

1 **Running title:** Spatial models for distance sampling
2 **Number of words:** ~??
3 **Number of tables:** ?
4 **Number of figures:** ?
5 **Number of references:** ?

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

8 **David L. Miller^{1*}, Louise Burt², Eric Rexstad²,**
9 **Len Thomas².**

- 10 *1. Department of Natural Resources Science, University of Rhode Island,*
11 *Kingston, Rhode Island 02881, USA*
12 *2. Centre for Research into Ecological and Environmental Modelling,*
13 *The Observatory, University of St. Andrews, St. Andrews KY16 9LZ,*
14 *Scotland*

15 *Correspondence author. dave@ninepointeightone.net

16

Summary

17

Since the initial work by Hedley & Buckland (2004), there have been

18

many advances to the methodology for density surface modelling in

19

distance sampling. This review aims to describe some of the recent

20

work, in particular from spatial smoothing. We offer a comparison of

21

the various options for the practitioner as well as an examples and

22

software.

23

Keywords: Distance sampling; spatial modelling; generalized additive mod-

24

els; Poisson processes; abundance estimation.

25 Introduction

26 When surveying biological populations it is increasingly common to record
27 spatially referenced data; for example: coordinates of observations, bathy-
28 metry or chlorophyll A levels. Mapping the spatial distribution of a pop-
29 ulation can be extremely useful for practitioners, especially when commu-
30 nicating results to non-experts. Spatial models allow for the vast databases
31 spatially-referenced data to be harnessed, allowing for interactions between
32 environmental covariates and population densities to be investigated. Includ-
33 ing spatial covariates into the model (for example, latitude and longitude)
34 can account for spatial autocorrelation. Recent advances in both methodo-
35 logy and software have made spatial modelling readily available to the non-
36 specialist (e.g. Wood (2006), Rue *et al.* (2009)). Note that here we use the
37 term “spatial model” to include any model which includes spatially referenced
38 covariates, not just those which contain smooths of location.

39 This article concerns combining spatial modelling techniques with dis-
40 tance sampling (Buckland *et al.* (2001), Buckland *et al.* (2004)). Distance
41 sampling takes simple strip sampling and extends it to the case where detec-
42 tion is not certain, for example when animals are cryptic.

43 Observers travel along transect centre lines or stand at points and record
44 the perpendicular distance from the centre line or point to the object of in-
45 terest (y). These distances are used to estimate the *detection function* ($g(y)$)
46 by modelling the decrease in detectability with increasing distance from the
47 line or point. The detection function may also include animal/observer spe-
48 cific covariates (Marques *et al.* (2007)). From the fitted detection function,

the probability of detection can be calculated, this gives the probability that an animal within the truncation distance is detected, which can then be used to calculate density and abundance (Buckland *et al.* (2001), Chapter 3).

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). If the objects' locations are not dependent on any spatially varying covariates (such as location, distance from coast, depth, etc) a homogenous process is assumed; so with respect to the line, the objects are distributed uniformly. It is often possible to design surveys such that this assumption holds (for example, 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).

Hedley & Buckland (2004) were the first to address spatial modelling of distance sampling data, allowing for a relaxation of the homogeneity of the point process, by including a rate parameter which is a function of spatially varying covariates. Thinking of the underlying placement of the objects as an inhomogeneous point process allows us to think of the detection process as a “thinning” (Cox & Isham (1980), Section 4.3) of the process, resulting in another inhomogeneous point process. By assuming the object placement and detection processes are independent, it is possible to separate these two processes (placement and thinning) in the likelihood.

Modelling the spatial process not only permits the use of spatially referenced data, it also gives practitioners the opportunity to use data from opportunistic surveys, for example “incidental” data arising from “ecotourism” cruises can be included in analyses (Williams *et al.* (2006)). Although with

74 such non-random designs, spatial placement is less important than placement
75 with respect to the range of covariate values expected to be encountered
76 within the area of interest.

77 The rest of the article is structured as follows: we describe two methods
78 which take the point process approach before going on to describe the two-
79 stage approach of Hedley & Buckland (2004). We then describes recent ad-
80 vances, along with some practical advice regarding the model fitting, formula-
81 tion and checking. Throughout this article a motivating data set is used to il-
82 lustrate the methods. These data are from a combination of several shipboard
83 surveys conducted on pan-tropical spotted dolphins in the Gulf of Mexico.
84 These data consist of 47 observations of groups of dolphins. The group size
85 was recorded, as well as the Beaufort sea state at the time of the observation.
86 Coordinates for each observation and depth at a series of points over the pre-
87 diction area were also available as covariates for the analysis. A complete ex-
88 ample analysis can be found at <http://www.github.com/dill/dsm/wiki/>.

89 Direct modelling of the process

90 From the point process description, two modelling procedures arise. One
91 approach is to directly model the point process, estimating the observation
92 process as the thinning of that point process (Niemi & Fernández (2010),
93 Johnson *et al.* (2010)). A second approach consists of performing a distance
94 analysis and using the fitted detection function as part of spatial model
95 (Hedley & Buckland (2004)).

