Running title: Spatial models for distance sampling
Number of words: ∼3879
Number of tables: 0
Number of figures: 5
Number of references: 29

Spatial models for distance sampling data: recent developments and future directions

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Date of submission: 21st December 2012

Summary

1. Our understanding of a biological population can be greatly enhanced by modelling their distribution in space and as a function of environmental covariates.
2. Density surface models consist of a spatial model of the abundance of a biological population which has been corrected for uncertain detection via distance sampling methods.
3. We offer a comparison of recent advances in the field and consider the likely directions of future research. In particular we consider spatial modelling techniques that may be advantageous to applied ecologists.
4. The methods discussed are available as R packages developed by the authors.
5. Density surface modelling enables applied ecologists to reliably estimate abundances and create maps of animal/plant distribution.

Keywords: abundance estimation, line transect sampling, point transect sampling, population density, wildlife surveys

Introduction

When surveying biological populations it is increasingly common to record spatially referenced data, for example: coordinates of observations, habitat type, elevation or (if at sea) bathymetry. Spatial models allow for vast databases of spatially-referenced data (e.g. OBIS-SEAMAP, Halpin *et al.*, 2009) to be harnessed, enabling investigation of interactions between environmental covariates and population densities. Mapping the spatial distribution of a population can be extremely useful, especially when communicating results to non-experts. Recent advances in both methodology and software have made spatial modelling readily available to the non-specialist (e.g., Wood, 2006; Rue *et al.*, 2009). Here we use the term "spatial model" to include any model that includes spatially referenced covariates, not just smooths of location. This article is concerned with combining spatial modelling techniques with distance sampling (Buckland *et al.*, 2001, 2004).

Distance sampling takes plot sampling (counting all the individuals or groups of objects within a strip or circle) and extends it to the case where detection is not certain. Observers travel along transect centre lines or stand at points and record the distance from the centre line or point to the object of interest (y). These distances are used to estimate the *detection function*, $g(y)$ (bottom left panel, figure 1), by modelling the decrease in detectability with increasing distance from the line or point (conventional distance sampling, CDS). The detection function may also include animal/observer specific covariates (multiple covariate distance sampling, MCDS; Marques *et al.*, 2007). From the fitted detection function, the probability of detection can be calculated. The estimated probability that an animal is detected, $\hat{p}_i$, can then be used to calculate abundance as

$$\hat{N} = \frac{A}{a} \sum_{i=1}^{n} \frac{1}{\hat{p}_i}, \tag{1}$$

where A is the area of the study region, a is the area covered by the survey (i.e., the sum of the areas of all of the strips/circles) and the summation takes place over the n observed individuals (Buckland *et al.*, 2001, Chapter 3). In general distance sampling is more efficient than plot sampling because all objects observed are recorded and only during analysis are observations discarded due to being too far from the line or point transect (outside of the *truncation distance*, specified when fitting the detection function).

When fitting the detection function in a distance sampling analysis, one assumes that the objects of interest are distributed according to some process (Buckland *et al.*, 2001, Section 2.1). It is usually possible to design surveys such that a homogenous process can be assumed so that (with respect to the line) objects are distributed uniformly. This can be achieved, for example, by ensuring that transect lines run perpendicular to geographical features that would attract (or repel) animals or by post-stratification (Buckland *et al.*, 2001, Section 3.7).

Estimators such as eqn (1) are referred to as *design-based* since they rely on the design of the study to ensure inference is valid. This article focusses on *model-based* inference. Using spatially explicit models one can investigate the response of biological populations to biotic and abiotic covariates that vary over the survey area. Model-based inference also enables the use of data from opportunistic surveys, for example, incidental data arising from "ecotourism" cruises (Williams *et al.*, 2006).

Our aims in a DSM analysis are usually two-fold: (i) estimating overall abundance and (ii) investigating the relationship between abundance and environmental covariates. As with any predictions which are outside the range of the data, one should heed the usual warnings regarding extrapolation. For example, in a terrestrial study predictions for unsampled habitats may be unreliable. Frequently, maps of abundance or density are required and any spurious predictions can be visually assessed, as well as by plotting a histogram of the predicted values. A sensible definition of the region of interest avoids prediction outside the range of the data.

This article focuses on those recent advances in spatial modelling of distance sampling data which are of most utility to applied ecologists. These methods are available in the R packages `Distance` and `dsm`, and will soon be available in the popular Windows application Distance (Thomas *et al.*, 2010).

