiveness of the mark-recapture methodology as a candidate to address distance sampling’s inflexibility with respect to $g(0)$.

Mark-recapture was suggested by Pollock and Kendall (1987) as a way to remove visibility bias. As described in Buckland *et al.* (2004, p.109), two methods utilising this technique were developed—one involving a single observer, whereby a sample of animals is marked and the proportion of them that is detected is measured, and the ‘double-count’ method of Graham and Bell (1989), whereby two observers, *i.e.* two platforms of observation, survey the same site and the observations of each serve as a marked sample for the other. We make use of the latter due to the double platform design of most of the project’s surveys. Each observed animal in the study area has associated ‘capture history’ possibilities:

$$\begin{aligned}\underline{\omega} &= (1, 0) - \text{detection by observer 1 only,} \\ \underline{\omega} &= (0, 1) - \text{detection by observer 2 only,} \\ \underline{\omega} &= (1, 1) - \text{detection by both observers (duplicates)}\end{aligned}$$

resulting in $n_1 + n_2 - n_3$ unique detections, where n_1 and n_2 are totals detected by observer 1 and 2 respectively, and n_3 represents duplicates. Estimators of the j^{th} observer’s average detection probability can then be written as $p_j = \frac{n_3}{n_{j-1}}$. These estimates are technically conditional probabilities, and so require observer independence for them to be accurate (Buckland *et al.*, 2004). Herein lies the crux of mark-recapture’s shortcomings, as any factors causing dependence in which particular individuals are detected by each observer induce bias, the one of primary interest in this paper being responsive movement. This dependence is known as ‘heterogeneity’, and any unmodelled heterogeneity results in correlation of the two observers’ detections, which in turn causes overestimation of unconditional detection probabilities p_1 and p_2 where this correlation is positive and underestimation where it is negative. In this way, although mark-recapture can eliminate some of the bias causing $p(0) < 1$ (henceforth using the notation of Buckland *et al.* (2004) of $p(y)$ to refer to the detection function where the trackline detection probability is less than or equal to one, rather than $g(y)$, for which trackline detection probability is assumed fixed at one), the method is generally susceptible to this unmodelled heterogeneity problem due to its independence assumption. From our hitherto descriptions, accurate estimation of abundance would seem elusive, however, a solution to the pitfalls of both approaches can be found in their combination under mark-recapture distance sampling.

Due to the increasing difficulty of detection at greater distances common to both observers, the principal source of heterogeneity in an observer’s detection probability under distance sampling is often distance itself, for which data is collected. Thus, in order to deploy the advantages presented by mark-recapture with respect to $p(0)$ ’s estimation, the two methods may be unified as mark-recapture distance sampling (MRDS), whose development was brought about by a number of studies in the 1980s and ‘90s. By this method, the detection function may be composed as

$$p \cdot (y, \underline{z}) = p \cdot (0, \underline{z}) g \cdot (y, \underline{z}). \quad (4)$$

Here $p \cdot$ represents the combined detection function probability (probability of detection by either observer) and \underline{z} represents a vector of covariates affecting detection

probability in addition to distance y)—a scaled form of that used in distance sampling. If we model detection probability only as a function of distance, as is the case in our simulation, the distance sampling component of the MRDS likelihood can be derived as

$$\mathcal{L}_y(\underline{\theta}) = \prod_{i=1}^{n.} \frac{p.(y_i)\pi(y_i)}{E(p.)}, \quad (5)$$

with $p.(y_i) = p_1(y_i) + p_2(y_i)[1 - p_{1|2}(y_i)]$ being the combined detection function probability for an animal i at distance y , and $E(p.)$ the average probability that an animal is detected at all. The related MRDS capture history likelihood component is given by

$$\mathcal{L}_\omega(\underline{\theta}) = \prod_{i=1}^{n.} \frac{\Pr(\underline{\omega}_i|y_i)}{p.(y_i)}, \quad (6)$$

where the numerator denotes the probability of observing a capture history $\underline{\omega}$ for an animal i at distance y_i . Although the MRDS detection function in equation 4 involves $p.(0)$, we know that distance sampling methods cannot estimate this as they are able to determine the detection function's shape but not its intercept. For this, the capture history likelihood is needed, and additionally, we must assume that dependence $\delta(y)$ between the two observers is zero at at least one distance. This is known as point independence, a method suggested by Laake (1999) to weaken the assumption of full independence, under which $\delta(y) = 1$ for all y . The point is usually chosen as zero distance, that is $\delta(0) = 1$, as this distance is least likely to be affected by heterogeneity on account of the observers both being most likely to detect an animal on the transect line; or as described by Buckland *et al.* (2010), at greater distances only the most detectable animals tend to be recorded, thus inducing greater observer dependence at increasing distance from the transect line.

Having now established most of the theoretical basis for our investigation, the final consideration in the MRDS framework is that of observer configuration, which determines how the data are collected but also how they can be analysed. There exist a number of ways that mark-recapture data can be gathered and they broadly differ with respect to the roles that each observer has in the study design. The only of the three observer configurations in which they are symmetric is the independent configuration, whereby each observer takes a sample of detected animals that serve as detection trials for the other, enabling estimation of both observers' detection functions. Animals in the survey area can take all possible capture histories $\underline{\omega}$ stated above with the following probabilities:

$$\begin{aligned} \Pr\{\underline{\omega} = (1, 0)\} &= p_1(y)[1 - p_2(y)] \\ \Pr\{\underline{\omega} = (0, 1)\} &= [1 - p_1(y)]p_2(y) \\ \Pr\{\underline{\omega} = (1, 1)\} &= p_1(y)p_2(y). \end{aligned}$$

This configuration design has been applied in many studies, including in Conn and Alisauskas' (2018) estimation of arctic waterfowl abundance. We described above how availability bias may influence mark-recapture methods despite their effort to reduce bias in $p(0)$, but the trial configuration of MRDS can help with this matter. In this set-up, one observer acts as the tracker, generating trials for the primary and creating binary data from which an estimation of the primary's detection function can be calculated (Burt *et al.*, 2014). Due to this configuration's observer asymmetry, only the latter two capture histories are possible and have probabilities of the same form as under independence, but with p_1 replaced by $p_{1|2}$. The tracker's detection function is not of interest and so its failure to detect certain animals poses no

issue for our ability to estimate abundance. Trial’s advantage over the independent configuration is that, if the tracker searches sufficiently far ahead of the primary, correlation in detections between them due to availability can be minimised (Buckland *et al.*, 2004). The other possible observer configuration is known as ‘removal’, which is implemented in cases where neither observer can survey independently of the other and only allows a limited MRDS analysis. Given the variety of analytical models outlined, we were presented with the choice of which of them to employ in order to most appropriately analyse our simulated data, and our decision was informed by consulting the survey design of our motivating project.

3 Methods

For our study to yield relevant results that could benefit the eventual analysis of the data collected by this project, we sought to adhere as closely as possible to the real survey design by incorporating its experimental parameters throughout the several sections of our investigation. The most fundamental of these parameters related to the dimensions of the survey area. Detections from the boat were truncated at 200m either side of the transect line so the width of the simulated survey area was set as the same. The length of the project’s transects vary due to topography, so they were simulated with a length $L = 2000$, *i.e.* 2km, determined to be an approximation of their average length from inspection of the effort survey maps. Sample size was an important consideration as too few simulated detections would result in less robust results. We chose to simulate the perpendicular distances of 1000 sea turtles per survey such that the number of duplicates would exceed 100 under no evasive movement. This is based on the recommendation by Buckland *et al.* (2001) that detections should number at least 60 – 80 for line transect surveys. Indeed, the number of turtles actually seen on each survey never approaches the number represented by our chosen sample size, and in fact a significant proportion of surveys do not detect any of the animals at all. In this respect, each simulated survey may be seen as being made up of pooled data, although for the purposes of this investigation we analyse each sample as representing a single survey. With the general survey parameters set, we needed to formulate a model for responsive movement. This was developed based on correspondence with the project leader Mariana Fuentes, from whom we gained knowledge regarding the sea turtles’ typical movement patterns. It has been noted from the surveys that the closer their position to the transect line, the further they were seen to be moving away from the travelling boat, according to a roughly linear relationship, with almost all animals responding. A value for the distance responded by turtles on the trackline itself was reckoned to be about 5m based on field observations. We thus modelled 95% of them responding in conformity to a range of evasive movement degrees with the trackline response varying from 0m (no movement) to 20m (extreme movement) by varying the parameter ρ in the following formula:

$$y = y_0 + \frac{\rho}{z}(z - y_0), \quad (7)$$

where y_0 is an animal’s perpendicular distance at its location before responding to the boat’s presence and y is its distance after responding, according to the relationship dictated by the value of the ρ parameter. The different degrees correspond to lines of different y -intercepts but with the same x -intercept of 100m, representing the approximate distance z at which the animals were seen not to be unaffected by the boat’s presence.