96 Johnson *et al.* (2010) propose a point process-based model for distance
 97 sampling data (henceforth referred to as DSpat). They first assume that
 98 the locations of all individuals in the survey area (not just those which were
 99 observed) are a realisation of an inhomogeneous Poisson process which is a
 100 function of space. The authors then take the novel approach of allowing
 101 for separate (disjoint) regions of the survey area to have different detection
 102 functions associated with them. The sum of these detection functions is then
 103 used as a thinning of the Poisson process. The parameters are then found via
 104 standard maximum likelihood methods for point processes (see, e.g. Badde-
 105 ley & Turner (2000)). In contrast to Hedley & Buckland (2004), parameters
 106 are estimated jointly so uncertainty from both the spatial pattern and the
 107 observation process is incorporated into variance estimates for the abund-
 108 ance. Concurrent estimation of the parameters also ensures that interactions
 109 between the thinning and underlying point process are estimated correctly.
 110 The authors also address the issue of overdispersion (commonly a symptom
 111 of animals or groups clustering), unmodelled by spatial covariates in a man-
 112 ner similar to that for GLMs (see *Recent Developments*, below, for another
 113 approach).

114 Niemi & Fernández (2010) also use Poisson processes but incorporate it
 115 into a fully Bayesian approach. Their intensity function takes the form of a
 116 product of a parametric function of the covariates and a mixture of Gaussian
 117 kernels as a spatial smooth. An appropriate degree of smoothing could be
 118 selected by putting prior distributions on the number and locations of the
 119 “knots” of the spatial smooth (the means of the Gaussian kernels) and then
 120 using reversible jump MCMC (Green (1995)). However, because the authors

only include a single precision parameter for all of the kernels, small and large scale variation cannot both be accommodated. As in Johnson *et al.* (2010), the detection function was used as a thinning of the process, although (unlike DSpat) only one detection function was used across the whole region with known parameters. This means that detection function uncertainty is not incorporated in the spatial model.

Both of the above Poisson process models do not account for group size, both stating 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 a two-stage approach is not large (Buckland *et al.* (2004), p. 313). For these reasons, the article focuses on method of Hedley & Buckland (2004) and the advances which can be applied to their methodology.

Density surface modelling

We refer to the approach of Hedley & Buckland (2004) as *density surface modelling* (DSM), this is used as a rather general description for modelling distance sampling data using spatially referenced data. The approach is incorporated into the popular software package Distance (Thomas *et al.* (2010)). **[[TKTKTK change this!]]** Rather than modelling the point process directly, DSM uses a spatial model for the survey area using the counts, abundance (of individuals or groups) or observation density as response.

144 The principle is simple: just as conventional and multiple covariate distance
 145 sampling (CDS and MCDS, respectively) extend strip transect sampling to
 146 the case where detection is not guaranteed, DSM extends a spatial model for
 147 strip transects to line and point transects.

148 First, consider conducting a strip transect survey. Strips are divided into
 149 contiguous *segments* (indexed by j), which are of length l_j ; small enough
 150 such that the density does not vary a lot in the segment. For each of these
 151 segments, the number of individuals observed (n_j) is used as the response
 152 (see *Practical advice*, below, for how to deal with size bias in grouped popu-
 153 lations). The count can then be modelled as a function of spatial and envir-
 154 onmental covariates (the \mathbf{z}_{jk} for k indexing the covariates: e.g. location, sea
 155 surface temperature, weather conditions) using a generalized additive model
 156 (GAM; e.g. Wood (2006)). The covered area enters the model as an offset
 157 (the area of segment j , $A_j = 2wl_j$, where w is the truncation distance). The
 158 model for the count per segment is:

$$\mathbb{E}(n_j) = \exp \left[\log_e (A_j) + \beta_0 + \sum_k f_k (\mathbf{z}_{jk}) \right], \quad (1)$$

159 where the f_k s are smooth functions of the covariates in the GAM case and
 160 β_0 is an intercept term. The distribution of n_j can then be modelled as over-
 161 dispersed Poisson, negative binomial, or Tweedie (see *Recent developments*,
 162 below) distribution.

164 If perpendicular distance is recorded, the per-segment abundance can be
 165 estimated and used as the response. We first fit a detection function to the
 166 distances using CDS or MCDS methods. We then replace n_j by a Horvitz-
 167 Thompson type estimator (Thompson (2002)) of abundance in the segment:

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

168 where \hat{p}_j is the probability of detection in segment j (although $\hat{p}_j = \hat{p}$, $\forall j$
 169 if there are no covariates other than distance in the detection function). R_j
 170 is the number observations in segment j and s_{jr} is the size of the r^{th} group
 171 in segment j (if the animals occur individually then $s_{jr} = 1$, $\forall j, r$).

172 Having estimated the response for the GAM, the following model is fitted:

$$\mathbb{E}(\hat{N}_j) = \exp \left[\log_e(A_j) + \beta_0 + \sum_k f_k(z_{jk}) \right], \quad (2)$$

173 where \hat{N}_j , as with n_j , is assumed to follow an overdispersed Poisson,
 174 negative binomial, or Tweedie distribution.

175 The above definition of the smooth terms is rather general because several
 176 covariates could be included in single smooth terms via tensor products of
 177 univariate bases (see Wood (2006), Section 4.1.8) or via multivariate spline
 178 bases (e.g. thin plate regression splines; Wood (2003)), as well as simple
 179 linear terms or random effects. A typical use of a bivariate spline in this
 180 setting is to smooth with respect to spatial coordinates by including the
 181 centroid of the j^{th} segment or point. Basis choice for spatial smooths is

covered below. Note that even if location is not used, the model is still spatial (in some sense), because the covariates used in the GAM are spatially referenced.

Data collected as point transects can also be analysed by setting $A_j = w\pi^2, \forall j$.

Figure 1 (top panel) shows the raw observations from 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. Further discussion of the plots follows in *Practical advice*, below.