Throughout this article a motivating data set is used to illustrate the methods. These data are from a combination of several shipboard surveys conducted on pantropical spotted dolphins (*Stenella attenuata*) in the Gulf of Mexico. 47 groups of dolphins were observed; group size was recorded, as well as the Beaufort sea state at the time of the observation. Coordinates for each observation and bathymetry data were also available as covariates for the analysis. A complete example analysis is provided as an online appendix.

The rest of the article follows this structure: we first introduce the density surface modelling approach of Hedley & Buckland (2004); explain how to estimate abundance and uncertainty; then go on to describe recent advances and provide practical advice regarding model fitting, formulation and checking. Before concluding, we look at two alternative (but less mature) methods which take a more direct approach to modelling spatial distance sampling data.

Density surface modelling

This section focuses on modelling the density/abundance estimation stage of distance sampling, using the "count model" of Hedley & Buckland (2004), which we refer to as *density surface modelling* (DSM). Both line and point transects can be used but if lines are used then they are are split into contiguous *segments* (indexed by j), which are of length l_j. Segments should be small enough such that the density does not vary appreciably within a segment (usually making the segments approximately square, $2w \times 2w$, is sufficient). Count or estimated abundance is then modelled as a smooth function of covariates using a generalized additive model (GAM; e.g. Wood, 2006). For each segment or point, the response is modelled as a function of environmental covariates (the z_{jk} with k indexing the covariates, e.g., location, sea surface temperature, weather conditions). The covered area enters the model as an offset: the area covered at segment j is $A_j = 2wl_j$ and at point j is $A_j = w\pi^2$ (where w is the truncation distance).

Count as response

The model for the count per segment is:

$$\mathbb{E}(n_j) = \exp\left[\log_e\left(\hat{p}_j A_j\right) + \beta_0 + \sum_k f_k\left(z_{jk}\right)\right],$$

where the f_ks are smooth functions of the covariates and β_0 is an intercept term. Multiplying the covered area (A_j) by the probability of detection ($\hat{p}_j$) gives the *effective area* for segment j. If there are no covariates other than distance in the detection function then the probability of detection is constant (i.e., $\hat{p}_j = \hat{p}$, $\forall j$). The distribution of n_j can then be modelled as overdispersed Poisson, negative binomial, or Tweedie distribution (see *Recent developments*, below).

Figure 1 (top panel) shows the raw observations of the dolphin data, along with the transect lines, overlaid on the depth data. Figure 2 shows a GAM fitted to the dolphin data, the top panel shows predictions from a model where depth was the only covariate, the bottom panel shows predictions where a (bivariate) smooth of spatial location was also included.

Abundance estimation is not the only information that can be derived from these models. Plots of marginal smooths of the spatially referenced covariates show the relationships between the covariates and abundance. The effect of depth on abundance for the dolphin data can be seen in Figure 3.

Estimated abundance as response

An alternative to modelling counts would be to use the per-segment/circle abundance can be estimated using distance sampling methods and the estimated counts used as the response. In this case we replace n_j by:

$$\hat{N}_j = \sum_{r=1}^{R_j} \frac{s_{jr}}{\hat{p}_j},$$

where R_j is the number observations in segment j and s_{jr} is the size of the r^{th} group in segment j (if the animals occur individually then $s_{jr} = 1, \forall j, r$).

The following model is then fitted:

$$\mathbb{E}(\hat{N}_j) = \exp\left[\log_e\left(A_j\right) + \beta_0 + \sum_k f_k\left(\boldsymbol{z}_{jk}\right)\right],$$

where $\hat{N}_j$, as with n_j, is assumed to follow an overdispersed Poisson, negative binomial, or Tweedie distribution. Note that the offset is now the area rather than effective area of the segment/point.

DSM with covariates at the observation level

The above models consider the case where the covariates are measured at the segment/point level. Often covariates (z_{ij}, for individual/group i and segment/point j) are collected on the level of observations; for example sex, group size or observer identity. In this case the probability of detection is a function of the individual level covariates $\hat{p}(z_i)$. Individual level covariates can be incorporated into the model by adopting the following estimator of the per-segment abundance:

$$\hat{N}_j = \sum_{r=1}^{R_j} \frac{s_{jr}}{\hat{p}(z_{ij})}.$$

By not including an offset, but instead dividing the count (or estimated abundance) by the area of the segment, we can also model density rather than abundance. We concentrate on abundance here, see Hedley & Buckland (2004) for further details on modelling density.

