

Ecography

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Supplementary material

Appendix 1

Hierarchical geostatistics models for wildlife populations

This model is a generalization of the Poisson kriging model introduced in Monestiez et al. (2006) where they proposed a corrected variogram estimator that takes account of variability added by the Poisson observation process in order to produce maps of relative abundance. The model presented here takes account explicitly of the observation process and of the deterministic trend often observed in species' spatial distributions (Bellier et al. 2010).

1 Expectation and variance of Z_s

From equations of the hierarchical model (Eq. 1 and 2 in the main text in the section '*a spatial hierarchical model for count data* ') as $Z_s | Y_s \sim P(\lambda)$ with a mean λ equal to the spatial field Y_s it follows directly that,

$$\mathbb{E}[Z_s|X_s] = Y_s = m_s X_s$$

$$\text{Var}[Z_s|X_s] = Y_s = m_s X_s$$

$$\mathbb{E}[(Z_s)^2|X_s] = Y_s + Y_s^2 = m_s X_s + m_s^2 X_s^2, \tag{A1}$$

and the unconditional (marginal) distribution of the observed data

$$\begin{aligned}\mathbf{E}[Z_s] &= m_s \\ \mathbf{Var}[Z_s] &= m_s^2 \sigma_X^2 + m_s.\end{aligned}\tag{A2}$$

For the covariance expression, the conditional independence of observations at different sites leads to

$$\begin{aligned}\mathbf{E}[Z_s Z_{s'} | X] &= \mathbf{Cov}[Z_s, Z_{s'} | X] + \mathbf{E}[Z_s | X_s] \mathbf{E}[Z_{s'} | X_{s'}] \\ &= \delta_{ss'} m_s X_s + m_s m_{s'} X_s X_{s'},\end{aligned}\tag{A3}$$

where $\delta_{ss'}$ is Kronecker's δ which is equal to 1 if $s = s'$ and 0 otherwise.

2 Variogram expressions

In order to characterize the relationship between the variograms of Z and X , we develop the expressions of the two first moments of $(Z_s - Z_{s'})$.

$$\begin{aligned}\mathbf{E}[Z_s - Z_{s'} | X] &= \mathbf{E}[Z_s | X_s] - \mathbf{E}[Z_{s'} | X_{s'}] = m_s X_s - m_{s'} X_{s'} \\ \mathbf{E}[Z_s - Z_{s'}] &= \mathbf{E}[X] (m_s - m_{s'}) = m_s - m_{s'}.\end{aligned}\tag{A4}$$

The second order moment can be derived from Eq. A2 and A3,

$$\begin{aligned}\mathbf{E}[(Z_s - Z_{s'})^2 | X] &= \mathbf{E}[(Z_s)^2 | X_s] + \mathbf{E}[(Z_{s'})^2 | X_{s'}] - 2 \mathbf{E}[Z_s Z_{s'} | X] \\ &= (Y_s + Y_{s'} - 2 \delta_{ss'} Y_s) + (Y_s - Y_{s'})^2. \\ \mathbf{E}[(Z_s - Z_{s'})^2] &= \mathbf{E}[(Y_s + Y_{s'} - 2 \delta_{ss'} Y_s) + (Y_s - Y_{s'})^2] \\ &= (m_s + m_{s'} - 2 \delta_{ss'} m_s) + \mathbf{E}[(m_s X_s - m_{s'} X_{s'})^2].\end{aligned}$$

2.1 Non-stationary theoretical variogram

In order to characterize the relationship between the variograms Z and Y and to determine adequate weights or correction terms, we developed conditional and non-conditional expectations related to $\left(\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}}\right)$ using Eq. A2,

$$\begin{aligned}\mathbb{E}\left[\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}} \middle| X\right] &= \frac{1}{m_s} \mathbb{E}[Z_s|X_s] - \frac{1}{m_{s'}} \mathbb{E}[Z_{s'}|X_{s'}] = X_s - X_{s'} \\ \mathbb{E}\left[\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}}\right] &= 1 - 1 = 0.\end{aligned}\tag{A5}$$