DSM WITH COVARIATES AT THE OBSERVATION LEVEL

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

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

202 Our aims in a DSM analysis are usually two-fold: estimating overall abund-
203 ance and investigating the relationship between abundance and environ-
204 mental covariates.

205 To calculate an abundance estimate for some region of interest, the ne-
206 cessary covariates (those included in the model) must be available for the
207 whole of the region, and they must also be available at the required resolu-
208 tion (using prediction grid cells that are smaller than the resolution of the
209 spatially referenced data will not have an effect on abundance/density estim-
210 ates). Having acquired the relevant data and calculated the associated areas
211 of the prediction cells, predictions can be made for the particular covariate
212 levels and abundance estimates calculated from summing predicted values
213 over the prediction grid cells.

214 As with any predictions which are outside of the range of the data, one
215 should heed the usual warnings regarding extrapolation. For example, in an
216 offshore study the effect of a continental shelf maybe cause significant issues
217 if there was not search effort on both sides of the shelf. Frequently, maps
218 of abundance or density are required and any spurious predictions can be
219 visually assessed, as well as by plotting a histogram of the predicted values.
220 A sensible definition of the region of interest is required to avoid prediction
221 outside the range of the data.

222 Abundance estimation is not the only information contained in these mod-
223 els. By looking at plots of marginal smooths of the spatially referenced
224 covariates, one can begin to understand the relationships between the covari-

225 ates and abundance. Going back to the dolphin data, we can see the effect
 226 of depth on abundance in Figure 3. There we can see that there is a large
 227 depth effect between 0 and 500m which then seems to level off (a straight line
 228 could be drawn inside the confidence band (dashed line)), indicating that the
 229 dolphins prefer water deeper than 500m. Note that the y axis in such plots
 230 is on the scale of the link function (log in this case), so care should be taken
 231 in their interpretation.

232 VARIANCE ESTIMATION

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

239 *Resampling-based methods*

240 Hedley & Buckland (2004) describe a method of calculating the variance in
 241 the abundance estimates using a parametric bootstrap, resampling from the
 242 residuals of the fitted model. The bootstrap then follows the following steps:

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

- 245 1. Resample (with replacement) the per-segment residuals, store the val-
 246 ues in \mathbf{r}_b .

- 247 2. Refit the model but with the response set to $\hat{\boldsymbol{\eta}} + \mathbf{r}_b$ (where $\hat{\boldsymbol{\eta}}$ are the
248 fitted values from the original model).
- 249 3. Take the predicted values for the new model and store them.

250 From the predicted values stored in the last step, the per-location and abund-
251 ance variance can be calculated in the usual manner. The total variance of
252 the abundance estimate can then be found by combining the variance es-
253 timate from the bootstrap procedure with the variance of the probability of
254 detection from the detection function model (using the delta method; Seber
255 (1982)). This assumes that the two components of the variance are independ-
256 ent and the method does not take into account spatial autocorrelation
257 (the individual segments are treated as independent).

258 The above procedure assumes that there is no correlation in space between
259 segments and that residuals can be swapped around. Clearly if many animals
260 are observed in a segment then we would expect there to be a relatively high
261 level in the next segment (especially because the segments are defined after
262 the survey). A moving block bootstrap (MBB) can account for some of
263 the spatial autocorrelation in the variance estimation. The segments are
264 grouped together into overlapping blocks, (so if the block size is 5, block
265 one is segments 1, ..., 5, the second block is segments 2, ..., 6, and so on).
266 Then, at step (2) above, resamples are taken of the blocks (i.e. groups of
267 segments together) rather than individual segments within the transects.
268 Using blocks should account for some of the autocorrelation between the
269 segments, inflating the variances accordingly.

270 Williams *et al.* (2006) use a slight variation on the MBB, resampling

271 either days or trips such that the total segment length was approximately
 272 the same as that in the original survey. The authors use a jackknife (Efron
 273 (1979)), removing one day (or trip) in turn and refitting the model to the
 274 remaining data. Predictions from the fitted model could be used to calcu-
 275 late a variance and from that confidence intervals (assuming that abundance
 276 estimates are log-normally distributed; Buckland *et al.* (2001), Section 3.6)
 277 can be calculated. By calculating variances for both day and trip, the au-
 278 thors also propose an informal test of between-day correlation: if adjacent
 279 days are independent then the variance estimates for trip and day should be
 280 similar, on the other hand if the adjacent days are autocorrelated then it
 281 would be expected that the trip variance would be lower (and the confidence
 282 intervals narrower). This test could then be used to decide which of the two
 283 resampling units should be used to calculate the abundance variance (if there
 284 was evidence of autocorrelation then trip should be used). The authors also
 285 used the jackknife approach to produce maps of the study area showing how
 286 the surface changed when different parts of the data were removed.

287 The methods detailed above account only for variability in the spatial part
 288 of the model, not the uncertainty in the detection function. The above mov-
 289 ing block bootstrap can be modified to take into account detection function
 290 uncertainty by generating new distances from the fitted detection function
 291 and then re-calculating the offset by fitting a detection function to the new
 292 data. The (new) procedure works as follows:

293 For $b = 1, \dots, B$ (where B is the number of resamples required):

- 294 1. Resample (with replacement) the per-block residuals, store the values
 295 in \mathbf{r}_b .