Prediction

To calculate an abundance estimate for a region of interest, covariates included in the model must be available at each prediction point at the required resolution (using prediction grid cells that are smaller than the resolution of the spatially referenced data will not have an effect on abundance/density estimates). The areas of the segments/points are included as an offset in the model, so the area of the prediction cells must be included in the prediction data. Predictions are made for the each grid cell using covariate values associated with each cell and abundance estimates are produced for a particular area by summing predicted values over corresponding grid cells.

Variance estimation

Estimating the variance of abundances calculated using a DSM is not straight forward: uncertainty from the estimated parameters of the detection function must be incorporated into the spatial model. A second consideration is that in a line transect survey, adjacent segments are likely to be correlated; failing to account for this spatial autocorrelation will lead to artificially low variance estimates and hence misleadingly narrow confidence intervals.

Hedley & Buckland (2004) describe a method of calculating the variance in the abundance estimates using a parametric bootstrap, resampling from the residuals of the fitted model. The bootstrap procedure is as follows.

Denote the fitted values for the model to be $\hat{\boldsymbol{\eta}}$. For $b = 1, \ldots, B$ (where B is the number of resamples required).

1. Resample (with replacement) the per-segment residuals, store the values in $\mathbf{r}_b$.
2. Refit the model but with the response set to $\hat{\boldsymbol{\eta}} + \mathbf{r}_b$ (where $\hat{\boldsymbol{\eta}}$ are the fitted values from the orginal model).
3. Take the predicted values for the new model and store them.

From the predicted values stored in the last step the variance originating in the spatial part of the model can be calculated. The total variance of the abundance estimate (over the whole region of interest or sub-areas) can then be found by combining the variance estimate from the bootstrap procedure with the variance of the probability of detection from the detection function model (using the delta method which assumes that the two components of the variance are independent; Seber, 1982).

The above procedure assumes that there is no correlation in space between segments however, if many animals are observed in a particular segment then we might expect there to be high numbers in the adjacent segments. A moving block bootstrap (MBB; Efron & Tibshirani, 1993, Section 8.6) can account for some of this spatial autocorrelation in the variance estimation. The segments are grouped together into overlapping blocks, (so if the block size is 5, block one is segments $1, \ldots, 5$, block two is segments $2, \ldots, 6$, and so on). Then, at step (2) above, resamples are taken of the blocks (contiguous collections of segments) rather than individual segments within the transects.

Using blocks should account for some of the autocorrelation between the segments, inflating the variances accordingly. However, because the block size dictates the maximum amount of spatial autocorrelation accounted for, this may not fully account for the autocorrelation. These bootstrap procedures can also be modified to take into account detection function uncertainty by generating new distances from the fitted detection function and then recalculating the offset by fitting a detection function to the new distances.

Recent developments

GAM uncertainty and variance propagation

Rather than using a bootstrap, one can use GAM theory to construct uncertainty estimates for DSM abundance estimates. This merely requires that we use the distribution of the parameters in the model to simulate model coefficients, using them to generate possible abundance estimated (further information can found in Wood, 2006, page 245). Such an approach removes the need to refit the model many times, making variance estimation much faster.

Williams *et al.* (2011) go a step further and incorporate the uncertainty in the estimation of the detection function into the variance of the spatial model, albeit only when only environmental covariates are in the DSM. Their procedure is as follows:

1. Fit a density surface model.

2. Re-fit the model with an additional term that characterises the uncer-

tainty in the estimation of the detection function (via the derivatives of the probability of detection, $\hat{p}$).

3. Variance estimates of the abundance calculated using standard GAM theory will include uncertainty from the estimation of the detection function.

We consider that propagating the uncertainty in this manner is not only more computationally efficient but also preferable from a technical perspective. A moving block bootstrap does not fully account for spatial autocorrelation; assuming that the residuals are exchangeable when they are not will lead to wider confidence intervals. In simulation the confidence intervals produced via the above method are narrower than their bootstrap equivalents, while maintaining good coverage.

DSM uncertainty can be visualised via a plot of per-cell coefficient of variation obtained by dividing the standard error for each cell by its predicted abundance. Figure 4 shows a map of the coefficient of variation for the model which includes both location and depth covariates using the variance propagation method.