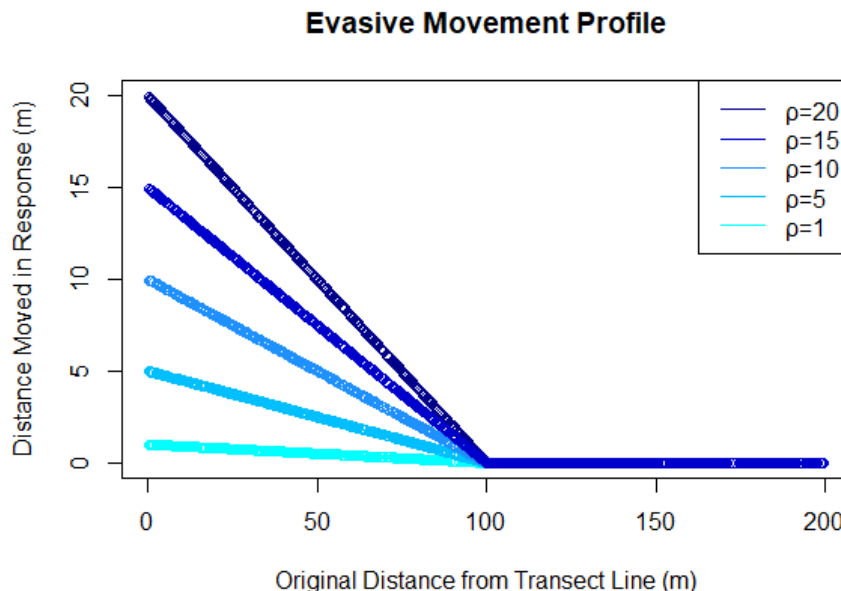


Figure 2: graph showing the responsive movement model for a range of example ρ values. ρ represents the trackline distance moved in response to the boat by sea turtles. Depending on its value, the distance responded by turtles at a given distance from the trackline can be calculated using equation 7. Under $\rho = 0$, the animals' distances from the trackline do not change, maintaining uniform distribution. (All distances are perpendicular.)

Our simulation consisted of three methods used for estimation of sea turtle abundance in the presence of our realistically-constructed evasive movement model. We first use conventional distance sampling in application to an analysis involving only the boat as the observation platform, and we subsequently use MRDS methods in two analyses representing two different configurations of the combined boat and drone observation platforms. The process of our study began with the simulation of distance data for the boat platform as a single observer in order to demonstrate the failure of the distance sampling method alone in producing accurate abundance estimates in situations where the trackline detection probability is appreciably less than 1. This is the case as pooling robustness of the distance sampling method does not apply when $p(0) < 1$, as explained by Buckland *et al.* (2004, p.182). This distance data were simulated under a half-normal model for the boat's detection function to reflect the gradually-decreasing ability of the human observers to make detections at greater distances from the transect line. The boat's trackline detection probability was set as 0.8 on the basis of reports from the field. By specifying the scale parameter σ for this half-normal function we could control how close to the transect line this observer's detection probability declined, with σ^2 denoting the variance of the distribution. As such, the θ vector governing equations 3, 5, and 6 above consists of only this parameter σ for half-normal detection function models. Its value was selected based on the assumption that $p(w) = 0.1$, *i.e.* that its detection probability at 200m was 10%. This comes from the recommendation of Buckland *et al.* (2001, p.104) that the greatest 5% of the distances be discarded if data are untruncated in the field, or to choose a truncation distance such that $\hat{g}(y) = 0.15$. We therefore chose an intermediate value of 10% here as the proportion of theoretical detection distances that would lie beyond the field-specified truncation

distance of 200m, resulting in a half-normal scale parameter of

$$\sigma = \sqrt{\frac{-200^2}{2\ln(\frac{0.1}{0.8})}} = 98.07 \text{ (2 d.p.)}. \quad (8)$$

After specifying the probability of the boat observer's detection on the trackline and the scale parameter, we could then assign detection probabilities to each of the turtles simulated in the study region according to the formula for the scaled half-normal:

$$p(y, \sigma) = 0.8 \exp\left(-\frac{y^2}{2\sigma^2}\right), \text{ for } 0 \leq |y| \leq w. \quad (9)$$

Although turtles were simulated on both sides of the transect line, resulting in both negative and positive y values, these probabilities were generated using the absolute distances $|y|$ on the basis that no asymmetry of the detection function was assumed, given the symmetrical nature of the underlying distribution from which distances were simulated, as well as of the evasive movement model described by equation 7. This assumption of symmetrical detection ability on either side of the platforms can be upheld experimentally by ensuring adequate observer rotation on the boat in the course of the surveys to minimise any discrepancy in their competency.

The detection probabilities were then used to generate detection data by performing a Bernoulli trial for each turtle, *i.e.* a Binomial trial with either a 0 (non-detection) or 1 (detection) outcome, resulting in a certain subset of the thousand simulated animals actually being detected from the boat. This subset served as the data which were then fitted with the CDS method and a half-normal key function. This key function was chosen as it is nearly median-unbiased when the data (detections) are generated by a half-normal (Gonzalez *et al.*, 2017), satisfying the aforementioned efficiency property for a robust detection function model. This function also reduces bias under responsive movement by not fitting the spike at small perpendicular distances due to its round shoulder shape constraint, and so also satisfies the shape criterion of a desired model for $g(y)$. To examine how well the data were fitted by this method we used the p -value of the χ^2 goodness of fit statistic given by Buckland *et al.* (2001, p.71) as

$$\chi^2 = \sum_{i=1}^u \frac{(n_i - n \cdot \hat{\pi}_i)^2}{n \cdot \hat{\pi}_i}, \quad (10)$$

which has a χ^2 distribution with $u - q - 1$ degrees of freedom. Here u denotes the number of groups that the n distance data are binned into, each with sample size of n_i and area under the fitted function of $\hat{\pi}_i$, and q denotes the number of parameters of the fitted detection function. More intuitively, this quantifies difference between the expected proportion of the data falling into a certain distance interval based on the fit and the proportion observed, across the whole range of the fitted data. Finally, we computed and extracted the abundance estimated from the CDS model fit as well as the standard error $\sigma_{\hat{N}}$ associated with it based on a Horvitz-Thompson-like estimator of form

$$\hat{N} = \hat{\tau} = \sum_{i=1}^n \frac{1}{\hat{P}_i}, \quad (11)$$

where \hat{P}_i is the probability that the i^{th} unit appears in the collected sample, and which gives unbiased estimation of the mean (Horvitz and Thompson, 1952). Distance data were simulated both under a uniform turtle distribution and also for

varying degrees of responsive movement to show how well sea turtle abundance estimates could be made based on data only from boat sightings. Two-hundred such surveys were simulated for a number of evasive movement degrees of extent ranging from none (uniform distribution), whereby none of the turtles in the study area move, to extreme, for which the distance responded by turtles on the line is $20m$, in order to observe its effect on abundance estimates.

We then simulated double observer data for the application of two methods constituting two observer configurations, independent and trial, as was the analytical procedure of Rankin *et al.* (2020), who used visual and acoustic observation teams to study rough-toothed dolphins (*Steno bradenensis*) in the Tropical Eastern Pacific. The removal method was not applicable to our analysis because we could consider the observers independent due to the fact that there was no communication between them, deliberate or otherwise. Under the independent configuration on the one hand, we specified the detection functions of both the boat and drone with half-normal curves of different scale parameters. Although the area in which the drone could make detections has a strict cutoff due to its limited field of view, its unconditional detection function was modelled with a half-normal due to the fact that the function called to fit the generalised linear models representing the observers' detection functions requires that they have the same shape parameter, meaning that if the boat's detection function was specified according to a half-normal, as is most sensible, the same must be done for the drone. The half-normal detection function of the drone was not scaled because its trackline detection could be assumed certain as the drone's considerable height above the boat affords it good visibility to much greater depths than is the case for the boat observers. Its detection function was thus modelled as in equation 9 but with the omission of the factor of 0.8, and with a scale parameter giving an effective strip half-width of $\mu = 28$, the half-width of the drone's actual view, which was evaluated as $\sigma_2 = 22.34$ (2 d.p.) by a calculation similar to equation 8. The effective strip half-width $\mu = w \cdot P_a$ refers to the distance within which as many animals are missed as are detected beyond it. The conditional detection functions were fitted to the binary detection data using a logistic mark-recapture model taking the form:

$$p_{j|3-j}(y) = \frac{\exp(\beta_0 + \beta_1 y + \beta_2 \text{platform})}{1 + \exp(\beta_0 + \beta_1 y + \beta_2 \text{platform})}, \quad (12)$$

and enabling estimation of the combined trackline detection probability $p.(0)$. Because we assumed point independence in all double observer analysis, this was combined with a CDS model using a half-normal key function which could subsequently fit the unconditional detection functions $p_j(y)$ and $p.(y)$ based on the simulated distance data. Full independence was not chosen as it represents a rather strong assumption with regard to the lack of heterogeneity at any distance, which is not expected to hold in this project.

When analysing the data under the trial configuration, the drone was chosen as the tracker setting up trial detections for the boat as the primary observer, since the drone's elevation at around $35m$ above the surface of the water means it can detect almost all sea turtles within its camera's view. Here, the drone's detection function was able to be modelled with a step function, more effectively reflecting its operation, and allowed by the fact the drone's unconditional detection function is of no interest under this configuration. This step function was characterised with a detection probability of 0.99 from 0 to $28m$ either side of the trackline, and 0 beyond $28m$. The conditional detection function was calculated as in equation 12,

but without the term denoting the platform effect, since only $p_{1|2}(y)$ is estimated and not $p_{2|1}(y)$. As for the single observer section, two-hundred surveys for a range of responsive movement parameter values were simulated for each double observer configuration. From these we obtained results for the effect of evasive movement on estimated abundance as compared to uniform animal distribution, as well as on the estimated value of $p(0)$ for the primary observer (boat). Truncation in the detection function fitting was not necessary for the fits under any method since none of the animals simulated moved outside the transect width of $200m$ due to the nature of our evasive movement model. There was thus no variability in the maximum distance of turtles from the boat and for this reason no issue was posed to the robustness of our analysis. In population surveys where the subject animals occur in clusters, cluster size and its variability would also naturally be considerations in the construction of a simulation. However, in the surveys conducted hitherto as part of the project this study is founded on, almost all sea turtles have been detected in isolation and so clusters were not incorporated into our model. Furthermore, although the real surveys actually record each detected animal's radial distance and angle from the transect line, it was not necessary to reflect this in the simulation since it complicates the process and ultimately results in the same outcome as simulating perpendicular distances.

In addition, we looked at the effect of the half-normal scale parameter on the turtle abundance estimates and their variance to see if the chosen parameters of the detection functions defined in our simulation would present a further source of bias. Here we used a single half-normal function tested with a range of σ values whose bounds contained those used in the abundance estimation section. For each σ , five-hundred surveys were generated and the mean abundance and standard error statistics across them were obtained. All analysis was conducted using the `mrds` library (Laake *et al.*, 2022) in R software (R Core Team, 2023).

4 Results

4.1 Single Observer

Owing to the fact that many of the surveys making up this project are conducted using a boat as the only platform of observation, we first investigated how accurately abundance could be estimated in these circumstances. Detections from the boat were simulated according to the previously-described parameters. As expected, a growing dearth of detections close to the transect line was found as the responsive movement parameter was increased, as shown in Figure 3, due to the greater distances moved by the simulated sea turtles away from the trackline. Thus, under uniform distribution, the histogram of detection distances reflects the shape of the half-normal detection function curve, and under greatest evasive movement, detection frequency increases sharply to a spike at $20 - 40m$, beyond which detection probability continually declines. Goodness of fit plots show close conformity of the fitted detection distances to the empirical ones for a random single survey under no responsive movement. With increasing evasive movement, greater deviation is seen between the fitted and empirical distances for turtles closer to the transect line due to the discrepancy in the observed animal density and the assumed constant density of the CDS model. This in turn leads to increasing overestimation of the proportion of turtles present at small perpendicular distances. For evasive movement greater than that represented by $\rho = 6$, the p -value of the χ^2 statistic was significant at the 5% level, indicating

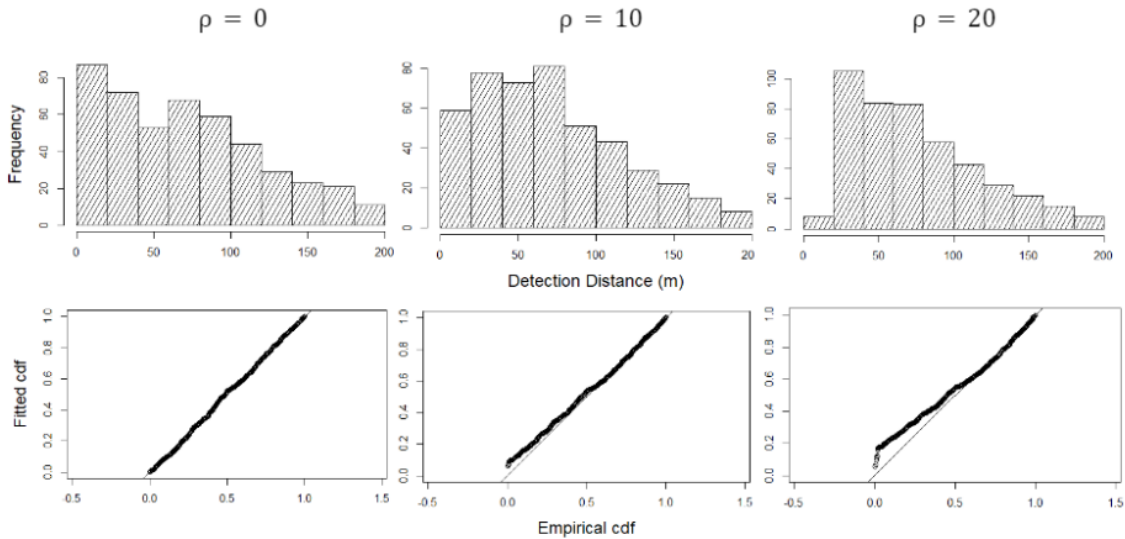


Figure 3: Upper: histograms showing the frequency of simulated detections from the boat at perpendicular distances from the transect line. Detections nearest the trackline decrease for increasing evasive movement. Thus, under constant animal density ($\rho = 0$) the bin closest to the trackline has the most detections, but under greatest responsive movement has the least. Lower: goodness of fit plots for the boat’s detections under the respective evasive movement degrees. The fitted CDF of the detections, which assumes uniformity, deviates more from the empirical under greater evasive movement.

poor fit of the detection function to the distance data in these circumstances.

The estimates of abundance produced from the single observer proved to be systematically negatively biased by roughly 20%—plainly attributable to the violation of the $g(0) = 1$ assumption. This is because the extent to which this method underestimates is directly proportional to the true detection probability at zero distance, as described by Buckland *et al.* (2004, p.22), which is modelled here as 80%. Estimates under evasive movement show even greater underestimation according to a linear relationship between ρ and estimated abundance \hat{N} given by: $\hat{N} = -3.67\rho + 801.89$. Thus, for every metre increase in the evaded distance by animals on the trackline, the estimated abundance decreases by 3.67 ± 0.14 . The greatest level of responsive movement whose error bars (representing one standard error— $\pm 1\sigma_{\hat{N}}$) contained the estimate made from uniform animal distribution was $\rho = 12$. This means that, in the presence of evasive movement characterised by a trackline responded distance greater than 12m, there is less than a 15.7% probability that the true abundance is obtained. For the most extreme evasive movement, \hat{N} is only 7.3% more biased than under no evasive movement; under the suspected level of responsive movement in the study sites constituted by $\rho = 5$, the bias in the estimated abundance is -21.6% , found by using the fitted trendline in Figure 4 to interpolate. From this initial analysis, we witnessed the manifestations of the two sources of bias causing underestimation of abundance— $p(0) < 1$ and evasive animal movement. We attempted to address the former in the following double observer analysis to be able to more accurately estimate $p(0)$ and thence provide more accurate values of \hat{N} .

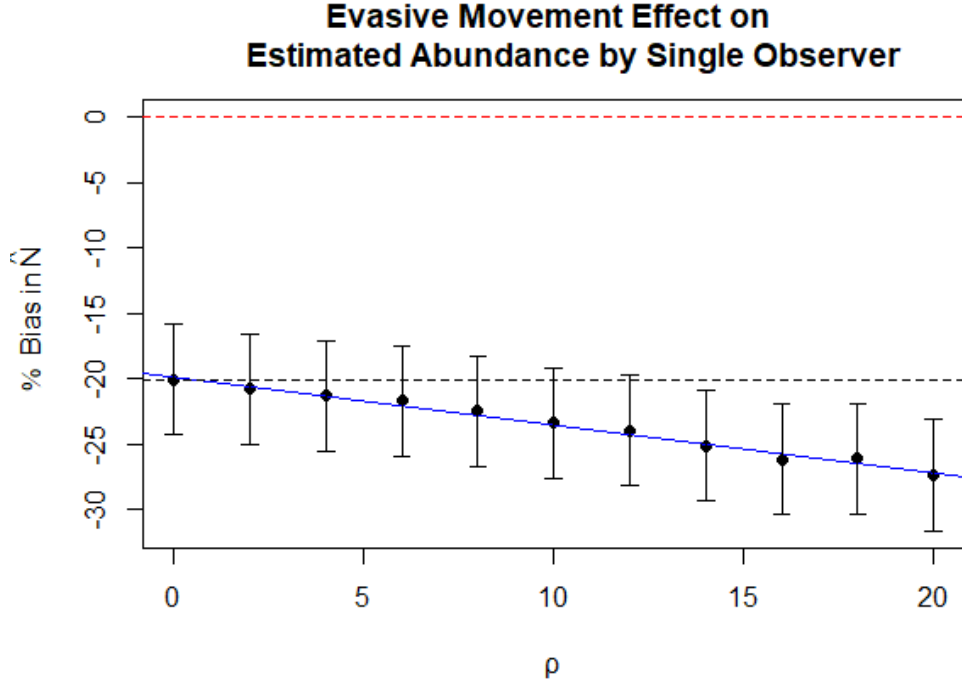


Figure 4: plot showing the percentage bias in the abundance estimate made using the boat as a single observation platform under a range of responsive movement degrees. Marked systematic bias is demonstrated by the discrepancy between the black and red dashed lines, representing the bias incurred by the CDS best estimate of abundance and an unbiased estimate respectively. A strong negative linear relationship is seen.

4.2 Double Observer

The analysis under the independence configuration simulated the detection functions of both the boat and drone with half-normal distributions of scale parameters $\sigma_1 = 98.1$ and $\sigma_2 = 22.3$ (3 s.f.) respectively. Their detections in the presence of uniform distribution of the sea turtles resulted in over a hundred duplicates on average on, and close to, the transect line. The boat’s detections can be seen to extend to either edge of the transect’s width, albeit with few detections at $y = 200$. The drone’s detections are more concentrated around the transect line due to the much smaller scale parameter of its modelled detection function. Although there are some simulated drone detections past $28m$, the drone’s real view half-width, as shown in Figure 5, this is acceptable due to the fact that we are bound by the constraints of the fitting software to approximate the drone’s step function with a half-normal, and that our choice of σ minimises inaccuracy to the real survey design. Detections by the observers decrease under increasing evasive movement since their detection probability remains highest on the trackline while the number of animals simulated there drops. This influences the turtle abundance estimates made using double observation data in a similar way to those from the single boat platform. A negative linear relationship is again observed—abundance estimates are increasingly underestimated for greater evasive movement according to the following equation: $\hat{N} = -5.97\rho + 890.33$, resulting in abundance estimates 5.97 ± 0.15 lower for each successive metre increase in trackline evaded distance. Although the pattern is comparable to that derived from the single observer, the estimates \hat{N} made under the independent configuration of double platform observation are more accurate

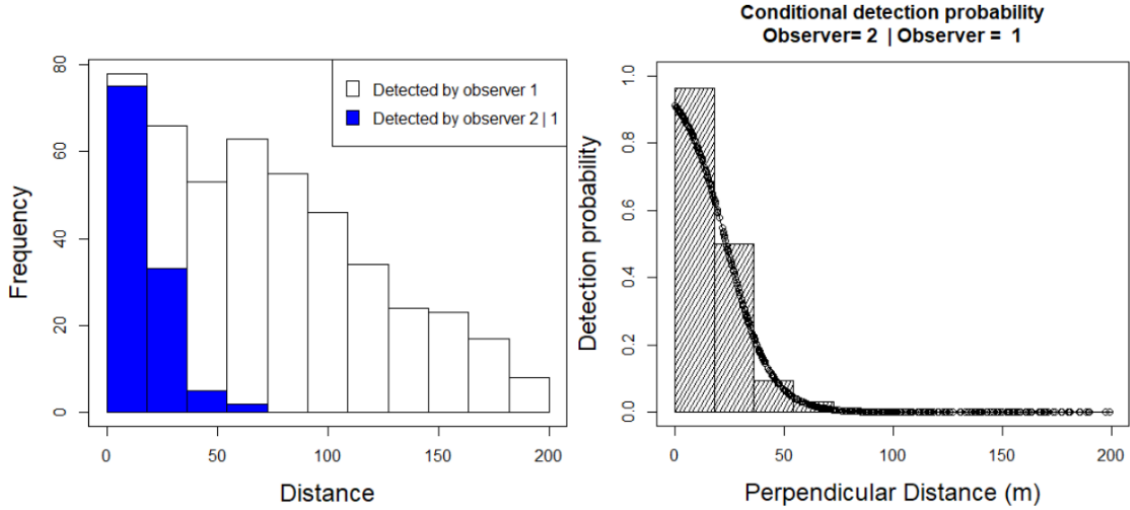


Figure 5: Left: histogram of double observer detections with those detected by the drone highlighted in blue. Their gradually-decreasing shape can be seen to reflect the half-normal model from which the detections were generated. Right: fit of the conditional detection function $p_{2|1}$ modelling the probability that the drone detected a turtle given that it was detected from the boat.

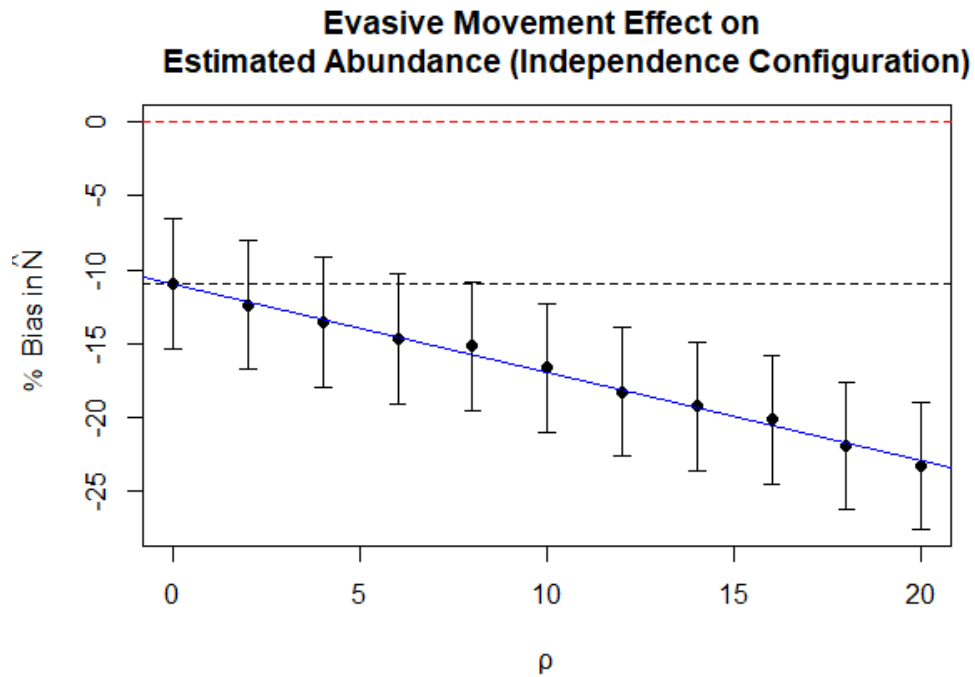


Figure 6: plot showing the percentage bias in the abundance estimates made based on simulated detection data from the boat and drone as double observers. Some systematic bias lingers, although less than for the single observer method.

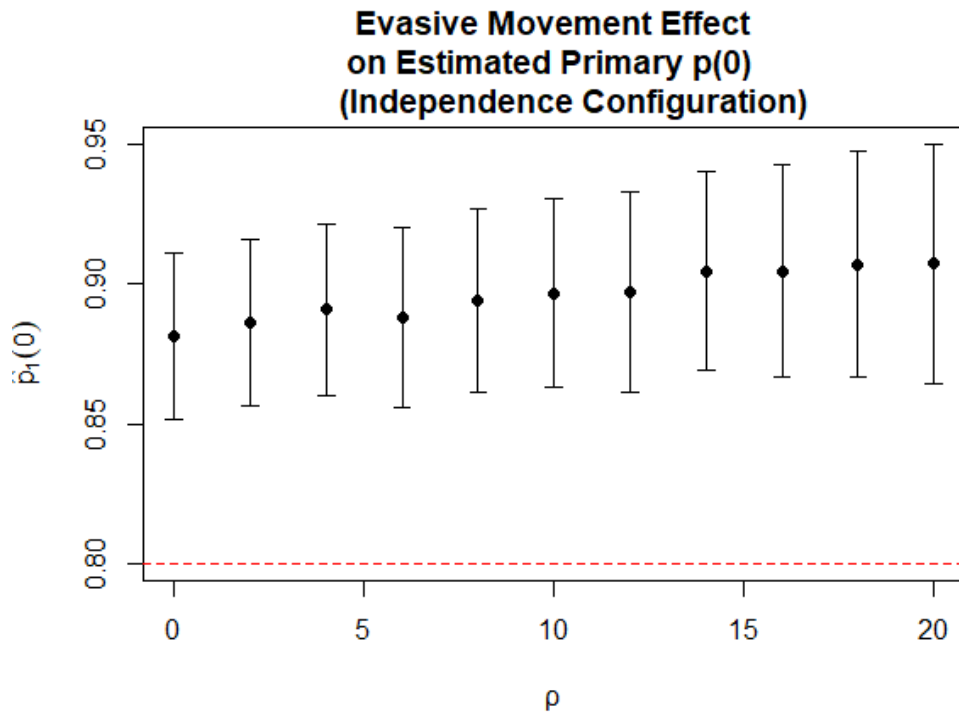


Figure 7: plot showing the absolute values of the boat platform’s probability of detecting turtles at zero distance estimated across a range of evasive movement degrees. $p_1(0)$ is overestimated under all ρ values, as seen by the estimates’ relation to the true modelled probability shown by the dashed red line.

across all ρ values, with the most extreme responsive movement being associated with a -23% bias rather than -27% . Estimated abundance under the suspected existent $\rho = 5$ gives a bias of -14.0% , rather than the -21.6% estimated from the single observer configuration.

This improvement in abundance estimation is largely due to the more accurate estimates of the primary observer’s (boat) trackline detection probability $p_1(0)$, shown in Figure 7. Under the conventional distance sampling model of the single observer design $p_1(0)$ is assumed 1, but the mark-recapture component of the double observer method allows better estimation, here giving $\hat{p}_1(0) = 0.88$ under uniform turtle distribution—10% greater than the true modelled probability. This is also manifest in the larger χ^2 p -values p_{χ^2} , which are significant only at ρ values greater than 10. As this is larger than the limit of $\rho = 6$ given by the single observer analysis, it shows the double observer method can deal with responsive movement more effectively. For greater ρ values, $\hat{p}_1(0)$ also increases, leading to decreased abundance estimates through the equation: $\hat{N} = \frac{n}{\hat{P}_a}$, where n is the number of detections and \hat{P}_a is the estimated average detection probability, which is dependent on $\hat{p}_1(0)$. Furthermore, the variance of the $p_1(0)$ estimates increases slightly for greater ρ values, with greater responsive movement leading to less precision. As a result of improved estimation of the boat’s detection probability on the transect line systematic bias is decreased from 20.1% to 11.0%, but despite this improvement over the single observer’s evaluation, overestimation of the boat’s trackline detection probability means that some systematic bias remains.

Since both platforms report fewer and fewer detections near the trackline for evasive movement of increasing severity, it follows that the number of duplicate detections falls sharply, as the distance responded by animals on the trackline rep-

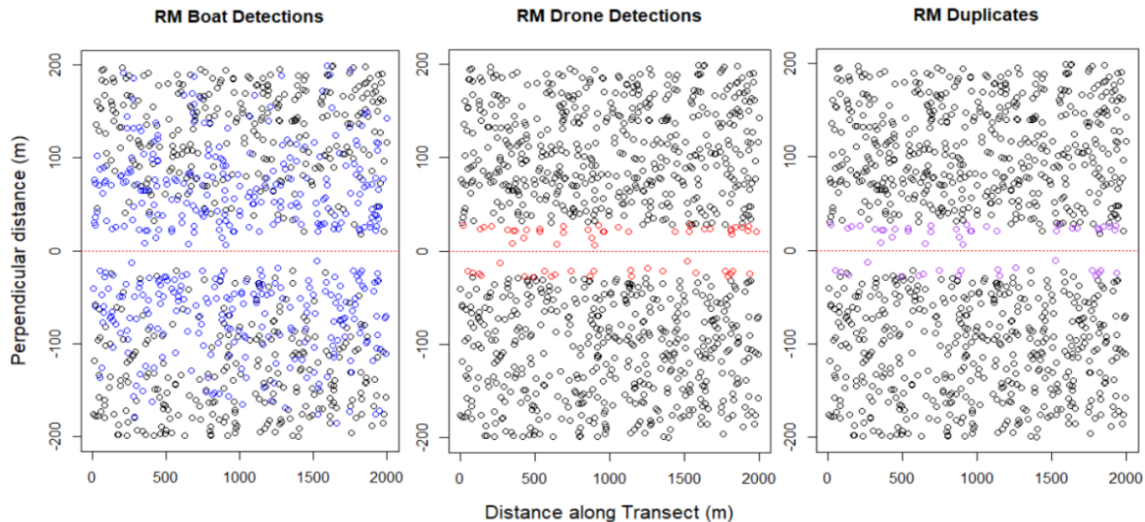


Figure 8: Detections by each of the two observation platforms in the presence of extreme responsive movement given by $\rho = 20$. There are relatively few duplicate detections due to the strict cutoff of the drone’s detection function at $|y| = 28$. The transect line is depicted by the dashed red line.

resents an increasingly large proportion of the drone’s strip half-width. Detections for this case are shown in Figure 8. Because the drone’s detection function was modelled using a step function in the trial configuration analysis, strong evasive movement posed an issue regarding the sufficiency of the number of generated trials (detections by the drone tracker). Figure 9 shows how the drone’s detections constitute only a small number of trials under evasive movement. This was manifest in the fact that the value of the fitted conditional detection function $\hat{p}_{1|2}$ often did not decrease quickly with increasing distance from the transect line or even increased, owing to the paucity of data needed to produce a good fit. Therefore, the randomised surveys which showed the pathological property of increasing fitted detection probability produced massive overestimates of abundance. To remedy this problem and give detection probability decreasing with distance from the transect line instead, it was necessary to constrain the slope of the mark-recapture logit-link equation by forcing the ‘distance’ coefficient to be negative, *i.e.* $\beta_1 < 0$.

Based on the trial configuration analysis, we obtained abundance estimates which showed very little systematic bias due to $p_1(0) < 1$, as the estimate in the absence of responsive movement was only 2.6% less than the true simulated abundance of $N = 1000$. Estimated sea turtle abundance was seen to obey the fitted linear relationship: $\hat{N} = -5.82\rho + 977.94$, giving values 5.82 ± 0.18 less for successive unit increases in ρ . In Figure 10, the estimates’ error bars include the true abundance up to a responsive movement constituted by $\rho = 12$, a value much greater than that expected in the study sites. We see only a -13.7% bias for the most extreme evasive movement given by $\rho = 20$, and -5.1% bias under the suspected value of $\rho = 5$. This can be linked to the appreciable accuracy of the estimated primary’s trackline detection probability, which is given under uniform animal distribution as $\hat{p}_1(0) = 0.82$. The responsive movement value at which the detection function fit deviates significantly from the data, shown by a significant χ^2 p -value, is again given by $\rho = 10$. As evasive movement increases, so do the estimates of $p_1(0)$ slightly, with $\rho = 20$ giving a value of 0.85. With that being said, the estimates of $p(0)$ under all

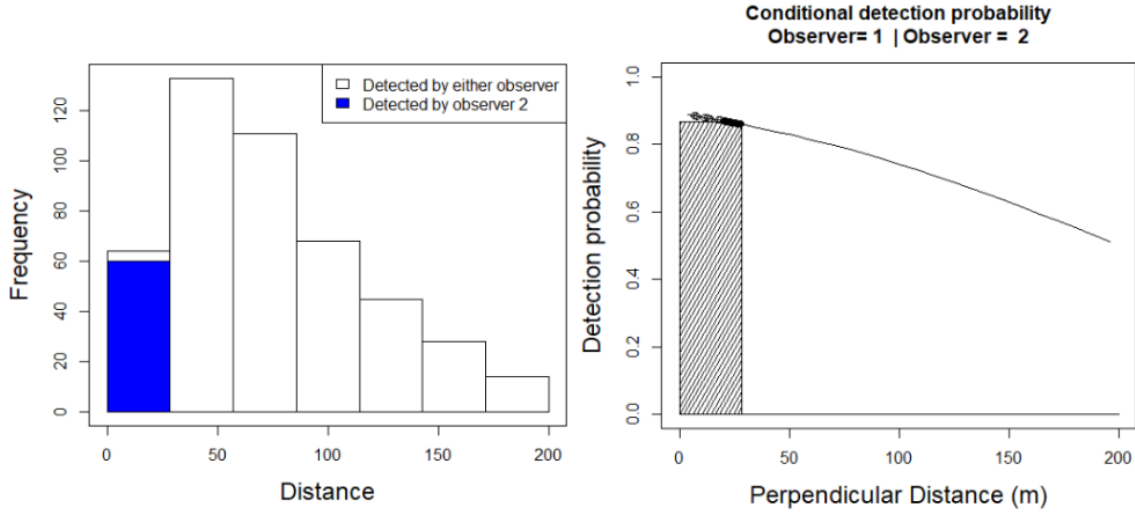


Figure 9: Left: histogram of double observer detections, with detections by the drone generated as trials highlighted in blue—there are less than 60 trials. Right: fitted conditional detection function $p_{1|2}$ based on these trials. A poor fit is produced, as seen by the discrepancy between the shapes of the fitted curve and the histogram of detections.

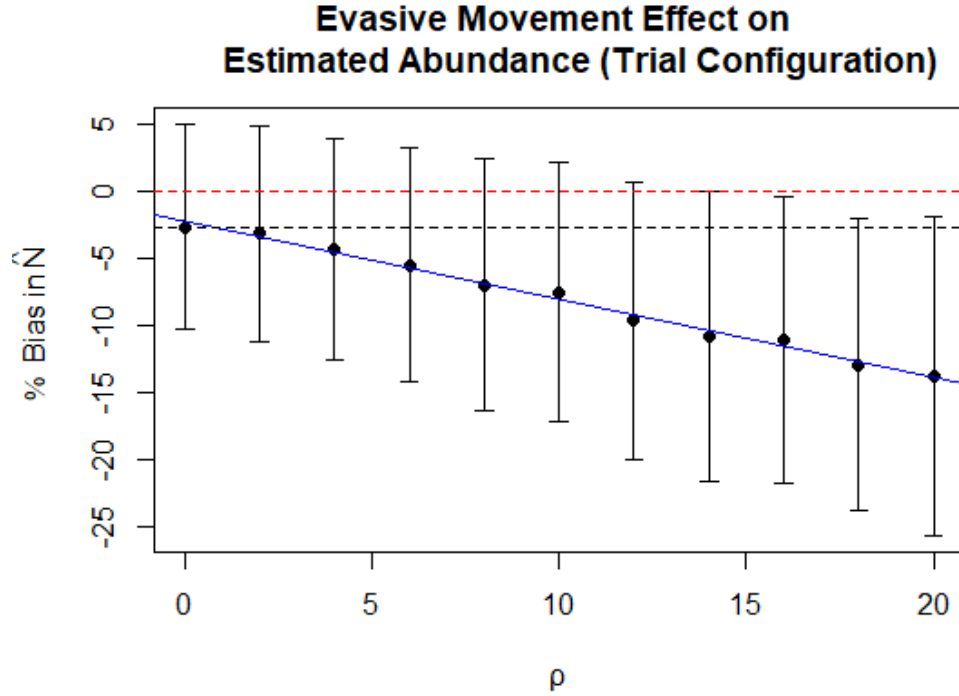


Figure 10: plot showing the percentage bias in the abundance estimates made based on simulated detection data from the boat and drone as double observers under the trial configuration. Systematic bias is significantly smaller than for the other two methods. Only the most extreme evasive movement degrees result in the true abundance lying further than 1 s.e. from the best estimate.

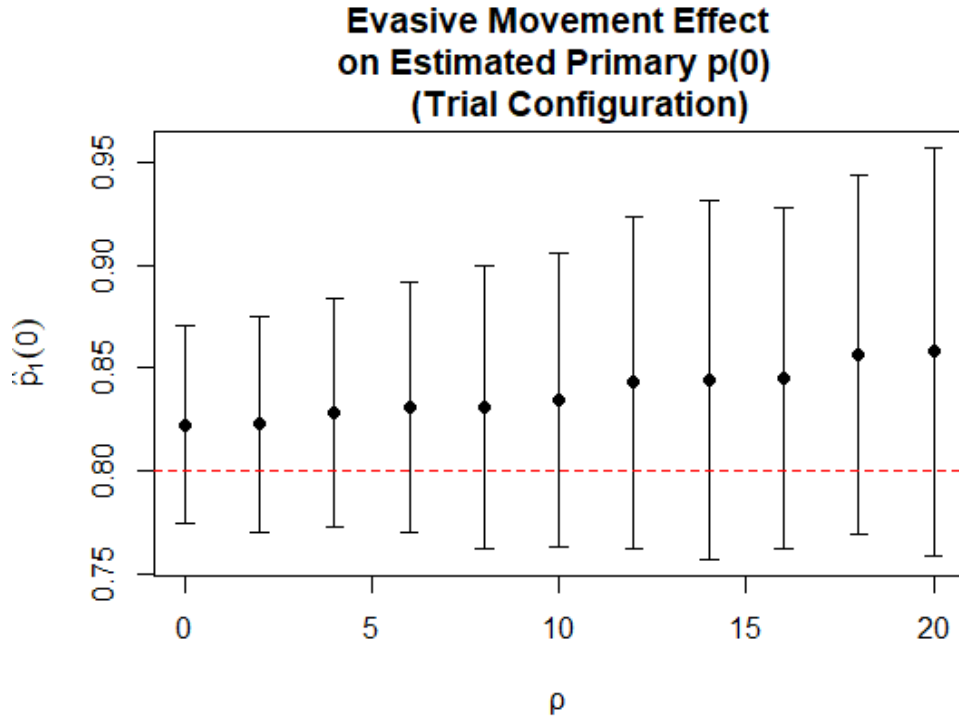


Figure 11: Percentage bias in the estimates of the boat's trackline detection probability based on trial configuration double observer analysis. The true value of $p_1(0)$ lies within one standard error of the best estimates across all degrees of evasive movement. The estimates increase slightly as ρ increases, as do their standard errors $\sigma_{\hat{p}_1(0)}$, as shown by increasingly wide error bars. Estimation under no responsive movement is associated with a $\sim 3\%$ bias.

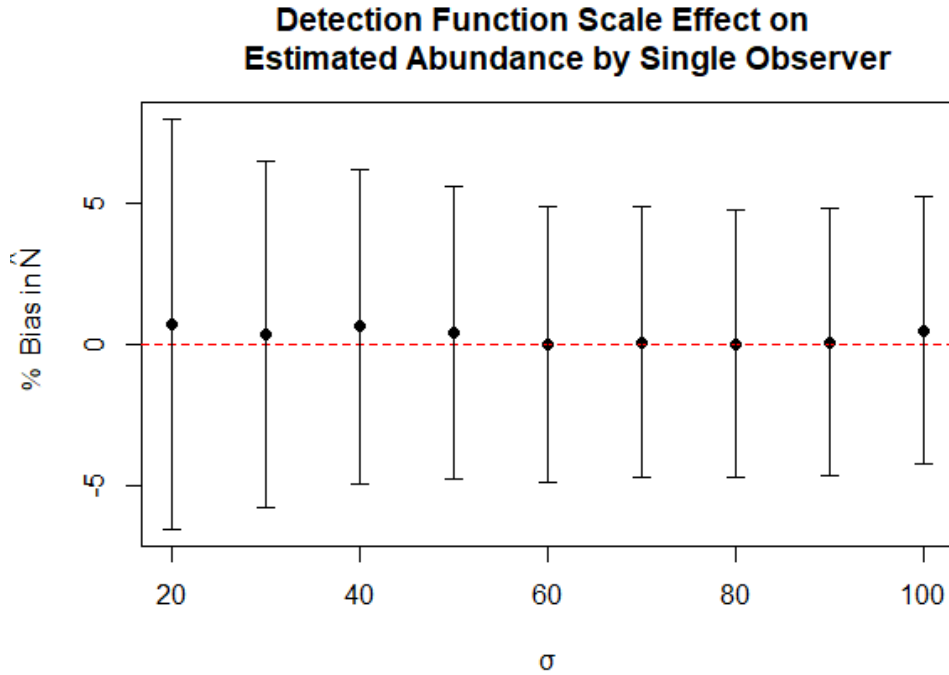


Figure 12: bias in the abundance estimates incurred using a half-normal detection function of various scale parameter values in the presence of uniform animal distribution. For each tried σ , abundance was estimated from each of five-hundred random surveys showing no responsive movement to obtain a baseline estimate of bias. Best estimates of abundance at all σ values produced minimal bias in abundance estimates ($< 1\%$).

ρ values contain the true transect line detection probability of 0.8. From this it can be judged that the trial configuration of the double observation platform design performs best across all levels of evasive movement in the accuracy of its estimates for the boat's $p(0)$ and therefore also for N .

In our additional investigation of the half-normal scale parameter's effect on abundance estimate bias, we tested σ values in the range of 20–100 to ensure that our chosen scale parameters for the boat and drone were included in the interval. Five-hundred random surveys were simulated for each parameter value under uniform animal distribution. From Figure 12, negligible bias can be seen across all tested scale parameters, but the variance of the estimates was seen to be slightly greater at lower values up to around $\sigma = 50$. On these grounds, the scale parameters used in the half-normal models ($\sigma = 22.3$ and $\sigma = 98.1$) should not present any significant source of bias in the estimated abundances. Results given by each of the three estimation methods are summarised in the appendix.

5 Discussion

Overall, we saw that greater evasive responsive movement leads to linearly greater negative bias in abundance estimates across all estimation methods. The phenomenon also increases the variance of the estimates of the primary's trackline detection probability more markedly than that of abundance. Estimation based on the single observer data seems to be less susceptible to bias caused by responsive movement, as the slope coefficient for ρ is significantly shallower than in the cases of both double observer configurations— -3.67 vs -5.97 for the independent config-

uration and -5.82 for the trial configuration. However, this was overshadowed by the fact that the CDS method of the single observer analysis was plagued by large negative systematic error, as was expected due to the infraction of the $g(0) = 1$ assumption. Under the independent configuration of the MRDS analysis, less systematic bias was seen, although $p_1(0)$ was still overestimated across all values of responsive movement. As a result, the true abundance was not contained within the 1 standard error bounds for the estimates across all ρ . With the use of real data, this bias could ordinarily be explained by unmodelled heterogeneity in the two observers' detection. However, this result was somewhat surprising given that our simulated data made use of no covariates other than distance and therefore contained no additional sources of dependence in their detection functions. Since $p_1(0)$ was overestimated by 10% under uniformity, this can be seen to contribute to almost all the of the 11% bias in \hat{N} for $\rho = 0$. This inaccuracy in $\hat{p}_1(0)$ subsequently led to inaccurate estimation of the detection functions, which, since no turtles responded out of the simulated study area on account of how the evasive movement model was defined, can be seen as responsible for the cause of the bias observed. The variance of the abundance estimates, as well as of the $p_1(0)$ estimates, stayed largely consistent. Under the trial configuration of the MRDS analysis, the abundance estimates up to $\rho = 14$ contained the true abundance within one standard error. Minimal bias was seen under uniform animal distribution. The true $p_1(0)$ lay within one standard error of the estimates across all ρ values. Because of the issue of inaccurate fitting of the conditional detection function slope caused by few trials, the variance of the estimates for both abundance and $p_1(0)$ increased noticeably with increasing responsive movement.