- 296 2. Let $n_b = \hat{\boldsymbol{\eta}} + \mathbf{r}_b$, rounding to the nearest integer.
- 297 3. Generate n_b new distances from the fitted detection function, refit a
 298 new detection function (with the same key function and adjustment
 299 terms and selecting the number of adjustments using AIC, if required).
- 300 4. Calculate \hat{P}_a and hence a new offset.
- 301 5. Refit the spatial model (with the same covariates but allowing the
 302 smoothing parameter to be selected), to the new response ($\hat{\boldsymbol{\eta}} + \mathbf{r}_b$)
 303 with the new offset.
- 304 6. Take the predicted values for the new model and store them.

305 By refitting the detection function in each bootstrap resample should
 306 account for the uncertainty in the detection function much much better than
 307 using the delta method to combine the variances.

308 *Variance propagation*

309 Rather than using the bootstrap methods above, Williams *et al.* (2011) cal-
 310 culate the variance without having to refit the model many times. Their
 311 method incorporates the uncertainty in the estimation of the detection func-
 312 tion into the variance of the spatial model, albeit only in the case where
 313 covariates are measured at a point/segment level only. Their procedure is as
 314 follows:

- 315 1. Fit the model described in eqn 2.

- 316 2. Re-fit the model with an additional random effects term. This term
317 characterises the uncertainty in the estimation of the detection function
318 (via the uncertainty of the probability of detection, \hat{P}_a).
- 319 3. Variance estimates of the abundance calculated (via the method given
320 in Wood (2006), page 245) from the model will include uncertainty
321 from estimation of the detection function.

322 We consider propagating the uncertainty in this manner not only to be more
323 computationally efficient but also preferable from a technical perspective.
324 The bootstrap methods described above do not fully account for spatial
325 autocorrelation, this failure to account for spatial autocorrelation will lead
326 to wider confidence intervals for the abundance (or density).

327 *Visualising uncertainty*

328 There are several ways to visualise the uncertainty measures calculated above.
329 For the bootstrap methods, if at each round of the bootstrap the predicted
330 values are stored per prediction grid cell, the coefficient of variation can be
331 calculated per cell and then displayed. Figure 4 shows maps of the coefficient
332 of variation for the model which includes both location and depth covariates.
333 The top panel shows the result of running 1000 bootstrap replications in-
334 cluding detection function uncertainty as above. The bottom panel shows
335 the same plot but using the variance propagation method.

Recent developments

EDGE EFFECTS

Recent work (Ramsay (2002), Wang & Ranalli (2007), Wood *et al.* (2008), Scott-Hayward et al (in prep) and Miller and Wood (submitted)) has highlighted the need to take care when smoothing over areas with complicated boundaries; for example, if the survey area includes rivers, peninsulae or islands. If two parts of the domain (either side of a peninsula, say) are inappropriately linked by the model (the distance between the points is measured “as the crow flies”, rather than “as the fish swims”) then the boundary feature can be “smoothed across” leading to incorrect inference. Ensuring that a realistic spatial model has been fit to the data (and, for example, that whales have not been estimated to dwell on land) 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 when using global smoothers, smoothing towards the plane can cause the fitted surface to “curl-up” as predictions move further away from the data. They suggest the use of *Duchon splines* (a generalisation of thin plate regression splines) to alleviate the problem by smoothing toward the intercept.

361 The Tweedie distribution offers a very flexible alternative to the quasi-Poisson
 362 distribution is the usual response distribution when modelling count data
 363 (Candy (2004)). Through the parameter p , many common distributions
 364 arise; varying p between 1 (Poisson) and 2 (gamma) leads to a random vari-
 365 able which is a sum of M gamma variables where M is Poisson distributed
 366 (Jørgensen (1987)). Although it is possible to perform optimization to find
 367 p , this is generally seen as unnecessary as the distribution does not change
 368 appreciably when p is changed by less than 0.1 (therefore trial and error is
 369 usually reasonable). Mark Bravington (pers. comm.) suggested plotting the
 370 square root of the absolute value of the residuals and if this plot is flat a
 371 “correct” p has been found. Additionally he suggests a value of 1.5/1.6 for p
 372 for fisheries and 1.2 marine mammal work is generally acceptable.

373 Practical advice

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

378 In the experience of the authors, it is sensible to start with a detection
 379 function without covariates and a simple smooth of spatial location and then
 380 add in more complicated features such as covariates in the detection function,
 381 or using a soap film smoother (perhaps afterwards dropping the location
 382 term). Model discrimination can be performed for the detection function

383 using goodness-of-fit tests (Buckland *et al.* (2004) and AIC. For the spatial
384 model, generalized cross validation (GCV) score and percentage deviance
385 explained are useful metrics, we also highly recommend the use of standard
386 GAM diagnostic plots. An example of such plots is given in Figure 6 along
387 with a description of their uses.

388 In the dolphin analysis, we include a smooth of location. This not only
389 doubles the percentage deviance explained (27.3% to 52.7%), it also allows us
390 to account for spatial autocorrelation (in a primitive way). One can see this
391 when comparing the two plots in Figure 2 and the plot of the depth in Figure
392 1, the plot of the smooth of depth alone looks very similar to the raw plot of
393 the depth data. A smooth of an environmental-level covariate such as depth
394 can be very useful for assessing the relationships between abundance/density
395 and the covariate, but estimates of abundance/density from such models may
396 be misleading.

397 In the analysis we have converted from latitude and longitude to metres
398 from the point (27.01, -88.3). This is because the bivariate smoother which we
399 use (the thin plate spline, Wood (2003)) is isotropic: it treats the wigglyness
400 of the smoother in each direction as equal: a move of 1 degree in latitude is
401 not the same as a move of 1 degree in longitude, the move to meters from
402 the centre of the study area is sensible (using SI units removes the need for
403 conversion later).