Edge effects

Recent work (Ramsay, 2002; Wang & Ranalli, 2007; Wood *et al.*, 2008; Scott-Hayward *et al.*, Submitted; Miller & Wood, Submitted) has highlighted the need to take care when smoothing over areas with complicated boundaries; e.g., those with rivers, peninsulae or islands. If two parts of the domain (either side of a river or inlet, say) are inappropriately linked by the model (the distance between the points is measured as a straight line, rather taking into account obstacles) then the boundary feature can be "smoothed across" leading to incorrect inference. Ensuring that a realistic spatial model has been fitted to the data is essential for valid inference. The soap film smoother of Wood *et al.* (2008) is particularly appealing as the model jointly estimates boundary conditions for a complex study area along with the interior smooth. This can be particularly helpful when uncertainty is estimated via a bootstrap as the model helps avoid large, unrealistic predictions which can plague other smoothers (Bravington & Hedley, 2009).

Even if the study area does not have a complicated boundary, edge effects can still be problematic. Miller *et al.* (In prep) show that global smoothers which have unpenalized plane components tend to cause the fitted surface to increase unrealistically as predictions move further away from the locations of survey effort. They suggest the use of Duchon splines (a generalisation of thin plate regression splines) to alleviate the problem.

Tweedie distribution

The Tweedie distribution offers a very flexible alternative to the quasi-Poisson and negative binomial distributions as a response distribution when modelling count data (Candy, 2004). Through the parameter λ, many common distributions arise; varying λ between 1 (Poisson) and 2 (gamma) leads to a random variable which is a sum of M gamma variables where M is Poisson distributed (Jørgensen, 1987). The distribution does not change appreciably when λ is changed by less than 0.1 therefore, a simple line search over the possible values of λ is usually reasonable. Mark Bravington (pers.

comm.) suggested plotting the square root of the absolute value of the residuals against fitted values; a “flat” plot (points forming a horizontal line) give an indication of a “good” value for λ. We additionally suggest using the metrics described in the next section for model selection.

Practical advice

Figure 5 shows a flow diagram of the modelling process for creating a density surface model for distance sampling data. The diagram shows which methods are compatible with each other and what the options are for modelling a particular data set.

In our experience, it is sensible obtain a detection function which fits the data as well as possible and only after a satisfactory detection function has been obtained, begin spatial modelling. Model selection can be performed for the detection function using AIC and model checking using goodness-of-fit tests given in Buckland *et al.* (2004). If animals occur in groups rather than individually, bias can be incurred due to the higher visibility of larger groups. Bias due to group size can be assessed by regressing evaluations of the fitted detection function onto the logarithm of group size, then comparing the expected and observed values of the group size at zero distance, if there is a large difference then it may be necessary to include size as a covariate in the detection function see (see Buckland *et al.*, 2001, Section 4.8.2.4). The bottom right panel of figure 1 shows a such a plot with the regression line overlaid.

For the spatial model, smooth terms can also be selected using (approximate) p-values. A useful technique for covariate selection is to have an additional penalty to each term in the GAM which allows smooth terms to be removed from the model during fitting (Wood, 2006, Section 4.1.6). Generalized cross validation (GCV) score (or related metrics such as UnBiased Risk Estimator or REstricted Maximum Likelihood score; UBRE and REML, respectively) and percentage deviance explained are useful for model selection. We highly recommend the use of standard GAM diagnostic plots. Wood (2006), Chapter 5, provides practical information on GAM model selection and fitting.

In the analysis of the dolphin data, we included a smooth of location. This not only nearly doubles the percentage deviance explained (27.3% to 52.7%), it also allows us to account for spatial autocorrelation (in a primitive way). One can see this when comparing the two plots in Figure 2 and the plot of the depth in Figure 1, the plot of the smooth of depth alone looks very similar to the raw plot of the depth data. A smooth of an environmental-level covariate such as depth can be very useful for assessing the relationships between abundance and the covariate (as in Figure 2). Caution should be employed when interpreting smooth relationships and abundance estimates, especially if there are gaps over the range of covariate values; large counts may occur at a high value of depth but if no further observations occur at such a high value, then investigators should be skeptical of any relationship. For this reason, a smooth of space is recommended for inclusion in candidate models. Limiting the “wigglyness” of smooths of spatial location (by limiting their basis size) can be a useful way of restricting their influence whilst still allowing them to “mop up” the residual spatial correlation in the data.

In the analysis presented we have converted from latitude and longitude to kilometres from the centre of the survey region (27.01, -88.3) because the bivariate smoother used (the thin plate spline; Wood, 2003) is isotropic, i.e. it treats the wigglyness of the smoother in each direction as equal. Moving 1 degree in latitude is not the same as moving 1 degree in longitude and so using kilometres from the centre of the study region makes the covariates isotropic (using SI units throughout would also remove the need for conversion).

Direct modelling of the spatial point process

[[**LEN**: Does some chat about Andy Royle's stuff fit in here?]]