The expression of the non-conditional order-2 moment is derived from Eq. A2 and A3,

$$\begin{aligned}\mathbb{E}\left[\left(\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}}\right)^2 \middle| X\right] &= \frac{1}{m_s^2} \mathbb{E}[(Z_s)^2|X_s] + \frac{1}{m_{s'}^2} \mathbb{E}[(Z_{s'})^2|X_{s'}] - \frac{2 \mathbb{E}[Z_s Z_{s'}|X]}{m_s m_{s'}} \\ &= \frac{X_s}{m_s} + \frac{X_{s'}}{m_{s'}} - 2\delta_{ss'} \frac{X_s}{m_s} + (X_s - X_{s'})^2. \\ \mathbb{E}\left[\left(\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}}\right)^2\right] &= \mathbb{E}\left[\frac{X_s}{m_s} + \frac{X_{s'}}{m_{s'}} - 2\delta_{ss'} \frac{X_s}{m_s} + (X_s - X_{s'})^2\right] \\ &= \left(\frac{m_s + m_{s'}}{m_s m_{s'}}\right) - 2\delta_{ss'} \frac{1}{m_s} + 2\gamma_X(ss').\end{aligned}$$

$$\frac{1}{2} \mathbb{E}\left[\left(\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}}\right)^2\right] = \frac{1}{2} \left(\frac{m_s + m_{s'}}{m_s m_{s'}}\right) - \delta_{ss'} \frac{1}{m_s} + \gamma_X(ss').\tag{A6}$$

Let $\gamma_{Z/m}(ss')$ denote the non-stationary theoretical variogram corresponding to the random field (Z_s/m_s) , we get for $s \neq s'$ the relationship :

$$\gamma_X(ss') = \gamma_{Z/m}(ss') - \frac{1}{2} \left(\frac{m_s + m_{s'}}{m_s m_{s'}}\right),\tag{A7}$$

we can check for $s = s'$ that Eq. A6 reduces to $\gamma_X(0) = \gamma_Z(0) = 0$.

Furthermore the conditionnal variance and its expectation for $s \neq s'$ are,

$$\begin{aligned}
\text{Var} \left[\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}} \middle| X \right] &= \mathbf{E} \left[\left(\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}} \right)^2 \middle| X \right] - \mathbf{E}^2 \left[\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}} \middle| X \right] \\
&= \frac{X_s}{m_s} + \frac{X_{s'}}{m_{s'}} + (X_s - X_{s'})^2 - (X_s - X_{s'})^2 \\
&= \frac{X_s}{m_s} + \frac{X_{s'}}{m_{s'}}. \\
\mathbf{E} \left[\text{Var} \left[\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}} \middle| X \right] \right] &= \mathbf{E} \left[\frac{X_s}{m_s} + \frac{X_{s'}}{m_{s'}} \right] = \left(\frac{m_s + m_{s'}}{m_s m_{s'}} \right). \tag{A8}
\end{aligned}$$

2.2 Estimation of $\gamma_X(h)$

Let Z_s be the values observed at a given cell s . The expectation of the modified sample variogram of X can be derived from the weight system from Eq. A8 and the minus-one bias-correction term from equation Eq. A7,

$$\gamma_X^*(\mathbf{h}) = \frac{1}{2 N(\mathbf{h})} \sum_{s,s'} \left(\frac{m_s + m_{s'}}{m_s m_{s'}} \left(\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}} \right)^2 - 1 \right) I_{d_{ss'} \sim \mathbf{h}}, \tag{A9}$$

where $I_{d_{ss'} \sim h}$ is the indicator function of pairs (ss') whose distance is close to \mathbf{h} , where

$N(\mathbf{h}) = \sum_{ss'} \frac{m_s + m_{s'}}{m_s m_{s'}} I_{d_{ss'} \sim \mathbf{h}}$ is a normalizing constant.

The sample variogram estimate $\gamma_X^*(\mathbf{h})$ can be difficult to obtain when computed from an area where few data are expected. For example, in our case study of the auks in the Bay of

Biscay, when the mean is inferior to 0.5 there were only 215 sightings and the total length of the transect was 2500 km. In such a case, the expression $\left(\frac{Z_s}{m_s} - \frac{Z_{s'}}{m_{s'}}\right)$ gives a strong weight to the variogram values when computed in this area where few data are expected. So a simpler estimate of γ_X can be proposed on subareas where the mean m_s can be assumed constant or when the empirical variogram estimate $\gamma_Z^*(\mathbf{h})$ is restricted to pairs of sampled sites with the same mean m_s ,

$$\gamma_X^*(\mathbf{h}) = \frac{1}{m^2} \left[\gamma_Z^*(\mathbf{h}) - m \right], \quad (\text{A10})$$

where m is the locally constant value of m_s .