404 If animals occur in groups rather than individually a size bias can occur
405 due to larger groups being more visible than smaller groups. The expected
406 group size can be obtained from a regression of probability of detec-
407 tion against the logarithm of group size. Having calculated the expected

group size, this can be used calculate the per-segment abundance, rather than simply summing the number of observed individuals.

Discussion

The field is quickly evolving to allow modelling of more complex data however the basic principle remains as in Hedley & Buckland (2004), albeit with various additions to the modelling process. We expect to see large advances in two areas: temporal inferences and the handling of spatial autocorrelation. These should become more mainstream as modern spatio-temporal modelling techniques are adopted. Petersen *et al.* (2011) provide a very basic framework for temporal modelling; their model includes extra smooth terms for their spatial and depth smooth terms after the construction of an offshore windfarm which are included via an indicator. 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 allows observations to cluster according to one of several states (e.g. “feeding” or “transit”) taking into account short-term agglomerations (“hot spots”).

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 and alerting him to the existence of the Markov modulated Poisson

429 process.

430 LEN: Do we need to say something about the Navy funding me
431 here?

References

- Baddeley, A. & Turner, R. (2000) Practical maximum pseudolikelihood for spatial point patterns. *Australian & New Zealand Journal of Statistics*, **42**, 283–322.
URL <http://onlinelibrary.wiley.com/doi/10.1111/1467-842X.00128/abstract>
- Bravington, M. & Hedley, S.L. (2009) Antarctic minke whale abundance estimates from the second and third circumpolar IDCR/SOWER surveys using the SPLINTR model.
URL http://www.iwcoffice.org/_documents/sci_com/sc61docs/SC-61-IA14.pdf
- Buckland, S.T., Anderson, D., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling*. Oxford University Press.
- Buckland, S.T., Anderson, D., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2004) *Advanced Distance Sampling*. Oxford University Press.
- Candy, S. (2004) Modelling catch and effort data using generalised linear models, the Tweedie distribution, random vessel effects and random stratum-by-year effects. *Ccamlr Science*, **11**, 59–80.
URL http://www.ccamlr.org/ccamlr_science/Vol-11-2004/04candy.pdf
- Cox, D.R. & Isham, V. (1980) *Point Processes*. Monographs on Applied Probability and Statistics. Chapman and Hall. ISBN 9780412219108.
- Efron, B. (1979) Bootstrap methods: another look at the jackknife. *The Annals of Statistics*, **7**, 1–26.
- Green, P.J. (1995) Reversible jump Markov chain Monte Carlo computation and Bayesian model determination. *Biometrika*, **82**, 711–732.
- Hardin, J. & Hilbe, J. (2003) *Generalized Estimating Equations*. Chapman and Hall/CRC, London, UK.
- Hedley, S.L. & Buckland, S.T. (2004) Spatial models for line transect sampling. *Journal of Agricultural, Biological, and Environmental Statistics*, **9**, 181–199.
- Johnson, D.S., Laake, J.L. & Ver Hoef, J.M. (2010) A model-based approach for making ecological inference from distance sampling data. *Biometrics*, **66**, 310–318.
- Jørgensen, B. (1987) Exponential dispersion models. *Journal of the Royal Statistical Society. Series B, Statistical Methodology*, **49**, 127–162.

- 465 Marques, F. & Buckland, S.T. (2003) Incorporating covariates into standard line
466 transect analyses. *Biometrics*, **59**, 924–935.
- 467 Marques, T.A., Thomas, L., Fancy, S. & Buckland, S.T. (2007) Improving estimates
468 of bird density using multiple-covariate distance sampling. *The Auk*, **124**, 1229–
469 1243.
- 470 Niemi, A. & Fernández, C. (2010) Bayesian Spatial Point Process Modeling of Line
471 Transect Data. *Journal of Agricultural, Biological, and Environmental Statistics*,
472 **15**, 327–345.
- 473 Petersen, I.K., MacKenzie, M., Rexstad, E., Wisz, M.S. & Fox, A.D. (2011) Com-
474 paring pre- and post-construction distributions of long-tailed ducks *Clangula*
475 *hyemalis* in and around the Nysted offshore wind farm, Denmark: a quasi-
476 designed experiment accounting for imperfect detection, local surface features
477 and autocorrelation. 2011-1.
- 478 Ramsay, T. (2002) Spline smoothing over difficult regions. *Journal of the Royal*
479 *Statistical Society. Series B, Statistical Methodology*, pp. 307–319.
- 480 Rue, H., Martino, S. & Chopin, N. (2009) Approximate Bayesian inference for
481 latent Gaussian models by using integrated nested Laplace approximations. *J.*
482 *R. Statist. Soc. B*, **71**, 319–392.
- 483 Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Paramet-*
484 *ers*. Blackburn Pr. ISBN 9781930665552.
485 URL [http://books.google.com/books?id=bnGaPQAACAAJ&dq=seber&cd=](http://books.google.com/books?id=bnGaPQAACAAJ&dq=seber&cd=10&source=gbs_api)
486 [10&source=gbs_api](http://books.google.com/books?id=bnGaPQAACAAJ&dq=seber&cd=10&source=gbs_api)
- 487 Skaug, H.J. (2006) Markov modulated Poisson processes for clustered line transect
488 data. *Environmental and Ecological Statistics*, **13**, 199–211.
- 489 Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley,
490 S.L., Bishop, J.R., Marques, T.A. & Burnham, K.P. (2010) Distance software:
491 design and analysis of distance sampling surveys for estimating population size.
492 *Journal of Applied Ecology*, **47**, 5–14.
- 493 Thompson, S.K. (2002) *Sampling*. Wiley, 2nd edn. ISBN 9781118162965.
494 URL [http://books.google.com/books?id=qukULxJ--QAC&printsec=](http://books.google.com/books?id=qukULxJ--QAC&printsec=frontcover&dq=intitle:sampling+inauthor:thompson&cd=1&source=gbs_api)
495 [frontcover&dq=intitle:sampling+inauthor:thompson&cd=1&source=gbs_](http://books.google.com/books?id=qukULxJ--QAC&printsec=frontcover&dq=intitle:sampling+inauthor:thompson&cd=1&source=gbs_api)
496 [api](http://books.google.com/books?id=qukULxJ--QAC&printsec=frontcover&dq=intitle:sampling+inauthor:thompson&cd=1&source=gbs_api)
- 497 Wang, H. & Ranalli, M. (2007) Low-rank smoothing splines on complicated do-
498 mains. *Biometrics*, **63**, 209–217.