Rather than use a GAM to model the spatially explicit part of the model, two recent articles (Johnson *et al.*, 2010; Niemi & Fernández, 2010) have modelled the process using point processes (Cox & Isham, 1980). In both cases the density of objects described by an intensity function, which can include spatially-referenced covariates.

Johnson *et al.* (2010) proposes a point process-based model for distance sampling data. They first assume that the locations of all individuals in the survey area (not just those observed) form a realisation of a Poisson process. Parameters of the intensity function are then estimated via standard maximum likelihood methods for point processes (Baddeley & Turner, 2000). In contrast to Hedley & Buckland (2004), all parameters are estimated jointly so uncertainty from both the spatial pattern and the detection function is incorporated into variance estimates for the abundance. This also ensures that correlations between the detection function and underlying point process are estimated correctly (and do not falsely inflate or deflate variance estimates). The authors also addressed the issue of overdispersion unmodelled by spatial covariates (i.e. counts that do not follow a Poisson mean-variance relationship) using a post-hoc correction factor.

Niemi & Fernández (2010) also use Poisson processes but incorporate them into a fully Bayesian approach. Model fitting proceeds in two stages: first the detection function is fitted, then the spatial model (via MCMC) assuming the detection function parameters are known, so detection function uncertainty is not incorporated in the spatial model.

Both of the above Poisson process models do not account for group size, but both state that this could be included by considering a marked point process (Cox & Isham, 1980, Section 5.5). Both methods offer direct modelling of the point process, although with some drawbacks compared to the methodology of Hedley & Buckland (2004). It should be noted that the loss of efficiency from using DSM is not large (Buckland *et al.*, 2004, p. 313) because distances contain little information about spatial variation due to how thin transects are compared to their lengths and how small circles are compared to the study area.

Discussion

The use of model-based inference for determining abundance and spatial distribution from distance sampling data presents new opportunities in the field of population assessment. Inference from a sample of sightings to a population in a study area does not depend upon a random sample design, and therefore data from "platforms of opportunity" (Williams *et al.*, 2006) can be used.

Unbiased estimates are dependent upon either (i) distribution of sampling effort being random throughout the study area (for design-based inference) or (ii) model correctness (for model-based inference). It is easier to have more confidence in the former than in the latter because our models are always wrong. Nevertheless model-based inference will play an increasing role in population assessment as the availability of spatially-references data increases.

The field is quickly evolving to allow modelling of more complex data building on the basic ideas of density surface modelling. We expect to see large advances in two areas: temporal inferences and the handling of spatial correlation. These should become more mainstream as modern spatio-temporal modelling techniques are adopted. Petersen *et al.* (2011) provided a very basic framework for temporal modelling; their model included smooth terms both before and after the construction of an offshore windfarm. Spatial autocorrelation can be accounted for via approaches that explicitly introduce correlations such as generalized estimating equations (GEEs; Hardin & Hilbe, 2003) or via mechanisms such as that of Skaug (2006), which allowed observations to cluster according to one of several states (e.g. “feeding” or “transit”) taking into account short-term agglomerations (“hot spots”). These advances should assist both modellers and wildlife managers to make optimal conservation decisions. [[**LEN**: don’t like this last sentence but feel like there should be some summing up here]]

Acknowledgments

DLM wishes to thank Mark Bravington and Sharon Hedley for their help and patience in explaining and providing code for their variance propagation method.[[**LEN**: N45 thanks?]]

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Figures

Fig. 1 Top: the survey area, transect centrelines and observations with size of circle corresponding to the group size overlaid onto depth data; bottom left, histogram of observed distances with fitted detection function; bottom right, plot of evaluations of the fitted detection function at given distances versus the logarithm of group size with linear trend showing the relation between probability of detection (given distance) and group size.

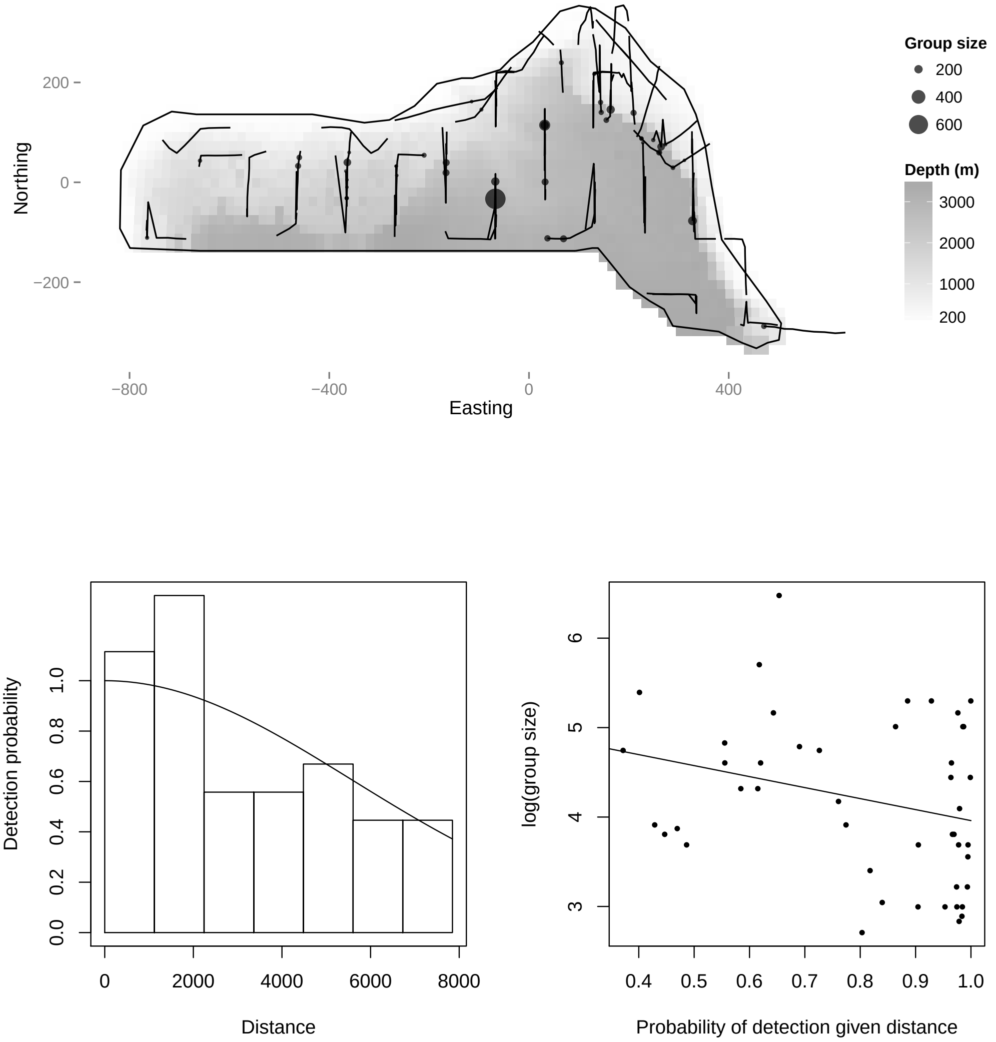
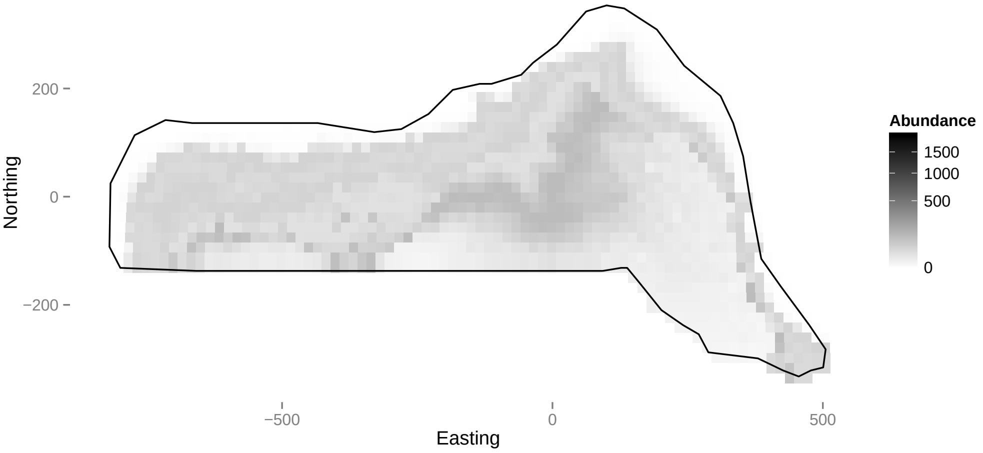


Fig. 2 Predictions for the dolphin data. Top: Predictions from the model using only depth as an explanatory variable, bottom: the model using both depth and location.



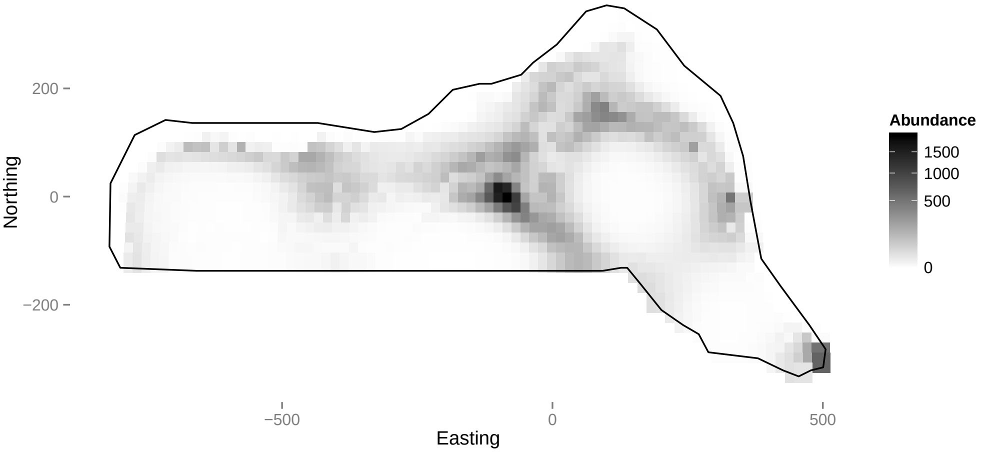


Fig. 3 Plot of the effect on the response of depth (from the model with both depth and location smooths), note that it is possible to draw a straight line between 750m and 3000m within the confidence band (between the dashed lines), so the wiggles in the smooth may not be indicative of any relationship. What is clear is that there is some effect up to about 500m. The rug ticks at the bottom of the plot indicate we have good coverage of the range of depth values in the survey area. Note that the y axis in such plots is on the scale of the link function (log in this case), so care should be taken in their interpretation.

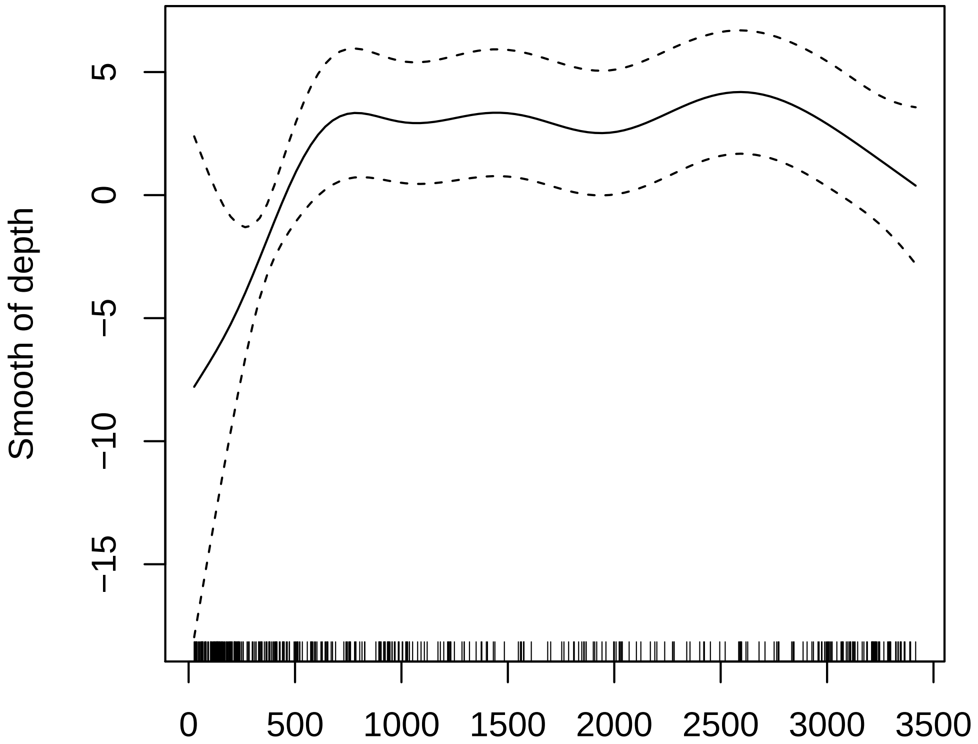


Fig. 4 Plot of coefficient of variation map for the model with smooths of both depth and location. Uncertainty was estimated using the variance propagation method of Williams *et al.* (2011). As might be expected, there is high uncertainty where there is low sampling effort (comparing to figure 1).

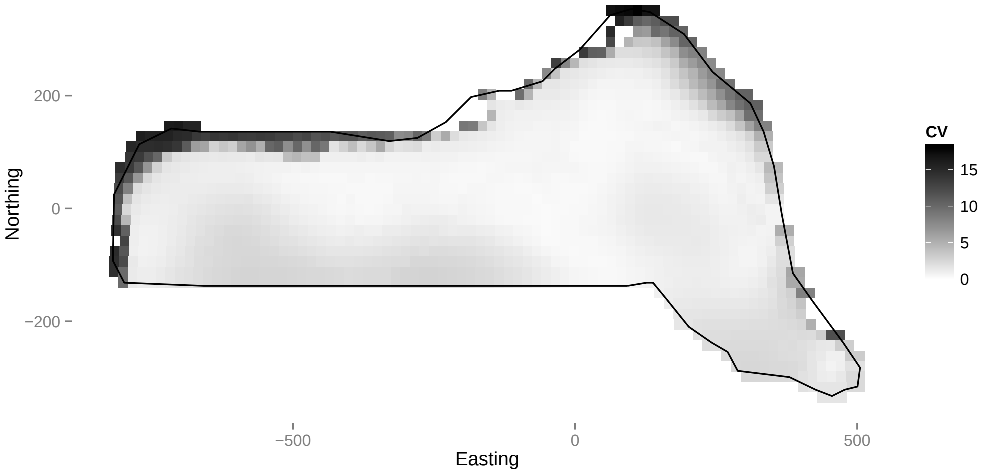
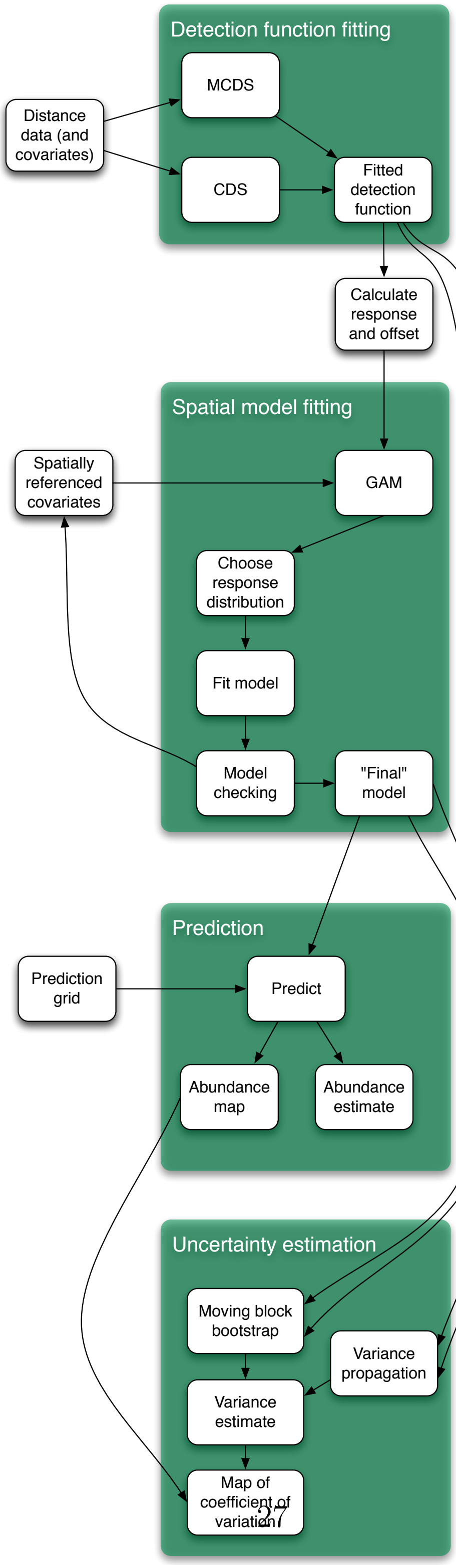


Fig. 5 Flow diagram showing the modelling process for creating a density surface model.


Detection function fitting
Distance data (and covariates)
MCDS
CDS
Fitted detection function
Calculate response and offset
Spatial model fitting
Spatially referenced covariates
GAM
Choose response distribution
Fit model
Model checking
"Final" model
Prediction
Prediction grid
Predict
Abundance map
Abundance estimate
Uncertainty estimation
Moving block bootstrap
Variance propagation
Variance estimate
Map of coefficient of variation