Our results were dependent on the evasive movement model used in the simulation and as such this presents a limitation of the investigation. The model was developed based on feedback from observers on the surveys, rather than on parameters which had already been determined through prior investigation, and so only represents an informed guess as to the true general pattern of the sea turtles' responsive movement to the boat. All responding turtles were modelled as moving perpendicularly away from the transect line, which of course constitutes a simplification of the turtles' movement patterns as their direction of response may in fact vary depending on proximity to the oncoming vessel in addition to their distance from the trackline. For example, sea turtles close to the boat may have a component of their motion parallel to, as well as perpendicular to, the transect line in order to outswim the vessel. Any such complexities in their evasive movement patterns were not included here. Field investigations to study the effect of survey effort on marine animals have been carried out in the past, such as Southall *et al.*'s (2016) measurement of behavioural responses of cetaceans to sonar. In this way, a simpler auxiliary study to quantify the turtles' behavioural response to the surveying boat on the line transect in our case would behoove this project by enabling a more rigorous parameterisation of their responsive movement profile in the study sites. Our results were also dependent on the modelled trackline detection probability of the boat primary, which was chosen based on a best guess from field observations. Although altering the value of $p_1(0)$ in our analysis would not change the results significantly, to obtain greatest applicability of the results to the real dynamics of the sea turtles, a deeper study to determine $p_1(0)$ could be carried out. This could be achieved by incorporating a dynamic availability hazard-rate model to address the principle source of bias giving rise to $p_1(0) < 1$ and enabling determination of $p_1(0)$ with greater rigour.

There are in fact many variables other than perpendicular distance from the transect line that may influence detectability and dependence between the detection functions of the boat and the drone. The surveys conducted for this project collect information on the species, size/stage class, timestamp, and depth of the detected turtles in addition to their location from the vessel. These were not modelled in our simulation to simplify the analysis, as the number of covariates describing these ancillary variables that could have been included is large and would complicate the analysis exponentially. When included in the analysis of the survey data, however, they could be used for stratification or incorporated as a vector \underline{z} of covariates by modelling detection probability as a linear function of them. The distance sampling component would then take the form of the multiple covariate distance sampling (MCDS) version of equation 3, and the mark-recapture component would incorporate a design matrix \mathbf{Z} including distance y and other covariates \underline{z} . Covariates that have a statistically significant effect on abundance estimation could be chosen by model selection based on AIC. Making use of these covariates in the analysis of the real survey data would not only likely improve estimation of abundance by recognising their impact on detectability, but also allow a more detailed demographic understanding of the sea turtle population with respect to the relative abundance of different species and their age structure.

The simulation code may be further customised in the analysis of the real data to recognise the variation between population abundances at each of the three study sites by incorporating their specific regional stratifications in the Horvitz-Thompson-like estimation of abundance (equation 11). For each region, multiple samples associated with different degrees of effort can be specified according to the length of the transects. Since the transects greatly vary in length due to the study sites' topography, the number of detectable sea turtles in them shall too, and therefore the amount of collectable data from which abundance can be estimated will vary across the transects. Acknowledgement of this variability in survey effort may result in more accurate abundance estimates across the sites.

Our chosen sample size was sufficiently large to give at least 60 total detections, a practical minimum for reliable estimation of the detection function using distance sampling given by Buckland *et al.* (2001, p.240). This was the case even under extreme responsive movement and so cannot be seen as a limitation of the validity of the abundance estimates produced. Furthermore, the number of duplicates always exceeded 30, the suggested minimum for valid estimation (Buckland *et al.*, 2004). For efficient simulation of distance data, it has been suggested that sample size should be generated from a discrete distribution. In our case, its value was instead fixed at $N = 1000$. This does not present an issue though because simulating sample size from a distribution would not change the estimates of bias, but in some cases would result in the generation of samples too small for accurate analysis, (even our sample size in some cases resulted in too few trials for accurate estimation under the trial configuration).

Our study simulated the spatial locations of turtles and the survey data based on them could be seen as describing a snapshot in time. Thus, time was not incorporated as a factor in the simulation model, meaning that detections were not simulated in the order they might occur. Time was not included as it would have greatly increased the simulation's complexity due to the additional considerations of the animals' speed, direction changes *etc.*, and made analysis much more difficult for no gain in relevance to our project. As the estimation methods used in our simulation were concerned only with perpendicular distances, the simulated along-trackline

distances provided no additional information in the analysis. Since the spatial locations of detected turtles are recorded in the real surveys by radial distance and angle from the boat, the along-trackline distances \underline{x} are also obtainable. To make use of this data, models based on two-dimensional spatial data that include along-trackline in addition to perpendicular distances could be implemented, as such models have been shown to contain information on the availability process (Cooke, 2001). This is because the proportion of duplicates detected by both observers at the same times relative to those detected at different times gives an indication as to how often the animals are available. As described by Buckland *et al.* (2004, p.173), however, such models only present a significant improvement over regular perpendicular distance models when applied to animals exhibiting discrete availability, that is becoming detectable for brief instants, and so may not bring a great advantage in this project since our sea turtle subjects' availability is demonstrably best characterised instead as intermittent (changeable availability for periods longer than an instant).

Finally, a consideration that could well be added in the analysis of the collected data is that of model selection. In our simulation, only one parameterisation of the fitted detection function was incorporated, *i.e.* the half-normal. A hazard-rate key function of form

$$g(y, \sigma, b) = 1 - \exp\left(-\left(\frac{y}{\sigma}\right)^{-b}\right) \quad (14)$$

was also considered to deal with the step function modelling of the drone's detection function, however, was not incorporated due to the shape parameter restriction of the detection functions fitted by the software used. Further investigations could include a key + series adjustment formulation of the detection function, *i.e.* $g(y) \propto \text{key}(y)[1 + \text{series}(y)]$, with cosine and Hermite polynomial series expansions applied to the half-normal key candidate, and cosine and simple polynomial expansion applied to the hazard-rate key, in line with the method of Gonzalez *et al.* (2017), to allow more flexibility in the detection functions and improve their fit. The best fitting model could then be selected by AIC. This would increase the robustness of the analysis in cases such as this project, where the true detection function of the observers is not known.

6 Conclusion

From our analysis, we obtained equations for the relationships between estimated abundance and evasive movement for the two double observer configurations. Consequently, if the distance moved in response by turtles on the transect line can be rigorously determined as $\hat{\rho}$ by field observations, one can arrive at accurate abundance estimates using the following equation:

$$N = \frac{1000}{a}(\hat{N} + b\hat{\rho}), \quad (13)$$

where the values of a and b represent the estimated intercept and slope coefficients respectively, and whose analytically-determined values are given in the results section for each estimation method. Of all three analysis methods, the trial configuration of the double observer MRDS method proved to be the best performing. We therefore recommend this method in the analysis of the real data collected by the surveys for which there is a double platform design. Since some of the surveys are necessarily conducted using only the boat, distance sampling rather than MRDS will need to be used, and we advise that it be used with caution due to its inability to deal with

bias due to $p(0) < 1$. However, using the equations given above, accurate abundance estimates may be recovered using any of the methods used here.

The results of this investigation are naturally relevant to, and beneficial for, informing the analysis strategy of the subject project to assess risk and conduct public outreach with the aim of reducing vessel-strikes on the sea turtle population of Florida's Gulf coastline. The applicability of this study's scope extends further, however. The Great Barrier Reef Dolphin Project (GBRDP) is currently being developed by marine biologist researchers at Southern Cross University and Flinders University to be carried out from September to November 2023 (Southern Cross University, 2023). Its objective is to assess the abundance and distribution of the threatened Australian snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback (*Sousa chinensis*) dolphin species in the northern Great Barrier Reef along the east coast of Queensland, Australia. The proposed method of data collection constitutes parallel line transects surveyed by double observer vessel platforms for implementation of the distance sampling method of abundance estimation. Since the dolphin subjects of this project are also expected to respond evasively to the surveying vessels' presence, in a way somewhat similar to the sea turtle project, the investigation presented in this paper may bear on addressing the issues brought about by such responsive movement.

Appendix

The R code in which this study's analysis was conducted can be accessed here: Code Supplement.

Single Observer Results:

ρ	\hat{N}	$\sigma_{\hat{N}}$	p_{χ^2}
0	799	42.2	0.494
2	792	42.2	0.443
4	787	42.2	0.275
6	783	42.3	0.0829
8	776	42.3	4.20e-3
10	766	42.3	1.23e-4
12	761	42.3	1.23e-5
14	749	42.2	2.37e-5
16	739	42.1	5.76e-7
18	739	42.3	9.16e-8
20	726	42.3	1.60e-11

Double Observer (Independence) Results:

ρ	\hat{N}	$\sigma_{\hat{N}}$	$\hat{p}_1(0)$	$\sigma_{\hat{p}_1(0)}$	p_{χ^2}
0	890	44.0	0.881	0.0298	0.383
2	876	43.8	0.886	0.0300	0.479
4	864	43.7	0.891	0.0305	0.429
6	853	43.7	0.888	0.0323	0.314
8	848	43.7	0.894	0.0327	0.184
10	834	43.6	0.897	0.0338	0.0735
12	817	43.4	0.897	0.0359	0.0267
14	808	43.4	0.905	0.0357	1.87e-3
16	799	43.4	0.905	0.0405	2.03e-4
18	781	43.2	0.907	0.0405	1.01e-5
20	768	43.1	0.907	0.0428	1.71e-6

Double Observer (Trial) Results:

ρ	\hat{N}	$\sigma_{\hat{N}}$	$\hat{p}_1(0)$	$\sigma_{\hat{p}_1(0)}$	p_{χ^2}
0	974	76.0	0.822	0.0480	0.464
2	969	80.2	0.823	0.0525	0.474
4	957	82.2	0.828	0.0556	0.330
6	945	87.0	0.831	0.0609	0.191
8	931	93.5	0.831	0.0688	0.103
10	925	96.3	0.835	0.0715	0.0305
12	904	103.1	0.843	0.0807	3.26e-3
14	892	108.1	0.844	0.0817	4.69e-4
16	889	106.3	0.845	0.0830	1.82e-5
18	871	108.5	0.857	0.0871	2.20e-6
20	863	118.5	0.858	0.0990	3.94e-7

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References

- Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *International Symposium on Information Theory, 2nd edn*, (eds B.N. Petran and F. Csáaki), Budapest: Akadémiai Kiadó, pp. 267–281.
- Buckland, S. T., Anderson D. R., Burnham, K. P., Laake, J. L., Borchers D. L., and Thomas L. (2001) *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. New York: Oxford University Press, ISBN: 978-0-019-850927-1.
- Buckland, S. T., Anderson D. R., Burnham, K. P., Laake, J. L., Borchers D. L., and Thomas L. (2004) *Advanced Distance Sampling: Estimating Abundance of Biological Populations*. New York: Oxford University Press, ISBN: 978-0-19-922587-3.
- Buckland, S. T., Laake, J. L., and Borchers, D. L. (2010) Double-Observer Line Transect Methods: Levels of Independence. *Biometrics*, 66(1), 169–177. Available at <http://www.jstor.org/stable/40663164>.
- Burt M. L., Borchers, D. L., Jenkins, K. J., Marques, T. A., Using Mark–Recapture Distance Sampling Methods on Line Transect Surveys, *Methods in Ecology and Evolution*, 5(11), pp. 1180–1191. Available at doi:10.1111/2041-210x.12294.
- Chaloupka, M., Bjørndal, K. A., Balazs, G. H., Bolten, A. B., Ehrhart, L. M., Limpus, C. J., Seganuma, H., Troeng, S. and Yamaguchi, M. (2008) Encouraging Outlook for Recovery of a Once Severely Exploited Marine Megaherbivore, *Global Ecology and Biogeography* 17. Available at <https://doi.org/10.1111/j.1466-8238.2007.00367.x>.
- Conn, P. and Alisauskas, R. (2018) Simultaneous Modelling of Movement, Measurement Error, and Observer Dependence in Mark-Recapture Distance Sampling: An Application to Arctic Bird Surveys. *The Annals of Applied Statistics*, 12. 96–122. 10.1214/17-AOAS1108. Available at <https://doi.org/10.1101/126821>.

Cooke, J. G. (2001) A Modification of the Radial Distance Method for Dual-Platform Line Transect Analysis, to Improve Robustness. Paper SC/53/IA31 presented to the IWC Scientific Committee. London (unpublished), 7pp.

Fewster, R. M., Southwell, C., Borchers, D. L., Buckland, S. T., and Pople, A. R. (2008). The Influence of Animal Mobility on the Assumption of Uniform Distances in Aerial Line-Transect Surveys. *Wildlife Research*, 35(4), 275-288. Available at <https://doi.org/10.1071/WR07077>.

Fuentes, M. M. P. B., Meletis, Z. A., Wildermann, N. E., Ware, M. (2021) Conservation Interventions to Reduce Vessel Strikes on Sea Turtles: A Case Study in Florida. *Marine Policy*, 128, 104471. Available at <https://doi.org/10.1016/j.marpol.2021.104471>.

Gonzalez, R. P., Thomas, L. and Marques, T. A. (2017) Estimation Bias Under Model Selection for Distance Sampling Detection Functions. *Environmental and Ecological Statistics* 24, 399–414. Available at <https://doi.org/10.1007/s10651-017-0376-0>.

Graham A., and Bell, R. (1989) Investigating Observer Bias in Aerial Survey by Simultaneous Double-Counts. *Journal of Wildlife Management*, 53, 1009-16. Available at <https://doi.org/10.2307/3809603>.

Heide-Jørgensen, M. P., and Lage, J. (2022) On the Availability Bias in Narwhal Abundance Estimates. *NAMMCO Scientific Publications*, 12. Available at <https://doi.org/10.7557/3.6518>.

Horvitz, D. G., and Thompson, D. J. (1952) A Generalization of Sampling Without Replacement From a Finite Universe. *Journal of the American Statistical Association*, 47(260), 663–685. Available at <https://doi.org/10.2307/2280784>.

Iijima, H. (2020) A Review of Wildlife Abundance Estimation Models: Comparison of Models for Correct Application. *Mammal Study*, 45(3), 177–188. 10.3106/ms2019-0082. Available at <https://doi.org/10.3106/ms2019-0082>.

Kingsland, S. (1982) The Refractory Model: The Logistic Curve and the History of Population Ecology. *Quarterly Review of Biology - QUART REV BIOL*, 57. 10.1086/412574.

Laake J., Borchers D., Thomas L., Miller D., Bishop J. (2022) mrds: Mark-Recapture Distance Sampling. R package version 2.2.8. Available at <https://CRAN.R-project.org/package=mrds>.

Laake, J. L. (1999) Distance Sampling with Independent Observers: Reducing Bias from Heterogeneity by Weakening the Conditional Independence Assumption. *Marine Mammal Survey and Assessment Methods* (eds G. W. Garner, S. C. Amstrup, J. L. Laake, B. F. Manly, L. L. Macdonald, and D. G. Robertson). Rotterdam: Balkema, pp. 137-48.

Marsh, H., and Sinclair, D. F. (1989) Correcting for Visibility Bias in Strip Transect Aerial Surveys of Aquatic Fauna. *Journal of Wildlife Management*, 53, 1017-24.

Available at <https://doi.org/10.2307/3809604>.

National Research Council (2010) *Assessment of Sea-Turtle Status and Trends: Integrating Demography and Abundance*. Washington, DC: The National Academies Press. Available at <https://doi.org/10.17226/12889>.

Pollock, K. H. and Kendall, W. L. (1987) Visibility Bias in Aerial Surveys: A Review of Estimation Procedures. *Journal of Wildlife Management*, 51, 502-10. Available at <https://doi.org/10.2307/3801040>.

R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org/>.

Rankin, S., Oedekoven, C. and Archer, F. (2020) Mark Recapture Distance Sampling: Using Acoustics to Estimate the Fraction of Dolphins Missed by Observers During Shipboard Line-Transect Surveys. *Environmental and Ecological Statistics*, 27, 233–251. Available at <https://doi.org/10.1007/s10651-020-00443-7>.

Rockwood, L. L. (2006) *Introduction to Population Ecology*. Oxford: Blackwell Publishing, pp.1, ISBN-13: 978-1-4051-3263-3.

Rosa, G., Salvidio, S., Trombini, E., and Costa, A. (2022) Estimating density of terrestrial reptiles in forest habitats: the importance of considering availability in distance sampling protocols. *Trees, Forests and People* 7:100184. Available at <https://doi.org/10.1016/j.tfp.2021.100184>.

Southall, B. L., Nowacek, D. P., Miller, P. J. O., and Tyack, P. L. (2016) Experimental Field Studies to Measure Behavioral Responses of Cetaceans to Sonar. *Endangered Species Research*, Vol. 31: 293–315. Available at doi: 10.3354/esr00764.

Southern Cross University (2023) GBR Dolphin Project Daniele Cagnazzi - Southern Cross University. Available at: <https://www.scu.edu.au/news/2023/gbr-dolphin-project-daniele-cagnazzi/> (Accessed: 29 August 2023).

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A. and Burnham, K. P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47: 5-14. Available at <https://doi.org/10.1111/j.1365-2664.2009.01737.x>

Turnock, B. J., and Quinn, T. J. (1991) The Effect of Responsive Movement on Abundance Estimation Using Line Transect Sampling. *Biometrics*, 47(2), 701–715. Available at <https://doi.org/10.2307/2532156>.