- 499 Williams, R., Hedley, S.L., Branch, T.A., Bravington, M.V., Zerbini, A.N. & Find-
500 lay, K.P. (2011) Chilean blue whales as a case study to illustrate methods to
501 estimate abundance and evaluate conservation status of rare species. *Conserva-*
502 *tion Biology*, **25**, 526–535.
- 503 Williams, R., Hedley, S.L. & Hammond, P. (2006) Modeling distribution and
504 abundance of Antarctic baleen whales using ships of opportunity. *Ecology and*
505 *Society*, **11**, 1.
- 506 Wood, S.N. (2003) Thin plate regression splines. *Journal of the Royal Statistical*
507 *Society. Series B, Statistical Methodology*, **65**, 95–114.
- 508 Wood, S.N. (2006) *Generalized Additive Models: An introduction with R*. Chapman
509 & Hall/CRC.
- 510 Wood, S.N., Bravington, M.V. & Hedley, S.L. (2008) Soap film smoothing. *Journal*
511 *of the Royal Statistical Society. Series B, Statistical Methodology*, **70**, 931–955.

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 distance versus group size with linear trend showing the relation between distance and group size.

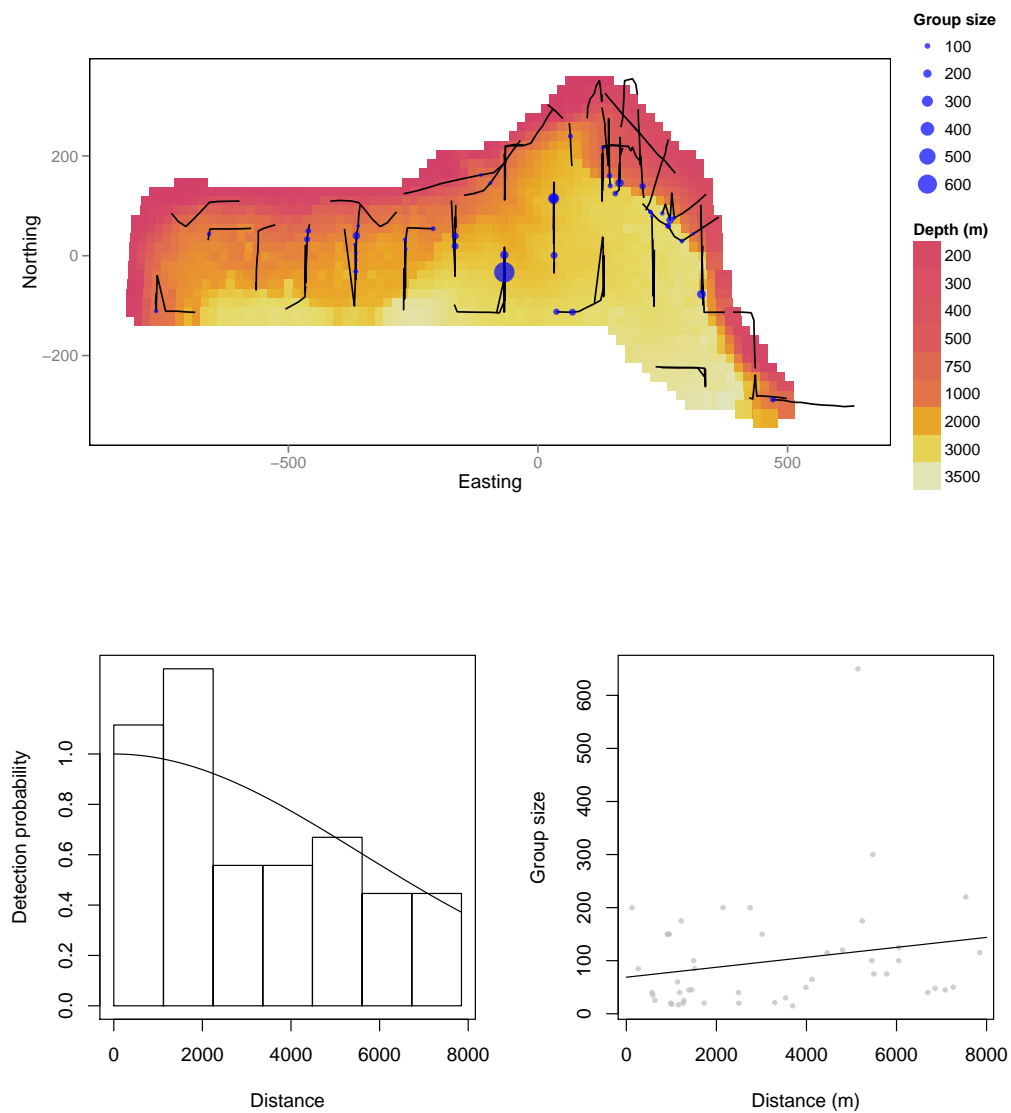


Fig. 2 Predictions for the dolphin data. Top: Predictions from the model using only depth as an explanatory variable, bottom: the model using both depth and location.

