Bayesian posterior prediction of the patchy spatial distributions of small pelagic fish in regions of suitable habitat

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Abstract :

Small pelagic fish aggregate within areas of suitable habitat to form patchy distributions with localized peaks in abundance. This presents challenges for geostatistical methods designed to investigate the processes underpinning the spatial distribution of stocks and simulate distributions for further analysis. In two-stage models, presence/absence is treated as separable and independent from the process explaining non-zero densities. This is appropriate where gaps in the distribution are attributable to one process and conditional abundance to another, but less so where patchiness is attributable primarily to the strong schooling tendencies of small pelagic fish within suitable habitat. We therefore developed a new modelling framework based on a truncated Gaussian Random Field (GRF) within a Bayesian framework. We evaluated this method using simulated test data, and then applied it to acoustic survey data for Peruvian anchoveta (*Engraulis ringens*). We assessed the method's performance in terms of posterior densities of spatial parameters, and the density distribution, spatial pattern, and overall spatial distribution of posterior predictions. We conclude that Bayesian posterior prediction based on a truncated GRF is effective at reproducing the patchiness of the observed spatial distribution of anchoveta.

Introduction

Acoustic surveys of small pelagic fish provide valuable information on their abundance and distribution (Simmonds and MacLennan 2005). The distribution of small pelagic fish typically can exhibit strong spatial structure (Fréon et al. 2005). A geostatistical approach is therefore ideal for inference and prediction because it takes into account spatial autocorrelation in the variance of the observed variable (Rivoirard et al. 2000). Geostatistical analysis may serve three broad purposes in fisheries ecology. First, structural analysis and inference may be used to investigate the relationship between the spatial distribution of stocks and environmental covariates, and the inherent spatial structure of fish stocks (Ciannelli et al. 2008, Lezama-Ochoa et al. 2011). Second, geostatistical methods may be used to estimate regional stock abundance (Rivoirard et al. 2000, Roa-Ureta and Niklitschek 2007). In recent years, conditional geostatistical simulation has been recognized as a useful tool for generating multiple spatial realisations of a variable and thus for estimating stock abundance given various sources of uncertainty (Gimona and Fernandes 2003, Walline 2007, Woillez et al. 2009). Third, conditional geostatistical simulation may be used to generate realisations of the spatial distribution of acoustic biomass over the survey region as a basis for analysing spatial associations, for instance between fishing fleets and fish stocks (see Bertrand et al. 2004b). The purpose of the geostatistical analysis presented here was to simulate the spatial distribution of small pelagic fish. The simulated spatial distribution was then used to analyse the foraging patterns of their predators (Boyd 2012). Nevertheless, we propose that the method described below is also of relevance to structural analysis and estimation of stock abundance and associated uncertainty.

The distribution of small pelagic fish is often characterized by intense patchiness (Petitgas 1993, Rivoirard et al. 2000), including gaps or areas of very low densities in the distribution. This leads to data with a high proportion of zeroes, and presents challenges for modelling (Ciannelli et al. 2008). The appropriate model structure for analysing these zeroes depends on the processes that underpin gaps in distribution. Gaps may be attributable to the association of the species with specific water masses or

53 suitable habitat at the stock scale and/or to intrinsic aggregative behaviours leading to the formation of
 54 schools and clusters of schools within suitable habitat (Fréon et al. 2005, Bertrand et al. 2008).

55 Where gaps in the distribution of small pelagic fish are attributable to areas of unsuitable habitat within a
 56 survey region, the distribution of suitable habitat and fish densities within suitable habitat may be
 57 modelled as separate processes. The conventional approach to modelling data with a high proportion of
 58 zeroes is consistent with this scenario. A two-stage model structure may be developed, in which
 59 presence/absence is treated as separable and independent from the process explaining non-zero densities
 60 (Maunder and Punt 2004). For example, Walline (2007) applied three simulation methods to acoustic data
 61 for walleye pollock (*Theragra chalcogramma*), including a two-stage model based on binary indicator
 62 simulation for presence/absence; Roa-Ureta and Niklitschek (2007) analysed repeated trawl survey data
 63 for squid (*Loligo gahi*) based on a binomial model for presence/absence; and Zwolinski et al. (2009)
 64 analysed acoustic data for sardine (*Sardina pilchardus*) based on a binomial distribution for
 65 presence/absence. In each case, the primary purpose was to estimate stock abundance.