References

- Bellier, E. et al. Geostatistical modelling of wildlife population : a non-stationary hierarchical model for count data. - geoENV VII - Geostatistics for Environmental Applications. 16: 1-12.
- Monestiez, P. et al. 2006. Geostatistical modelling of spatial distribution of *Balaenoptera physalus* in the Northwestern Mediterranean Sea from sparse count data and heterogeneous observation efforts. - Ecological Modelling 193: 615-628.

Appendix 2

Variogram models

We present here the theoretical variogram formulas used in this study. They are standard variogram models and more detailed explanations can be found in Cressie (1993), Wackernagel (2003) and Webster and Oliver (2007). We deal with them in their isotropic form, so that the lag vector $|\mathbf{h}|$ becomes a scalar measure of distance only, h in any direction.

Here, $\gamma(h)$ is the theoretical variogram at distance h , the nugget parameter is c_0 , the sill parameter is c_1 and a is the range. There are two main families of variogram model, one represents bounded variation while the other unbounded variation.

Spherical model. This model is a bounded variogram, so that the spherical model may reach its sill at a finite lag distance, the range and the semi-variance has a maximum (i.e. the sill) which is *a priori* the variance of the process. The value of the range corresponds to the average diameter of the patches. This makes the range values easily interpretable when investigating the spatial structure of a species' distribution. This model is well-suited to model spatial processes generating regular patches. A spherical model (c_0, c_1, a) is defined

by

$$\gamma(h) = \begin{cases} c_1 \left[\frac{3h}{2a} - \frac{1}{2} \frac{h}{a} \right] & \text{for } h \leq a_1 \\ c_0 + c_1 & \text{for } h > a_1. \end{cases} \quad (\text{A11})$$

The following models are unbounded variogram models meaning that the variance is infinite and the sill is approached only asymptotically and so they do not have a finite range. In this case the range values might be more difficult to interpret when analysing a species 'distribution. These are the variograms of transition processes and are well-suited to model very broad-scales structures generated by environmental gradients (i.e., trends) when applied to ecological data.

Exponential model. The exponential model has a near linear behaviour when approaching distance zero (i.e. origin of the variogram) and may be well-suited to model processes with irregular patches and very broad-scale variation. An exponential model (a, c_0, c_1) is defined by

$$\gamma(h) = c_0 + c_1 \left\{ 1 - \exp\left(-\frac{h}{a}\right) \right\}. \quad (\text{A12})$$

Stable model. This model has a reverse curvature when approaching the origin, the curvature varies with α . A stable model (c_0, c_1, a, α) is defined by

$$\gamma(h) = c_0 + c_1 \left\{ 1 - \exp \left(-\frac{h}{a} \right)^\alpha \right\}. \quad (\text{A13})$$

Bessel model. This model might be used to model a variogram that fluctuates more or less periodically, rather than increasing monotonically. This model might be useful to model processes with periodicity. The user of this function should ask what evidence there is of periodicity in the ecological process being investigated. If there is none and the apparent periodicity or hole is weak, then the user should not try to force a periodic model on the variogram. A Bessel model (c_0, c_1, a, w_j) is defined by

$$\gamma(h) = c_0 + c_1 \left\{ 1 - \exp \left(-\frac{h}{a} \right) J_0 \left(-\frac{2\pi h}{w_j} \right) \right\}, \quad (\text{A14})$$

where J_0 is the Bessel function of the first kind and w_j is a distance parameter corresponding roughly to the wavelength.

The following models are multi-scale models that combine two models and they are the ones used to fit the sample variograms for simulations A, B and C.

Two-scale variogram model with a Bessel and a spherical model used in sim-

ulation A

$$\gamma(h) = c_0 + c_{fine} \left\{ 1 - \exp\left(-\frac{h}{a_{fine}}\right) J_0\left(-\frac{2\pi h}{w_j}\right) \right\} + c_{broad} \left[\frac{3h}{2a_{broad}} - \frac{1}{2} \frac{h}{a_{broad}} \right]. \quad (\text{A15})$$

Two-scale variogram model with a spherical and an exponential model used in simulation B

$$\gamma(h) = c_0 + c_{fine} \left[\frac{3h}{2a_{fine}} - \frac{1}{2} \frac{h}{a_{fine}} \right] + c_{broad} \left\{ 1 - \exp\left(-\frac{h}{a_{broad}}\right) \right\}. \quad (\text{A16})$$

Two-scale variogram model with an exponential and a spherical model used in simulation C

$$\gamma(h) = c_0 + c_{fine} \left\{ 1 - \exp\left(-\frac{h}{a_{fine}}\right) \right\} + c_{broad} \left[\frac{3h}{2a_{broad}} - \frac{1}{2} \frac{h}{a_{broad}} \right]. \quad (\text{A17})$$

References

Cressie, N. A. C. 1993. Statistics for spatial data. Revised edition. Wiley Inter-Science, New York.

Wackernagel, H. 2003. Multivariate Geostatistics: An introduction with application. 3 rd edition. Springer-Verlag, Berlin.

Webster, R. and M. A. Oliver. 2007. Geostatistics for Environmental Scientists. John Wiley Sons Ltd, Chichester, England.

Appendix 3

Estimation of Y by multiplicative Poisson kriging

This appendix details the derivation of multiplicative Poisson kriging. The aim of the multiplicative Poisson kriging is to map the non-stationary latent density of sightings of animals. A comparison between Poisson kriging (Monestiez et al. 2006) and the multiplicative Poisson kriging presented here can be found in Bellier et al. (2010).

The spatial interpolation of Y is implemented through ordinary kriging (OK) at any site $s_p \in \mathcal{D}$. This kriging is a linear predictor of Y_{s_p} combining the observed data Z_s weighted by the drift terms m_s and m_{s_p} ,

$$Y_{s_p}^* = \sum_{s=1}^n \lambda_s \frac{m_{s_p} Z_s}{m_s}. \quad (\text{A18})$$

The unbiasedness of $Y_{s_p}^*$ leads to the usual condition on values λ_s 's :

$$\sum_{s=1}^n \lambda_s = 1. \quad (\text{A19})$$

The expression of the Mean Square Prediction Error (MSPE) can also be derived from the kriging estimate expression,

$$\mathbb{E}[(Y_{s_p}^* - Y_{s_p})^2] = m_{s_p}^2 \left(\sigma_X^2 + \sum_{s=1}^n \frac{\lambda_s^2}{m_s} + \sum_{s=1}^n \sum_{s'=1}^n \lambda_s \lambda_{s'} C_{ss'} - 2 \sum_{s=1}^n \lambda_s C_{s s_p} \right). \quad (\text{A20})$$

By minimizing this expression C20 on λ_i 's subject to the unbiasedness constraint, we obtain the following kriging system of $(n + 1)$ equations where μ is the Lagrange multiplier.

$$\begin{cases} \sum_{s'=1}^n \lambda_{s'} C_{ss'} + \frac{\lambda_s}{m_s} + \mu = C_{s s_p} & \text{for } s = 1, \dots, n \\ \sum_{s=1}^n \lambda_s = 1. \end{cases} \quad (\text{A21})$$

The kriging system expressed with covariance is preferably used for computation when both variogram and covariance exist. The kriging system may be expressed from the variogram using the usual relation $C_{ss'} = \sigma_X^2 - \gamma_X(ss')$.

The expression of the prediction variance resulting from this kriging system reduces to :

$$\text{Var}(Y_{s_p}^* - Y_{s_p}) = m_{s_p}^2 \left(\sigma_X^2 - \sum_{s=1}^n \lambda_s C_{s s_p} - \mu \right). \quad (\text{A22})$$

It can be easily shown that the kriging of X_{s_p} defined as $X_{s_p}^* = \sum_{s=1}^n \lambda_s \frac{Z_s}{m_s}$ gives the same solutions in λ 's and μ , so kriging of $Y_{s_p}^*$ or $X_{s_p}^*$ become equivalent using the relationship $Y_{s_p}^* = m_{s_p} X_{s_p}^*$.

References

Bellier, E. et al. Geostatistical modelling of wildlife population : a non-stationary hierarchical model for count data. - geoENV VII - Geostatistics for Environmental Applications. 16: 1-12.

Monestiez, P. et al. 2006. Geostatistical modelling of spatial distribution of *Balaenoptera physalus* in the Northwestern Mediterranean Sea from sparse count data and heterogeneous observation efforts. - Ecological Modelling 193: 615-628.

Appendix 4

Segmented line regression model

We used the segmented line regression (Eq. 6 in the main text) to model the non-constant mean of the population of auks in the Bay of Biscay. The estimated parameters are given in the Table A1 below. The standard errors in bracket were obtained by parametric bootstrap.

Table A1: Estimated parameters of the segmented line (Eq. 6) and their standard errors.

	α	B_1	B_2	B_3	w_1	w_2
December 2001	2.49 (1.18)	41.65 (12.50)	55.29 (6.97)	179.08 (27.09)	0.56 (0.28)	0.04 (0.05)
January 2002	3.90 (1.29)	42.27 (10.37)	57.28 (3.40)	182.77 (20.65)	0.86 (0.35)	0.05 (0.05)
February 2002	3.97 (1.33)	41.10 (11.50)	57.07 (3.40)	181.76 (22.87)	0.83 (0.29)	0.05 (0.05)
Mars 2002	5.55 (2.20)	41.00 (12.45)	56.64 (5.72)	181.45 (23.84)	1.23 (0.48)	0.09 (0.09)

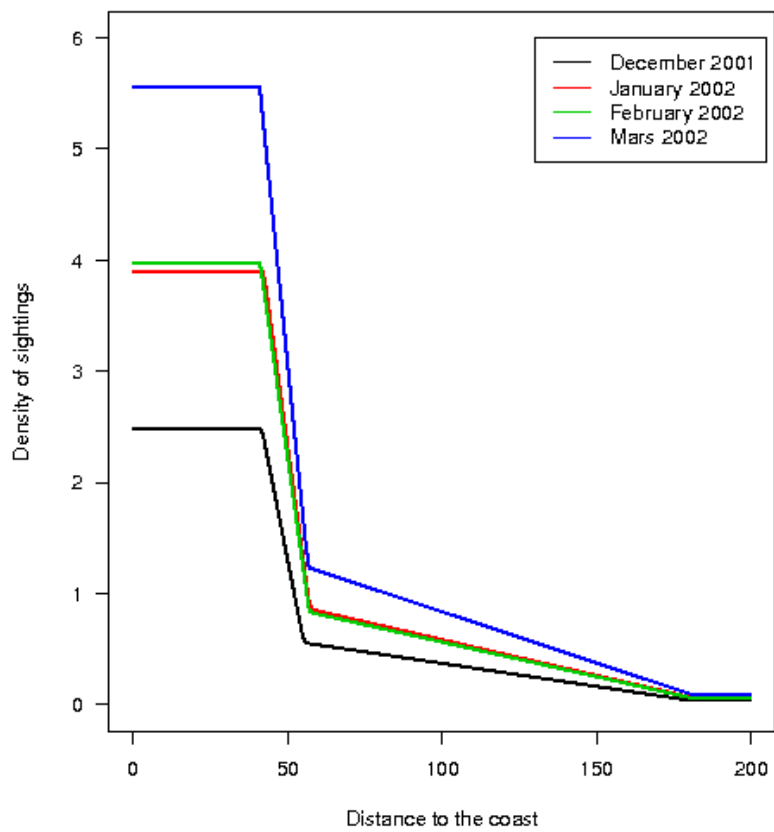


Figure A1: Density of auk sightings as a function of the distance to the coast (dots) estimated by fitting a segmented line regression model (i.e. estimation of the spatial trend m).

Appendix 5

Multi-scale variogram and multi-scale map of the spatial
distribution of the auks in the Bay of Biscay in

November 2001

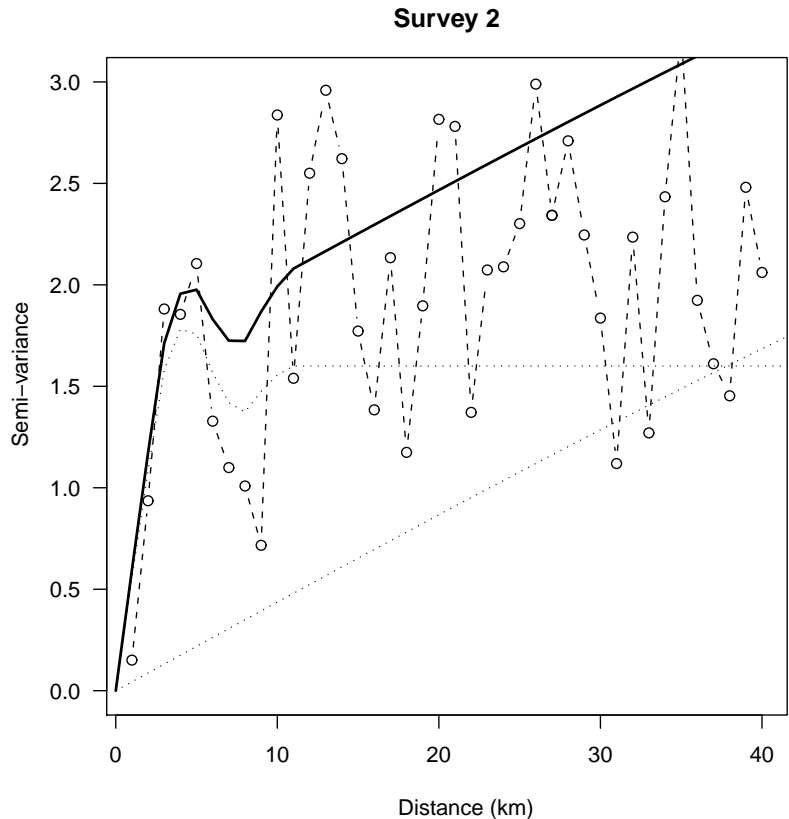


Figure A2: Two-scale variogram models fitted to sample variograms of X (i.e. corrected variograms of Z) for the survey of November 2001: sample variogram of X (dotted-and-dashed line) ; multi-scale variogram model (solid line) ; variogram models used when composing the nested variogram model (dotted lines). The x-axis represents the distance in km while the y-axis corresponds to the semi-variance. The approximate AIC value for the spherical model was 420.73, for the single wave-model was 570.86, and for the two-scale model was 401.23. The estimated parameters for the two-scale model (with their associated standard error given in brackets) were $c_{wave} = 1.6(1.52)$, $conc_{wave} = 3.3(1.18)$, $a_{1-wave} = 2.5(0.89)$, $a_{2-wave} = 5(1.17)$, $c_{sph} = 3.5(1.2)$, $a_{sph} = 120(42.8)$.

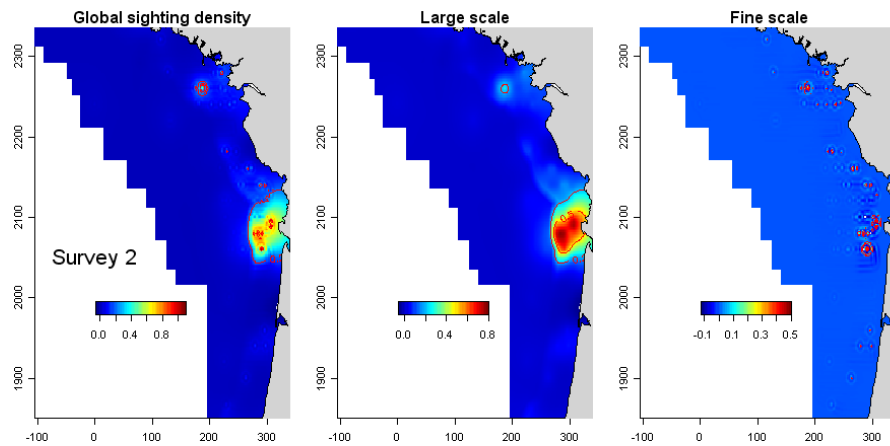


Figure A3: Left panel: map of the auk sighting expectations (expected sighting density per km) obtained by multi-scale kriging for the survey of November 2001. Centre panel: map of broad-scale auk sighting distributions. Right panel: map of fine-scale auk sighting distributions. A 2-km resolution prediction grid was defined for all maps. All data points were used in the kriging system for spatial prediction.