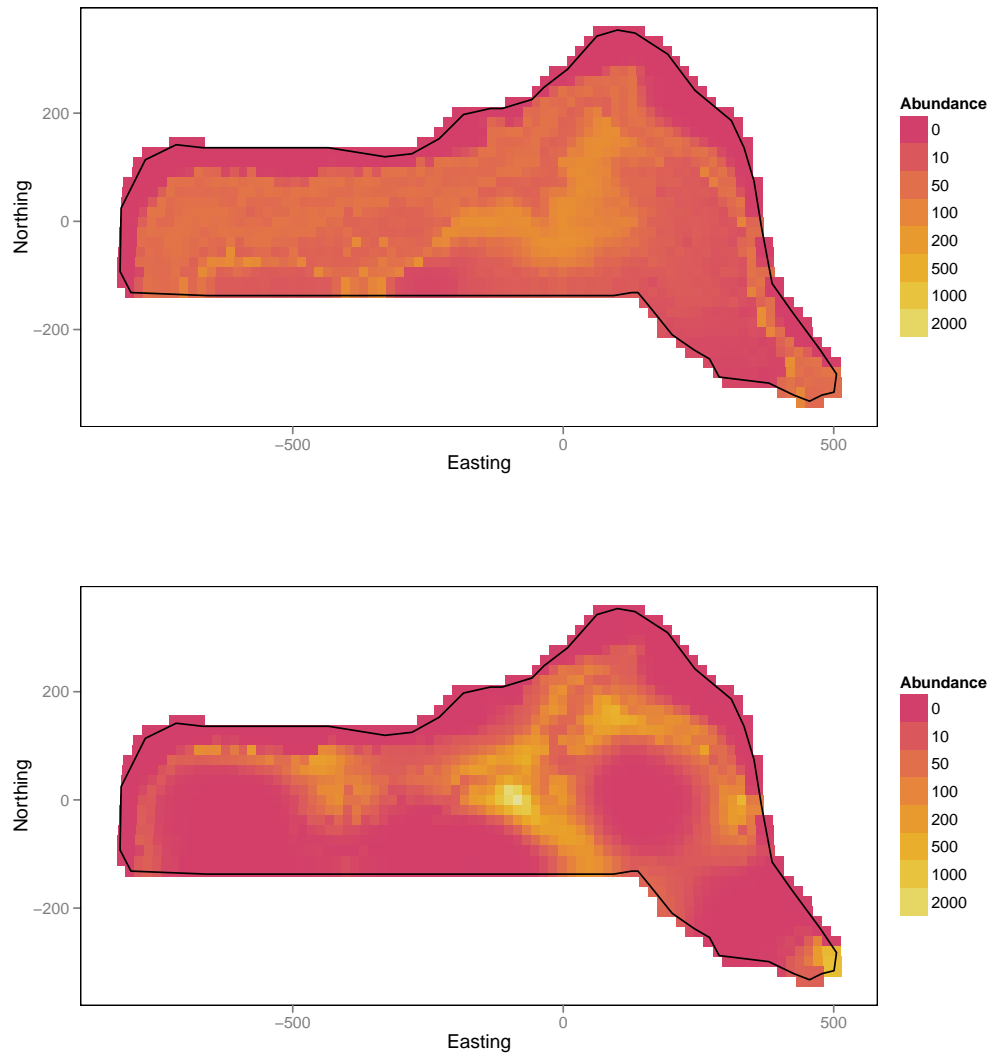


Fig. 3 Plot of the effect on the response of depth, note that it is possible to draw a straight line between 750m and 3000m within the confidence band, so the wiggles in the smooth may not be indicative of any relationship. What is clear is that there is some effect up to about 500m. The number in brackets on the y axis indicates the effective degrees of freedom of the smooth term. The rug ticks at the bottom of the plot indicate where the data were collected.