66 However, where patchiness is mostly attributable to aggregative behaviours within suitable habitat, the
 67 density data would ideally be modelled as the outcome of a single continuous process with the observed
 68 zeroes corresponding to very low densities. Analogously, it is typically assumed that observed data are
 69 censored below some detection threshold in the analysis of rainfall or contaminant data. Values below the
 70 threshold may occur, but remain undetected. A complete spatial analysis therefore incorporates these
 71 unobserved low-level values or ‘censored’ data based on the observed data above the detection threshold
 72 (Stein 1992, De Oliveira 2005). The focus of inference is on the underlying distribution process that
 73 generated the data, rather than the boundary between censored and non-censored data which depends on
 74 the detection threshold and is a function of the observation process. Truncated Gaussian random fields
 75 (GRFs) are well-established in some areas of geostatistics for modelling censored data such as rainfall
 76 data (e.g. Sanso and Guenni 1999) and contaminant data (e.g. Fridley and Dixon 2007), but have been
 77 applied to fisheries data only recently. Woillez et al. (2009) developed an integrated approach to model

the distribution of Scottish herring (*Clupea harengus*) as a continuous distribution using a transformed truncated GRF.

The method developed by Woillez et al. (2009) was founded in classical geostatistics, which does not require that the dependent variable follow a known parametric distribution (Ecker 2003). In contrast, likelihood-based approaches require an explicit assumption about the distribution of the dependent variable as the basis for parameter estimation and analysis of uncertainty (Diggle et al. 1998). There are several advantages to likelihood-based approaches for structural analysis of spatial processes and parameter estimation (Ecker 2003, Roa-Ureta and Niklitschek 2007). Classical geostatistics typically involves a stage-based approach to parameter estimation, whereas likelihood-based approaches allow for simultaneous estimation or analysis of all parameters. In likelihood-based approaches, parameter uncertainty may be evaluated through likelihood profiles, and models may be compared using information criteria such as Akaike's Information Criterion (AIC) (Burnham and Anderson 2002).

Likelihood-based approaches support both frequentist and Bayesian approaches to inference. In frequentist approaches, estimation and prediction are treated as separate processes: the geostatistical model is assumed to have fixed but unknown parameters, parameters are estimated and then point estimates of the parameters are plugged back into the geostatistical model to generate predictions (Diggle and Ribeiro 2007). In contrast, Bayesian prediction takes full account of uncertainty in parameters and any latent variables. Uncertainty in both parameters and latent variables is characterized through posterior distributions (i.e. probability distributions conditioned on the data) and prediction is based on samples from the joint posterior distributions of all unknown quantities (Royle and Dorazio 2008). A Bayesian approach was preferred for the analysis presented here, given uncertainty in parameters and the latent distribution of interest.

We therefore extended the approach developed by Woillez et al. (2009) to a fully Bayesian approach.

Woillez et al. (2009) used non-parametric Gaussian anamorphosis (or normal-score transformation) to transform the observed non-zero densities into a left-truncated GRF, while the zero densities were transformed to a spike of equal values at the truncation point. It was not possible to infer the variogram of

the underlying GRF directly because of this spike of equal values, so it was inferred analytically based on the functional relationship between the variogram of the left-truncated GRF and the latent underlying GRF (Woillez 2007). Gibbs sampling was then used to simulate Gaussian values at the locations of the zero densities. In the final step, conditional geostatistical simulation was used to evaluate uncertainties associated with abundance estimates derived from a combination of acoustic and trawl data.

In the Bayesian approach presented here, a parametric distribution was assumed for the non-zero densities, and used as the basis for transformation into a left-truncated GRF. Locations with observed zeroes were assumed to represent low-level values below some detection threshold (see section on Observed Data below). Information on the locations of observed zeroes was incorporated into the analysis using Bayesian data augmentation methods (Tanner and Wing 1987). Gibbs sampling was used to sample from imputed low-level values at the locations of observed zeroes and infer the variogram. The posterior densities of model parameters and imputed low-level values were then used to support prediction to a set of prediction points. This Bayesian approach thus allowed for uncertainty in the variogram parameters as well as imputed values at the location of observed zeroes.

The performance of the Bayesian integrated method was evaluated using a simulated test dataset and then applied to acoustic survey data for Peruvian anchoveta (*Engraulis ringens*). The purpose of the testing was to assess whether this method is effective at identifying the spatial parameters, density distribution, and the spatial pattern of a censored process in a case where the true underlying distribution was known. The purpose of the application to anchoveta was to simulate the spatial distribution of these forage fish as the basis for spatial analysis of the foraging patterns of anchoveta predators (Boyd 2012). The priority was therefore to reproduce the observed spatial pattern as closely as possible.

Peruvian anchoveta occurs in the Humboldt Current system off the coasts of Peru and northern Chile (Mathisen 1989), and supports one of the largest single species fisheries in the world (Fréon et al. 2008). Off Peru, anchoveta stocks are concentrated close to shore, at distances between the shoreline and 100 nautical miles from the coast, depending on the year (Simmonds et al. 2009). Stocks are strongly associated with recently-upwelled nutrient-rich cold coastal waters (CCW) (Bertrand et al. 2004a,

Swartzman et al. 2008). In most years, the CCW are spread in a broad shallow layer over the continental shelf, but in some years the CCW may be restricted to isolated pockets associated with persistent upwelling during warm water anomalies (Bertrand et al. 2004a). As with other small pelagic fishes, the distribution of anchoveta within suitable habitat is characterized by nested aggregation structures (Fréon and Misund 1999). Anchoveta exhibits strong schooling tendencies, and schools may form clusters of schools within broader aggregations (Bertrand et al. 2008). Both factors, the strong association of stocks with particular water masses and the formation of clusters, can lead to a high degree of patchiness in the distribution of anchoveta.

Methods

Observed data

The Instituto del Mar del Perú (IMARPE) conducted an acoustic survey along the Peruvian coastline from approximately 11.4°S to 12.2°S on the RV “Olaya” during 2-5 December 2008 and 4-7 December 2009. The survey was designed to provide data on the distribution of anchoveta coincident with data on the movement patterns of seabirds collected at the island group of Pescadores (11.77°S). The survey comprised systematic, parallel, equally-spaced, onshore-offshore transects approximately 10 km apart (Fig. 1). The eastern end of each transect was near shore, approximately 1 km from the coast. The western end of most transects fell within the shelf break approximately 60 km from the coast, with every third transect continuing approximately 25 to 45 km beyond the shelf break to cover the observable range of anchoveta. Sampling effort therefore differed between the on-shelf and off-shelf area. For the purposes of this analysis, the study region was restricted to the on-shelf area covered by the survey.

Acoustic backscattering data were collected using a calibrated Simrad scientific echosounder (EK60) operating at 120 kHz. The acoustic data were processed by IMARPE, using Echoview acoustic postprocessing software (Myriax Software, Hobart, Tasmania, Australia). Acoustic backscatter was identified to species based on known backscattering characteristics, ground-truthed using biological samples taken from mid-water trawls during the survey (Castillo et al. 2009, Simmonds et al. 2009). The

155 nautical area scattering coefficient (NASC) attributable to anchoveta was computed from the volume
 156 backscattering strengths over 1 nautical mile transect segments (elementary distance sampling units,
 157 EDSUs). Only backscatter attributed to anchoveta was used in this analysis. Geolocations were
 158 transformed into the Universal Transverse Mercator coordinate system using the package `rgdal()` in R
 159 (Keitt et al. 2011, R Development Core Team, 2011).

160 In both 2008 and 2009, the distributions of acoustic densities attributed to anchoveta were characterized
 161 by high proportions of zero values (approximately 40% of the total in 2008 and 60% in 2009), and the
 162 distributions of non-zero densities were strongly right-skewed. In December 2008, observed data indicate
 163 that anchoveta was broadly distributed throughout the study region, with some areas of zero or low
 164 densities in the distribution (Fig. 1a). This pattern is consistent with the hypothesis that the shelf area
 165 covered by the acoustic survey mostly encompassed suitable habitat for anchoveta, and that the gaps in
 166 the distribution are mostly attributable to the aggregative behaviour of anchoveta within suitable water
 167 masses. In contrast, in December 2009, there were larger areas of zero or low densities (Fig. 1b). At the
 168 time of 2009 survey, observed water masses in the study region (CCW and mixed CCW and subtropical
 169 surface waters) provided suitable habitat for anchoveta, but the biomass of anchoveta in the study region
 170 was rather low. This suggests that gaps in the distribution in 2009 were mostly attributable to a
 171 combination of low regional biomass and the aggregative behaviours of anchoveta within suitable habitat.

172 **Test data**

173 Test data were generated using a process that matched the assumptions of the integrated method (see
 174 below). A set of prediction points encompassing the study region was created. A single isotropic GRF
 175 with exponential correlation function was simulated to the 2008 transect locations and the prediction
 176 points (Fig. 2a). The parameters governing spatial autocorrelation were chosen to be close to values
 177 indicated in exploratory analysis of the observed anchoveta data for 2008. Due to the random nature of
 178 the process, the realised parameters of a simulated GRF are not expected to correspond exactly to the
 179 simulation parameters. The mean and variance of the test data were standardized for convenience. Two

censored datasets were then derived from the single test dataset by censoring values less than a censoring point, defined as (i) the 40th percentile (Fig. 2b) and (ii) the 60th percentile, corresponding to the proportion of observed zeroes in the anchoveta data for 2008 and 2009 respectively. Values at the transect locations were then extracted to form two estimation datasets (Fig. 2c), leaving values at the prediction points to provide two evaluation datasets.

Geostatistical model

A standard geostatistical model (following Diggle and Ribeiro 2007) may comprise a trend surface, a spatial signal process, and additional non-spatial or residual variance:

$$(1) \quad Y_i \sim \sum_{j=1}^J \beta_j D_{ji} + S_i + \varepsilon_i$$

where Y is a random variable observed at a set of sampling locations $i = 1 \dots N$; D_{ji} are $j = 1 \dots J$ measured spatial coordinates or environmental covariates and β_j are the corresponding parameters; S_i is the spatial signal process, $E[S_i] = 0$; and ε_i are independent and identically distributed with zero mean and non-spatial variance τ^2 . The theoretical variogram is used to characterize the spatial signal process. In the stationary and isotropic case, this simplifies to:

$$(2) \quad V(h) = \sigma^2[1 - \rho(h)]$$

where σ^2 is the variance of the spatial signal process (the ‘partial sill’), which is constant in the stationary case; $\rho(h)$ is the correlation function; and h is the absolute Euclidean distance between two locations. In the case of second-order stationarity, the covariance depends only on the absolute distance between two locations. The correlation function, $\rho(h)$, is usually chosen from a range of standard families which are known to be positive definite, but are otherwise sufficiently flexible to meet the needs of geostatistical data (Diggle and Ribeiro 2007). Based on exploratory analysis of the acoustic survey data, an exponential correlation function was assumed throughout the analysis presented here:

$$(3) \quad \rho(h) = \exp\left(-\frac{h}{\varphi}\right)$$

where the scale parameter, $\varphi > 0$, is approximately one third of the practical range, i.e. the distance at which correlation is 0.05. Spatial autocorrelation may be isotropic or anisotropic. However, in this case,

the spatial distribution was assumed to be isotropic (i.e. spatial continuity is similar in all directions) as the study region was small. We further assumed a constant trend or mean (i.e. $E(Y_i) = \beta_j D_{ji} = \mu$). The restricted maximum likelihood estimator for a stationary GRF is:

$$(4) \quad LL(\varphi, \sigma^2, \tau^2) = -0.5 \{ n \cdot \log(2\pi) + \log|\sigma^2 V_\varphi| + \log|D'(\sigma^2 V_\varphi)^{-1} D| + Z'(\sigma^2 V_\varphi)^{-1} Z \}$$

where n is the number of observations; $V_\varphi = R_\varphi + v^2 I$, R_φ is the correlation matrix; $v^2 = \frac{\tau^2}{\sigma^2}$; D is a vector of 1s in the case of a constant trend; and Z is the vector of observed minus expected values (see Diggle and Ribeiro, 2007, p. 117).

Bayesian data augmentation, inference, and posterior prediction

Test data

For the two estimation datasets, the variable underlying the censored and non-censored values was known to follow an isotropic GRF with zero mean (i.e. $\mu = 0$), and the sampling distribution on which the log-likelihood in Equation 4 was based. Bayesian data augmentation (Tanner and Wing 1987) was used to impute values at the locations of the censored data. Bayesian data augmentation is useful when the data comprise a combination of observed and unobserved or latent data, and the posterior density of the parameters is difficult to calculate without the latent data but would be comparatively straight-forward if the latent data were fully observed. The Bayesian data augmentation solution is to generate many sets of values for the latent data, and then approximate the posterior density over the many sets of imputed values (see De Oliveira 2005 for a relevant geological example). Here, a Gibbs sampler was used to impute the censored values and sample from the posterior densities of the parameters φ , σ^2 , τ^2 . Imputed values were drawn from a continuous uniform distribution with the upper bound set at the censoring point corresponding to the dataset being analysed and the lower bound set to a value (-5) with probability density <0.00001 under the standard Gaussian distribution. Following Diggle and Ribeiro (2007), both φ and v^2 were discretized to reduce computation time. The priors for parameters φ , σ^2 , v^2 were assumed to be independent. For $\varphi > 0$, a uniform discrete prior $\{1, 2, 3, \dots, 50\}$ was chosen, with the upper limit set to

50 km. For $v^2 = \frac{\tau^2}{\sigma^2}$, a uniform discrete prior $\{0, 0.1, 0.2, \dots, 1\}$ was used. The prior for the inverse of σ^2 was $\Gamma(0.1, 0.1)$. The Gibbs sampler was implemented in JAGS (Just Another Gibbs Sampler, Plummer 2003). For each estimation dataset, two parallel chains were generated with a thinning rate of 50. After discarding the first 250 parameter sets, 250 parameter sets were saved from each chain. Convergence was evaluated using the Geweke and Gelman-Rubin diagnostic statistics (Geweke 1992, Gelman and Rubin 1992, Brooks and Gelman 1998).

Posterior predictions were then generated to the set of prediction points following development of the posteriors for ϕ , σ^2 , v^2 . One hundred parameter sets (including imputed values) were sampled at random from the two chains for each estimation dataset. For each sampled parameter set, conditional geostatistical Gaussian simulation (Goovaerts 1997) was used to generate posterior densities of values at the prediction points, based on a single realisation of the GRF for each of the 100 parameter sets. The posterior predictions were conditioned on the non-zero densities and the locations of the censored data, while the model parameters and the imputed values at the locations of censored data were treated as uncertain. For the posterior predictions, values less than the 40th or 60th percentile of the standard Gaussian distribution were then censored as appropriate to check whether the proportion of censored values in the posterior matched the true population value in the test data. (R code for reproducing the simulations and Bayesian data augmentation, inference and prediction is available in the Supplementary Material.)

Observed data

For the observed data, the first step in the modelling process was to transform the non-zero densities for each survey year into a left-truncated Gaussian distribution with the censoring point corresponding to the observed proportion of zero values. In likelihood-based geostatistics, zero-truncated right-skewed continuous distributions may be modelled using a linear model following Box-Cox transformation (Box and Cox 1964). Preliminary analysis indicated that log-transformation provided the best fit to the non-zero acoustic densities (Fig. 3). Following log-transformation, the Anderson-Darling test for normality indicated that the observed data were consistent with a Gaussian distribution (p-value = 0.815) in 2009

but not in 2008 (p-value = 0.019). Nonetheless, a log-Gaussian distribution was assumed in both cases, and the effects of this assumption are discussed further below. For each survey year, probability points were calculated for the non-zero densities based on a log-Gaussian distribution and then rescaled to allow for the observed proportion of zero values in each year, i.e. the rescaled probability points fell within the range ~0.4-1 for the 2008 data and ~0.6-1 for the 2009 data. The non-zero densities were then transformed into standard Gaussian space with zero mean and unit variance using the rescaled probability points. (R code for transforming a variable to a truncated Gaussian distribution is available in the Supplementary Material.) The transformed variable (combining transformed non-zero densities and latent values corresponding to the observed zeroes) was then assumed to follow an isotropic GRF with zero mean (i.e. $\mu = 0$) and log-likelihood as in Equation 4. Environmental covariates were not included in the analysis presented here, but could have been included as per Equation 1 (see also Diggle and Ribeiro, 2007, p. 117).

Bayesian data augmentation, inference, and posterior prediction were implemented as for the test data, with the following adjustments. The upper limit for $\phi > 0$ was extended to 100 km, approximately the maximum distance between survey locations. The step size in the uniform discrete prior for $v^2 = \frac{\tau^2}{\sigma^2}$ was refined to $\{0, 0.025, 0.05, \dots, 1\}$. For each observed dataset, two parallel chains were generated with a thinning rate of 200. After discarding the first 250 parameter sets, 250 parameter sets were saved from each chain. The 2009 survey did not extend as far south as the 2008 survey (Fig. 1), so the set of prediction points for 2009 was cropped to avoid extrapolation from the observed data. Finally, values less than the predefined censoring point were censored, and the vector of non-censored data was back-transformed to the observed data space using the inverse of the procedure described above.

Results

Performance of the Bayesian integrated method was assessed in terms of the posterior densities for the spatial parameters, and the density distribution, spatial pattern, and overall spatial distribution of posterior predictions.

Test data

Posterior densities of the spatial parameters

Samples from the posterior densities of the spatial parameters of the uncensored and censored test data are shown in Figure 4. The posterior density distributions are similar, with some increase in uncertainty as 40% and 60% of values are censored.

Density distributions of the posterior predictions

In the case of the test data, the mean and variance of the simulated GRF are known (Fig. 5). Differences between descriptive statistics for the estimation and evaluation datasets are indicative of sampling error and are not attributable to the analytical method. In the case of the variance, the difference is partly structural. Spatial autocorrelation implies that the variance between points that are close together is less than the variance between points that are far apart. The prediction locations are interpolated among the transect locations – each prediction location therefore has more close neighbours and the overall variance is consequently lower.

The mean and variance of the simulated GRF are well reproduced in posterior predictions, as is the proportion of values that fall below the censoring point and the density distribution of non-censored values when 40% of values are censored (Fig. 5a). The mean and variance of the simulated GRF are less well reproduced when 60% of values are censored (Fig. 5b). Nevertheless, the proportion of values that fall below the censoring point and the density distributions of the non-censored values are well-reproduced (Fig. 5b).

Spatial pattern of the censoring process and of the non-censored values

The performance of the Bayesian integrated method in terms of reproducing the spatial pattern of the underlying process can be evaluated by comparing boxplots of empirical variograms derived from the posterior predictions with the empirical variogram of the simulated GRF after censoring (Fig. 6).

Overall, the spatial patterns in the posterior predictions correspond well to the patterns in the evaluation datasets, especially at short distances. Spatial autocorrelation in the censoring process (approximating presence/absence) is well-reproduced, (Fig. 6a). Sampling error is more pronounced for the non-censored values (approximating conditional abundance). The variograms calculated from posterior predictions of non-censored values generally fall between variograms calculated from values at the prediction points and transect locations.

Overall spatial distribution

Figure 7 shows the simulated GRF after censoring, together with sample posterior predictions. The posterior predictions reproduce the spatial distribution of the censored GRF, in terms of the distribution of censored values and peaks in non-censored values.

Observed data

Posterior densities of the spatial parameters

Samples from the posterior densities of the spatial parameters based on analysis of the acoustic survey data for anchoveta are shown in Figure 8. Overall, the posterior distributions for the spatial parameters compare well to those for the test data after allowing for the broader prior distribution for the scaling parameter, ϕ , used in the analysis of observed data. The posterior distribution for the non-spatial variance, τ^2 , is notably more concentrated.

The posterior densities indicate several differences in the spatial process underlying the distribution of anchoveta in 2008 versus 2009 (Fig. 8). Posterior densities of the scaling parameter, ϕ indicate that the distance over which spatial autocorrelation decays was likely longer in 2009 than 2008, consistent with fewer larger clusters in 2009. Posterior densities of the variance parameters indicate that non-spatial variance was relatively low and hence the spatial signal represented a greater proportion of the overall variance in 2009, consistent with better-defined clusters.

Density distributions of the posterior predictions

In posterior predictions based on the 2008 data (Fig. 9a), the proportion of zero densities and the mean of the non-zero densities correspond closely to the data observed at transect locations. The mode of the variance of non-zero densities also corresponds to the variance at transect locations, but the variance ranges quite broadly among posterior predictions. In posterior predictions based on the 2009 data (Fig. 9b), the proportion of zero densities tends to be higher than observed at transect locations, while the mean and variance of non-zero densities correspond more closely to data observed at transect locations. Posterior predictions effectively reproduce the density distribution of non-zero values observed in 2009 (Fig 9b). In contrast, posterior predictions based on the 2008 data do not reproduce the spike of low values in the observed data because this is not consistent with the assumed log-Gaussian distribution (Fig 9a).

Spatial pattern of presence/absence and conditional abundance

Comparison of empirical indicator variograms derived from the posterior predictions with empirical indicator variograms for the transect data (Fig. 10a) indicates that the non-spatial variance in the presence/absence process is over-estimated, especially in 2008. The contrast with the test data is striking, and suggests that the edges of anchoveta clusters are more consolidated than in the test data.

Overall spatial distribution

Figure 11 shows the observed transect data for 2008 and 2009, together with sample posterior predictions for each year. The posterior predictions reproduce the overall spatial distribution of the observed data in terms of the distribution of censored values and peaks in non-censored values. Anchoveta was broadly distributed across the study region with some gaps in the distribution in the northwest and the southeast in 2008, whereas it was mostly concentrated nearshore, with some more diffuse clusters near the shelf break in 2009.

Discussion

A new modelling framework

The appropriate method for spatial analysis of the distribution of small pelagic fish depends on the processes underlying the observed distribution and the purpose of the analysis. Two-stage models are appropriate where the processes leading to gaps in the distribution are distinct from those determining conditional abundance. Here, we developed an approach suitable for modelling distributions in which patchiness is largely attributable to the aggregation of small pelagic fish within a region of suitable habitat. Following Woillez et al. (2009), the patchy distribution was modelled as the outcome of a continuous but censored aggregation process, based on a transformed truncated GRF. We developed a fully Bayesian approach, using Bayesian data augmentation to impute censored values and accounting for uncertainty in the parameters of the spatial distribution.

Performance testing revealed that this Bayesian integrated method was effective at identifying the spatial parameters of a simulated GRF from censored data at transect locations, and at reproducing the density distribution of non-censored data. Performance deteriorated slightly when 60% of values were censored. The spatial pattern of the censoring process and the non-censored values was well-reproduced in posterior predictions, together with the spatial and density distribution of the censored variable. While the posterior predictions are based on samples from a wide range of parameter values, the spatial distributions that emerge are consistent with the simulated GRF across posterior predictions. This is attributable to conditioning on the values at transect locations, which provide a consistent skeleton on which posterior predictions are constructed.

In performance testing, the data-generating process was known to be a censored isotropic GRF, whereas the spatial processes underlying the observed data were unknown. Differences in performance of the Bayesian integrated method when applied to test data versus observed data point towards possible deviations from the assumptions underlying implementation of the method. Poor identification of spatial parameters, for example, would suggest that the spatial process underlying the observed data was poorly

represented by a censored GRF. Overall, the Bayesian integrated method performed well when applied to the anchoveta data for both 2008 and 2009, with two notable exceptions. First, the Bayesian integrated method effectively reproduced the spatial pattern of the observed non-zero densities, but the non-spatial variance in the censoring process was notably higher in posterior predictions than in the transect data, especially for 2008. This suggests that the edges of clusters are more clearly-defined than shown in the posterior predictions, while the interior spatial structure is better-represented. One hypothesis to explain the relatively low contribution of non-spatial variance to the presence/absence process would be differences in the inherent aggregative behaviours underpinning presence/absence versus conditional abundance. The impulse that underlies the formation of schools by small pelagic fish may be strong, contributing to low non-spatial variance, whereas spatial structure within schools may be more heterogeneous contributing to higher non-spatial variance (Gerlotto and Paramo 2003, Bertrand et al. 2008). Second, the observed non-zero densities were not consistent with a log-Gaussian distribution in 2008. Consequently, the density distributions of posterior predictions more closely follow a Gaussian distribution than the observed log-transformed data for 2008. In likelihood-based approaches, effective inference depends on how well the assumed distribution approximates the true distribution of the variable of interest (Isaaks and Srivastava 1989, Matheron 1978). Where the observed data do not follow a parametric distribution, researchers must choose between a parametric and non-parametric approach. This choice will depend on the purpose of analysis, the extent of deviations from a parametric distribution, and an assessment of whether these are representative of the true distribution or reflect sampling error. Analysis of the observed anchoveta data using the Bayesian integrated method following non-parametric transformation is presented in the Supplementary Material. Comparison of the results following parametric and non-parametric transformations indicates that the posterior densities for the spatial parameters and spatial pattern are very similar. However, when the analysis was extended to include simple estimates of regional abundance following back-transformation, substantial differences emerged attributable to the deviations of the observed sample distribution from a true log-Gaussian distribution.

The primary purpose of our analysis was to simulate the spatial distribution of small pelagic fish as the basis for analysing the foraging patterns of their predators, and we chose to use a fully parametric approach. Other researchers may choose a non-parametric transformation, especially for the purposes of abundance estimation.

Comparison with existing approaches

Where the primary focus of spatial analysis is the presence/absence process rather than conditional abundance, alternative geostatistical methods may be considered. Indicator simulation (Goovaerts 1997) provides one option for simulating presence/absence (e.g. Walline 2007), but falls outside the likelihood-based framework so the advantages of a likelihood-based approach for structural analysis would be lost. In likelihood-based geostatistics, the conventional approach to modelling a presence/absence process is based on a binomial model (e.g. Roa-Ureta and Niklitschek 2007). However, a major challenge for spatial analysis based on a single Bernoulli trial at each location, as in the anchoveta data, is the limited information available to estimate the spatial signal (Diggle and Ribeiro 2007). Repeated surveys may be necessary to generate sufficient information to estimate the parameters of the binomial model. This strategy was shown to be useful in analysis of Patagonian squid (*Loligo gahi*) (Roa-Ureta and Niklitschek 2007), but its effectiveness will depend on the time interval between surveys versus the mobility of the stock. The binomial geostatistical model is based on the assumption that the spatial signal process takes the form of a hypothetical GRF which is transformed into a probability field through the inverse logit function. The response variable is then assumed to follow a Bernoulli distribution based on the probability field. In the final step, an indicator value is drawn independently for each location based on the inferred spatially-dependent probability field. This step is inappropriate for species with strong inherent aggregative behaviours, such as anchoveta. For these species, presence/absence at a location is not independent of presence/absence at neighbouring locations, even after the underlying probability of occurrence has been taken into account. Binomial simulation leads to a more fragmented pattern than the

integrated method (Boyd 2012), and is inappropriate for species with inherent aggregative behaviours that extend beyond the scale of analysis.

In conclusion, truncated GRFs are well-established in other fields of geostatistics, but have only recently been applied to fisheries data. The analysis presented here demonstrated that Bayesian posterior prediction using a truncated GRF can be effective at reproducing the patchy spatial distribution of anchoveta. This method is broadly applicable to the patchy distributions of small pelagic fish and krill within suitable habitat and the three main purposes of geostatistical analysis for fisheries ecology identified in the Introduction. There are several differences in the overall spatial distribution simulated using the Bayesian integrated method compared to a two-stage model. In two-stage models, no information is passed from the presence/absence stage to the conditional abundance stage on the probability of occurrence at a location. All points with predicted presence are treated as equal in the second stage, so high values may be predicted in areas with low probability of occurrence. In contrast, all information is retained throughout the posterior prediction process in the integrated method. As a result, the integrated method generally predicted low values, if any, in areas near where the acoustic survey returned zero values. The integrated method may prove more efficient for structural analysis and inference on the relationship between the spatial distributions of fish and environmental covariates because the analysis is not split into two separate and independent stages. Furthermore, in the integrated method, predicted values near the edge of clusters are constrained by low neighbouring densities whereas they are unconstrained by nearby zero values in two-stage models. The greater spatial structure in the integrated method is therefore expected to reduce the variance in posterior predictions of stock abundance. The purpose of our analysis was to simulate the spatial structure of aggregations of anchoveta, as the basis for spatial analysis of the foraging patterns of anchoveta predators (Boyd 2012). As tracking data on marine predators and fishing fleets become more widely available, we anticipate that similar analyses of the spatial pattern of forage fish, their natural predators, and fishing fleets will become an important tool for strengthening understanding of spatial structure and function in marine ecosystems as an input to ecosystem-based management.

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Figure legends

Figure 1. Proportional representation of acoustic backscatter (m^2 per nautical mile²) in (a) 2008 and (b) 2009. Elementary distance sampling units (EDSUs) are marked by crosses (zero values for anchoveta) and circles (positive values, diameter of the circles proportional to the logarithm of relative anchoveta abundance). The shelf break (200 m isobaths) is indicated by the dashed line.

Figure 2. (a) A standard isotropic GRF was simulated to the 2008 transect locations and prediction points. Darker shades indicate higher densities. (b) Values less than the 40th percentile were censored. White indicates censored values. (c) The transect locations were extracted. Steps (b) and (c), were repeated with values less than the 60th percentile censored (not shown).

Figure 3. Histograms of the observed log-transformed non-zero acoustic densities by EDSU for (a) 2008 and (b) 2009, with Gaussian density distributions overlaid.

Figure 4. Samples from the posterior densities for the test data when (a) 0%, (b) ~40%, and (c) ~60% of values are censored. Parameter values used to generate the test data are indicated by dashed vertical lines.

Figure 5. Posterior densities for the test data when (a) ~40%, and (b) ~60% of values are censored: from left to right, the mean of the simulated GRF prior to censoring; the variance of the simulated GRF prior to censoring; and the proportion of values censored. In each case, the dashed vertical line represents the population value estimated from the evaluation points, and the dotted vertical line represents the sample value from the estimation datasets. In the far right panel, histograms show the density distributions of the simulated GRF after censoring. The solid line shows the mean; dashed lines show the 2.5th and 97.5th percentile of the corresponding posterior densities.

Figure 6. Quantitative summaries of the spatial pattern of (a) the censoring process (approximating presence/absence) and (b) the non-censored values (approximating conditional abundance). Box plots represent empirical variograms computed from posterior predictions. Dashed lines represent empirical variograms for the simulated GRF; dotted lines represent empirical variograms for the transect data.

Figure 7. The simulated GRF after censoring when (a) ~40% and (b) ~60% of values are censored (far left panel), together with three sets of sample posterior predictions. Darker shades indicate higher densities in quantiles and white indicates censored values.

Figure 8. Samples from the posterior densities for observed data on anchoveta from (a) 2008 and (b) 2009. From left to right, panels show the scaling parameter, spatial variance, and non-spatial variance.

Figure 9. Samples from the posterior densities for observed data on anchoveta from (a) 2008 and (b) 2009. From left to right, panels show the proportion of values censored, the mean of non-zero densities, and the variance of non-zero densities, with the dotted vertical line representing the value from the transect data. In the far right panel, histograms show the distributions of the observed log-transformed non-zero densities; the solid line shows the mean; dashed lines show the 2.5th and 97.5th percentile of the corresponding posterior densities.

Figure 10. Quantitative summaries of the spatial pattern of observed data on anchoveta of (a) presence/absence and (b) conditional abundance. Box plots represent empirical variograms computed from posterior predictions. Dotted lines represent empirical variograms for the observed data.

Figure 11. The observed transect data from (a) 2008 and (b) 2009, together with three sets each of sample posterior predictions. Darker shades indicate higher densities in quantiles and white indicates censored values.