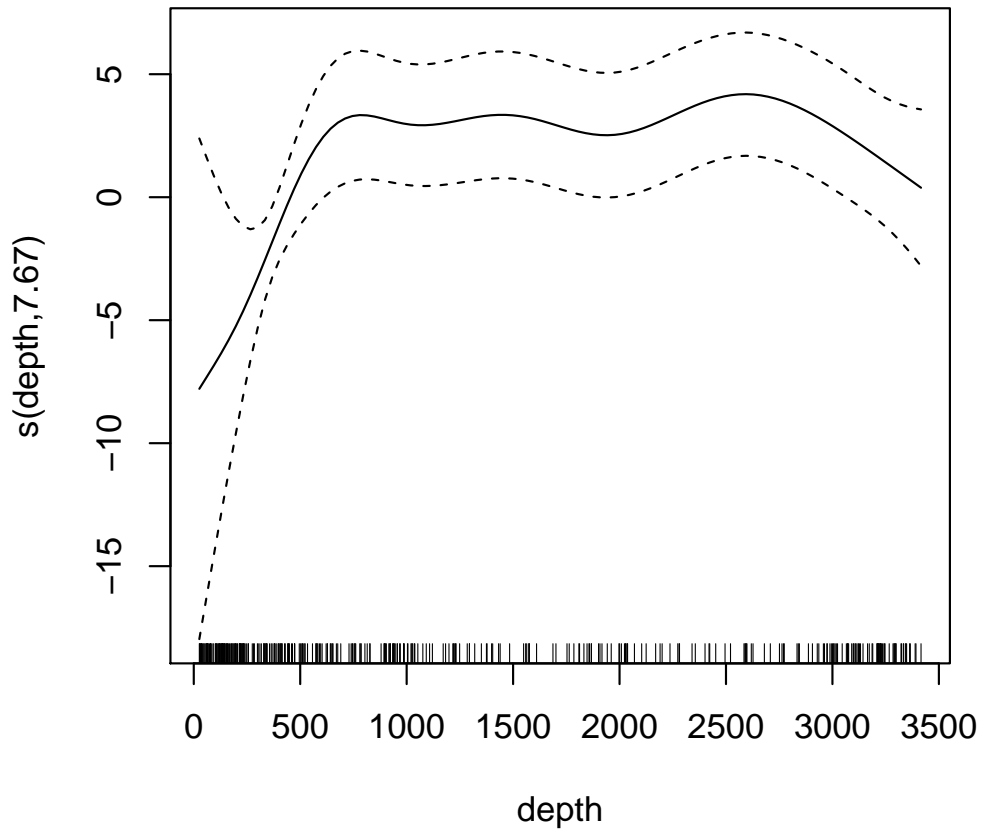


Fig. 4 Plot of coefficient of variation maps, showing the uncertainty in the fitted model. The top panel shows the estimate using the moving block bootstrap incorporating detection function uncertainty, the bottom panel shows the same plot using the variance propagation method. The bootstrap plot seems far more noisy.

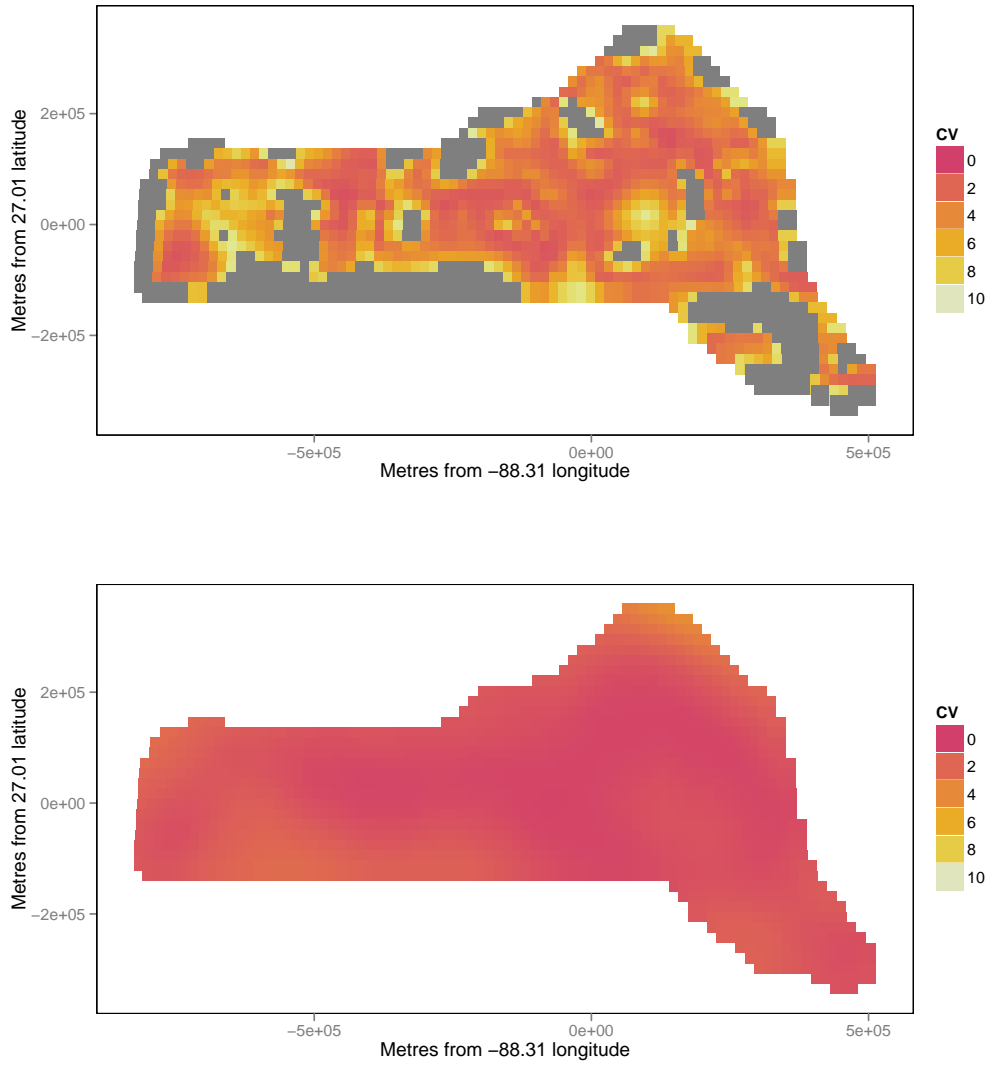


Fig. 6 Example of model diagnostics for the model which included both location and depth covariates for the dolphin data. From top left clockwise:

