The treatment of spatial autocorrelation in biological surveys: the case of line transect surveys

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Abstract: Marked spatial autocorrelation was encountered in an extensive data set on Antarctic seal densities as well as Antarctic pack ice characteristics. Whilst the methodology of measuring spatial autocorrelation is well developed, there is no established infrastructure for statistical inference in terms of correlation analysis or ANOVA. We survey the literature that deals with these problems, as well as some of the approaches that have been proposed for taking autocorrelation into account in inferential statistics. We apply these approaches to a data set comprising Antarctic pack ice seal counts as well as a few environmental measures. In contrast to the predictions from the existing literature, nonlinear estimation suggested that Pearson’s r substantially overestimates the true correlation between seal densities and environmental variables. When compared to spatially adjusted analysis of variance, conventional ANOVA that compared seal densities or pack ice characteristics in different areas overestimated the degree of difference between these areas in proportion to the degree of spatial autocorrelation of the particular data set. In our case, the effects of spatial autocorrelation were not neutralised by treating entire transects as single points. These results emphasise the need for a methodology that takes spatial autocorrelation into account for interpreting the spatial data on Antarctic seals collected during the Antarctic pack ice seal (APIS) program. New software written for performing these analyses is available from the senior author.

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Introduction

A large proportion of ecological studies includes the handling of spatial information. Such data may represent the geographical movements of animals, population densities in different areas, the spatial distribution of resources such as food plants or prey, or the distribution of infection rates. In these cases, we would not be primarily interested in the spatial data themselves, but in the way that a biological or environmental variable of interest (the ‘response variable’) is affected by space or locality. It has been generally accepted that few animals or their resources are either evenly or randomly distributed: in fact, a spatially clumped distribution characterizes the traits of many animals (Caughley 1977). With the advent of geographical information systems (GIS), the handling of spatial data has reached a new level of complexity, enabling the management, manipulation and interpretation of volumes of spatial information that was not possible previously. This technology has given rise to studies that focused on diverse ecological and evolutionary problems (e.g. Sokal & Oden 1978, Legendre & Legendre 1984).

If spatial data often originate from observations based on a clumped distribution, it means that special consideration needs to be given to the planning of data collecting and to the interpretation of such data. One of the problems inherent in large numbers of spatial data sets is spatial autocorrelation. This is merely the fact that, having made a spatial measurement of a particular response variable (e.g. population density at a specific location), an equivalent measurement in any closely situated locality is likely to have a fairly similar value to that of the original measurement. This is due to close-range geographical similarity of environmental conditions. A similar argument could be used when considering the altitude (above sea level) of towns on a particular landscape. Knowing the altitude of a particular town frequently enables one to predict something about the altitude of a neighbouring town since, generally, the altitudes of such towns are similar. On the other hand, animal data sets could exhibit negative spatial autocorrelation: if local effects such as competition for a territory or for food, or access to water causes some animals to drive away others, this would cause localities with animals to be surrounded by a zone with fewer animals than expected from a random distribution. Sokal (1978), Sokal & Oden (1978) and Legendre (1993) give excellent accounts of the effects of spatial autocorrelation within a biological setting. One type of study that needs to take autocorrelation into account is the spatial estimation of animal abundance. Whenever census data arise from closely situated sampling sites, the probability of spatial autocorrelation arises. Although an argument can be made that a suite of uniform random sampling sites, chosen beforehand, would allow a design-based analysis of the data (Brewer et al. 1979), most geographical survey data are not appropriate for such an
Recent analyses have shown that autocorrelation is present amongst some of these data (Fig. 1) requiring methods to be found for dealing with this phenomenon. The purpose of this paper is twofold. Firstly, we review the methods available for dealing with inferences from spatially autocorrelated data sets and, secondly, we review the computer software available for performing such analyses. Our aim is to review the material in a way accessible to biologists and to focus on two of the most frequent types of inferential analyses using locality-based data sets: correlation analyses and analyses for comparing means. We then demonstrate ways of adjusting analyses for spatial autocorrelation by using a data set of seal counts from the Lazarev Sea, Antarctica.

Results and discussion

The statistical consequences of spatial autocorrelation

The measurement of spatial autocorrelation is relatively simple compared with statistical inferences involving autocorrelated data. Moran (1950) proposed an index \( I \) that has affinities with the Pearson product-moment correlation coefficient \( r \) (it includes dividing the equivalent of the covariance between measurements from closely-situated sites by the variance of the response variable) as follows:

\[
I = \frac{1}{n(n-1)} \left( \sum_{i=1}^{n} \sum_{j=1}^{n} w_{ij} z_i z_j - \overline{z}^2 \right),
\]

where \( n \) is the number of observations; \( A \) is the number of data pairs (i.e., joins) used in the calculation and \( z \) is the deviation from the overall mean. \( E(I) = -1/(n-1) \) and converges to 0 but is not zero. However, \( I \) differs from \( r \) in that the limits of \( I \) are not [-1, +1] but are determined by the spatial arrangement of the particular data set. An estimate of the maximal value of \( I \) can be made (Cliff & Ord 1981) and in most analyses \( \max(I) \) is greater than 1.0 and \( \min(I) < -1.0 \). This allows scaling of Moran’s \( I \) in a way similar to a normal correlation coefficient, thus resulting in a pseudo-correlation coefficient \( \rho_p \) useful for data sets from some 50 or more locations. A spatial autocorrelation estimate that falls within the [-1, +1] interval could be obtained through maximum likelihood estimation (Cliff & Ord 1981). Spatial autocorrelative patterns are often described by calculating the degree of autocorrelation at successive and increasing spatial distances within a data set, resulting in a graphical representation as a correlogram (Fig. 1b). The correlogram is similar in use to the variogram which describes the magnitude of variance between observations at different distances of separation with autocorrelation we would expect closely situated observations to be similar and therefore to have a low variance, while the variance between observations at greater distances would be larger. In fact, correlograms and variograms are mathematically related (Cliff & Ord 1981). The statistical properties of \( I \) have been well studied (Moran 1950, Cliff & Ord 1973) and it is possible to test the hypothesis that a particular estimate of \( I \) differs significantly from zero. On the other hand, it is possible to circumvent the problems associated

\[\text{Fig. 1. a. A sample of a single strip census of crabeater seals in the inner region of the Lazarev Sea near to the edge of the fast ice. Spatial autocorrelation is evident from the fact that points with large values tend to cluster. b. Correlogram indicating the overall spatial autocorrelation at varying distances from a particular observation. Moran's } I \text{ is used as a measure of autocorrelation. Results are given for seven strip counts in the inner pack ice (close to the edge of the fast ice) as well as in the outer pack ice. Significant degrees of spatial autocorrelation are indicated by an asterisk.}\]
with \( I \) by calculating the true spatial autocorrelation \((\rho; \text{see Cliff \\& Ord 1981, Griffith 1993})\) using techniques described below.

Spatial autocorrelation has the effect of reducing the variance within a data set (Griffith 1993). Since neighbouring observations of a response variable are not independent, the probability of fortuitously obtaining a measurement that strongly deviates from the mean is reduced. The second and subsequent observations therefore contribute less to our understanding of the system than does the first. From a statistical point of view, the differences between observations and the population mean (i.e. the residuals \( e \)) are not independent of one another. Consider now the effect of this on a statistical test that compares the means of seal densities in two different geographic areas. Since the within-sample variance is reduced as a result of spatial autocorrelation, small but fortuitous differences between the areas are emphasised, resulting in an increased probability that the test statistic may indicate significantly different seal densities between the areas. This effect is evident from the following formulation for the expectation of the sample variance:

\[
E[s^2] = s^2 (1-\rho),
\]

where \( \rho \) is the mean autocorrelation between all the pairs of observations and \( s^2 \) is the population variance (Brown \\& Rothery 1993). In addition to the above problem, the accuracy with which the population mean could be estimated for spatially autocorrelated data sets is lower than would normally be the case. Mathematically, \( \text{var}[\bar{Y}] = \frac{(s^2/n)}{[1+(n-1)\rho]} \) where \( s^2 \) and \( \rho \) are defined as above and \( n \) is the number of observations in the data set (Brown \\& Rothery 1993). Diggle (1990, pp. 87–90) gives worked numerical examples of these effects. Since the standard error of the estimate of the mean is increased, it has a negative effect on attempts to show differences between the mean values of a response variable from different geographical areas (see below). The same type of problems also arise in other statistical procedures, e.g. correlation and regression analyses. Therefore, since spatially autocorrelated data sets have observations that are not truly independent, the assumptions of traditional parametric as well as nonparametric statistical tests are violated.

Below we present some of the characteristics of part of a data set of seal counts collected during a survey of pack ice seals in the Lazarev Sea, Antarctica during 1991–93. We present the descriptive and spatial characteristics of the data set and describe how these were interpreted. The methodology of the counts is described in detail in Bester \textit{et al.} (1995, 2002). Briefly, aerial strip census counts of seals on pack ice were performed within 200 nautical miles (n.m.) of the Antarctic fast ice. Counts were performed along pairs of north–south strips, 10 n.m. apart. The east–west position of each of these pairs of strips was determined by the distance the ship steamed at half-speed overnight, normally at intervals of some 100 n.m. (see Bester \textit{et al.} 2002 for a map). Strips were about 60 n.m. long and counts of seals were accumulated into 3 n.m. long compartments (‘frames’) along the flight path of the helicopter. This strategy represents a modified systematic sampling of the study area. Spatial autocorrelation was measured at three scales: the 3 n.m. distances between compartments within a strip, the 10 n.m. distance between two strips forming a pair, and the 100 n.m. distance between strip pairs. This design was necessitated by limits imposed by the cost of the survey as well as safety precautions that prevented the aircraft from flying too distantly from the ship. Seal counts were expressed as densities in terms of number of seals n.m.\(^{-2}\). For the purpose of ANOVA, we compared the seal densities and pack ice characteristics in three spatial zones with increasing distance from the edge of the Antarctic fast ice.

**Descriptive statistics of the pack ice seal data**

Seal densities within compartments were highly left-skewed and unsuitable for most parametric statistical procedures (see figures in Bester \textit{et al.} 1995). The frequency distribution of log-transformed seal densities was bimodal. A large number of frames had no seals, but those that contained seals had a unimodal frequency distribution that did not differ from normality (Kolmogorov-Smirnov \( P > 0.2 \)). Inferential statistics relating to seal densities were based on log-transformed data.

Figure 1a is a representative sample of seal counts during the 1992/93 survey, indicating the clumped distribution of seals along a particular transect. This trend was much clearer on strips with high seal densities (close to the fast ice) than on those with low densities (far from the fast ice). The clumped distribution of seals gave rise to a significant degree of spatial autocorrelation in frames separated up to some 20 n.m. for transects near the fast ice. Figure 1b indicates that the spatial autocorrelation was not consistently observed along every transect. This would indeed be expected from spatially autocorrelated data based on sparsely distributed counts along transects and would need to be taken into account when making statistical inferences.

For counts of crabeater seals, there was an overall significant degree of spatial autocorrelation \((\rho = 0.2–0.3; P < 0.0001)\) among the data points. However, when the three spatial zones were considered separately, only the zone closest to the fast ice contained significant spatial autocorrelation \((\rho = 0.2–0.4; P < 0.0001)\). The other two zones had negligible amounts of autocorrelation \((\rho = 0.01)\). These results therefore indicate that, within the inner zone of pack ice adjacent to the fast ice, the effect of spatial autocorrelation was strong between compartments within a transect and extended for distances up to 30 n.m., thus including the distances within transect pairs. However, the groups of transect pairs (separated by some 100 n.m.) were probably not affected by autocorrelation.

**Inferential statistics on spatially autocorrelated data**

There are several approaches towards minimising the effect of spatial autocorrelation. A first approach may be to plan the
data collection at a scale where the effects of spatial autocorrelation would be neutralised, enabling the use of conventional statistical tests. For instance, our evidence indicates that, if seal densities were measured at points further than some 30 n.m. apart, spatial autocorrelation would be minimal (Fig. 1). However, this set-up may be impractical since the financial cost of sampling 500 data points (as in this study) on the pack ice at 30 n.m. intervals (transects comprising 15,000 n.m.) would be prohibitive. In any case, since the degree of spatial autocorrelation cannot be predicted ahead of the survey, higher resolution surveying would be required in order to establish the between location distance required to minimise the effects of spatial autocorrelation. If the analysis included systematically omitting observations from the original fine scale analysis in order to decrease spatial autocorrelation, the information inherent in those dropped observations would be wasted. The situations where such an approach would be useful at all would therefore be exceptional. Secondly, each strip could be treated as an individual sampling point. Although this would allow the comparison of counts from different geographical areas, it does not automatically eliminate spatial autocorrelation. Since no a priori knowledge of the degree of spatial autocorrelation would be available, the problem in data interpretation would not be solved. In addition, correlation analyses between animal densities and environmental variables would not be possible if single strips cover a range of environmental variables. A third approach is to apply a correction factor to a standard statistical test in order to correct for the degree of spatial autocorrelation. One such example is outlined below as Cliff & Ord’s t-test. A fourth way of achieving valid results is to incorporate the estimation of autocorrelation in the statistical analysis itself. Below, we describe some examples of such an approach.

**Comparison of means from different geographic areas**

Cliff & Ord (1981) presented two algorithms for correcting Student’s t-test for use on locality-based data. This involves using the spatial autocorrelation ρ in a corrected formula for calculating t and allows the comparison of mean values of a response variable from two areas. In the case of positive spatial autocorrelation (as is the case with most strip census data) the calculations are relatively simple and simulations by those authors suggested robustness of the test. Legendre et al. (1990) used a random permutation based approach for performing spatially-adjusted ANOVA on response variables that have been collected from a rectangular geographical lattice.

Griffith (1978) presented an analytical algorithm that incorporates the estimation of spatial autocorrelation in an ANOVA through the use of nonlinear regression analysis, using the simultaneous autoregressive approach. Within the framework of conventional statistical inference, if y is the value of each observation, x is the true parameter being estimated (e.g. population mean) and ε is the error of the estimate, then y = x + ε and ε is normally distributed with a mean of zero. For spatial data sets with autocorrelation, the values of ε are not independent. In this case, y = x + zε, where z represents the effect of autocorrelation on ε. A way to handle this problem in ANOVA is to turn the ANOVA into a regression analysis (Griffith 1978, Cliff & Ord 1981), as follows. This type of ANOVA usually yields asymptotic standard errors. Compared to the Cliff-Ord t-test, the ANOVA bears a cost of 1 degree of freedom for simultaneously estimating the spatial autocorrelation (ρ) as well as the mean values for the different areas.

Draper & Smith (1966) showed how a regression analysis could be used to perform an ANOVA. A common expression for a regression relationship is

\[ Y = \beta_0 + \beta_1 x_1 + \varepsilon \]

where \( \beta_0 \) is a regression constant equivalent to a Y-intercept, \( \beta_1 \) is a regression parameter equivalent to a slope and \( x_1 \) is the value of an independent variable. For multiple regression analyses, the series \( \beta_1 x_1 \) is expanded to include more parameters, e.g. \( Y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \varepsilon \). A one-way classification ANOVA with i classes can be rewritten in the form of a multiple regression:

\[ Y = \mu x_0 + t_1 x_1 + t_2 x_2 + \ldots + t_i x_i + \varepsilon \]

where \( \mu \) is the overall mean across all classes of the ANOVA, \( t_i \) (a new term not related to the t-test above) is the difference between \( \mu \) and the mean value for class i, \( \varepsilon \) is a normally distributed error term with mean of 0, and \( x_i \) is a set of variables of which all have zero values except for \( x_0 \) and the \( X \)-value connected with the class from which \( Y \) originated, both of which equal 1. Thus, if \( Y \) originates from class j with \( i \geq j \), the equation above reduces to \( Y = \mu + t_j + \varepsilon \). Regression techniques can be used to estimate the t-values, thus accomplishing an ANOVA.

Griffith (1978) showed that ANOVA on a spatially autocorrelated response variable can be written in the form

\[ Y = \mu + t + (I-\rho X)^{-1} \varepsilon \]

where the term in brackets contains the degree of spatial autocorrelation (\( \rho \)) and a matrix (X) with information on the geographic location of the study sites. \( \mu \) is a vector with all elements equal to the overall mean and t is a vector of t-values for each observation as defined above. In this equation, \( \varepsilon \) represents a vector of independent error values that are normally distributed with mean zero. However, the term in brackets is the component associated with the spatial autocorrelation of the data and which causes the values of the error term to comprise non-independent values, violating the assumptions of conventional ANOVA. Estimation is also complicated by the Jacobian of the transformation from an autocorrelated to a non-autocorrelated attribute space, i.e. the normalizing factor that ensures integration of the probability density function equals 1.0 (Griffith 1988). After the equation above has been rewritten as a regression, taking into account the normalizing
Table I. A comparison of three techniques for comparing the seal densities or pack ice characteristics in two geographical areas of the Antarctic pack ice. The results of conventional t-tests (variances assumed not equal) are compared to Cliff & Ord’s (1973) modification of the t-test as well as with Griffith’s (1978) regression approach towards solving ANOVA’s. \( p = \) the spatial autocorrelation of the data set. Figures are presented as the estimated difference between the two different areas with associated variance in brackets. Within each row, statistical significance tends to decrease among the three tests from left to right.

### Variable

<table>
<thead>
<tr>
<th>Variable</th>
<th>( \rho )</th>
<th>Conventional ANOVA</th>
<th>Spatially adjusted ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>t-test</td>
<td>Cliff-Ord t-test</td>
</tr>
<tr>
<td>Large floes cover</td>
<td>0.276</td>
<td>0.301 (.056)</td>
<td>0.308 (.062)</td>
</tr>
<tr>
<td>Ross seal density</td>
<td>0.316</td>
<td>0.052 (.019)</td>
<td>0.052 (.027)</td>
</tr>
<tr>
<td>Vast floes cover</td>
<td>0.359</td>
<td>0.337 (.161)</td>
<td>0.330 (.135)</td>
</tr>
<tr>
<td>Crabeater seal density</td>
<td>0.373</td>
<td>2.24 (.000)</td>
<td>2.24 (.000)</td>
</tr>
<tr>
<td>Small floes cover</td>
<td>0.428</td>
<td>0.038 (814)</td>
<td>0.038 (437)</td>
</tr>
<tr>
<td>Cake ice cover</td>
<td>0.476</td>
<td>0.072 (.676)</td>
<td>0.072 (.390)</td>
</tr>
<tr>
<td>Total ice cover</td>
<td>0.485</td>
<td>0.752 (.012)</td>
<td>0.74 (.0151)</td>
</tr>
</tbody>
</table>

factor (which, by itself, is dependent on \( \rho \), one of the parameters being estimated), the analysis is performed using an equation of the form

\[
Y \exp(J^{2}) = WY. \exp(J^{2}) + (1-\rho W)X\beta. \exp(J^{2}) + e.\exp(J^{2})
\]

where: \( Y = \) vector containing the observed data,

\( \beta = \) vector containing the regression coefficients being estimated,

\( W = \) weighted, stochastic connectivity matrix,

\( \exp(J^{2}) = \) the Jacobian term which is dependent on \( \rho \)

\( X = \) matrix of predictor variables (Griffith 1993).

This equation can be solved using nonlinear regression techniques, resulting in a spatially adjusted ANOVA that yields reliable estimates of \( \rho \). The analysis could be thought of as a nonlinear analysis of covariance (ANCOVA) in which the spatial autocorrelation is the covariate and in which the vertical difference in positions of graphs from different geographical areas is compared. Griffith (1993) illustrated this approach within the SAS environment (SAS Institute, Cary, NC).

Table II. Comparison of the results of conventional ANOVA with those of spatially adjusted ANOVA for seven data sets. \( \rho \) indicates the degree of spatial autocorrelation within each data set. The columns for each of the two analyses indicate the estimated difference between the inner pack ice and the outer pack ice with the standard error of the estimate in brackets. The relative magnitude of the standard error of the estimate when performing a conventional analysis, compared to that of a spatially adjusted analysis, is indicated in the rightmost column. The statistical significance of tests are indicated by an asterisk (*). $p < 0.05$ or by ‘ns’.

<table>
<thead>
<tr>
<th>Variable</th>
<th>( \rho )</th>
<th>Conventional ANOVA</th>
<th>Spatially adjusted ANOVA</th>
<th>Relative magnitude of conventional s.e</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ross seal density</td>
<td>0.274</td>
<td>0.039 (0.011)*</td>
<td>0.027 (0.114) ns</td>
<td>0.09</td>
</tr>
<tr>
<td>Vast floes cover</td>
<td>0.343</td>
<td>0.393 (0.115)*</td>
<td>0.359 (0.156)*</td>
<td>0.74</td>
</tr>
<tr>
<td>Large floes cover</td>
<td>0.344</td>
<td>0.329 (0.082)*</td>
<td>0.306 (0.111)*</td>
<td>0.74</td>
</tr>
<tr>
<td>Crabeater seal density</td>
<td>0.384</td>
<td>1.660 (0.209)*</td>
<td>1.950 (0.247)*</td>
<td>0.85</td>
</tr>
<tr>
<td>Cake ice cover</td>
<td>0.508</td>
<td>0.126 (0.100) ns</td>
<td>0.218 (0.152) ns</td>
<td>0.66</td>
</tr>
<tr>
<td>Small floes cover</td>
<td>0.521</td>
<td>0.361 (0.084)*</td>
<td>0.354 (0.126)*</td>
<td>0.66</td>
</tr>
<tr>
<td>Total ice cover</td>
<td>0.588</td>
<td>1.208 (0.161)*</td>
<td>1.217 (0.249)*</td>
<td>0.65</td>
</tr>
</tbody>
</table>

Table III. Comparison of spatially adjusted ANOVA results on crabeater seal densities on the Lazarev Sea pack ice, comparing analyses using counts from individual compartments and mean counts from whole transects treated as single points. The analysis compares the seal densities in three zones in the pack ice at different distances from the edge of the Antarctic fast ice shelf. The overall degree of spatial autocorrelation is given, as well as that within the inner zone adjacent to the fast ice.

<table>
<thead>
<tr>
<th>Unit of analysis:</th>
<th>Compartments Estimate ( s ) e</th>
<th>Whole transects Estimate ( s ) e</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of units analysed (( n ))</td>
<td>540</td>
<td>31</td>
<td>0.001</td>
</tr>
<tr>
<td>Spatial scale of analysis</td>
<td>3.8 n.m.</td>
<td>15 n.m.</td>
<td>0.04</td>
</tr>
<tr>
<td>Overall ( p )</td>
<td>0.38 0.04 &lt; 0.001</td>
<td>0.28 0.18 0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>Inner zone ( p )</td>
<td>0.42 0.04 &lt; 0.001</td>
<td>0.36 &lt; 0.14 &lt; 0.02</td>
<td>0.02</td>
</tr>
<tr>
<td>Overall density (seals/n.m.(^{-2}))</td>
<td>1.88 0.24 &lt; 0.001</td>
<td>1.83 0.44 &lt; 0.001</td>
<td>0.03</td>
</tr>
<tr>
<td>Difference inner/outer zones</td>
<td>1.63 0.29 &lt; 0.001</td>
<td>1.67 0.51 &lt; 0.003</td>
<td>0.03</td>
</tr>
<tr>
<td>Difference central/outer zones</td>
<td>-0.55 0.36 0.13</td>
<td>-0.62 0.65 0.35</td>
<td></td>
</tr>
</tbody>
</table>

Comparison of spatially adjusted ANOVA results on crabeater seal densities on the Lazarev Sea pack ice, comparing analyses using counts from individual compartments and mean counts from whole transects treated as single points. The analysis compares the seal densities in three zones in the pack ice at different distances from the edge of the Antarctic fast ice shelf. The overall degree of spatial autocorrelation is given, as well as that within the inner zone adjacent to the fast ice.
the difference between mean density, this was not a consistent trend. Thus, for this particular data set, the main effect of spatial autocorrelation was to reduce the standard error of estimates, making it more likely to obtain a significant statistic. This effect is exemplified in the case of the ANOVA’s testing for differences in the densities of Ross seals. The Ross seal densities were based on only 34 Ross seals observed in over 500 compartments. Spatial autocorrelation caused the conventional ANOVA to indicate a significant difference in densities, while the spatially adjusted counterpart indicated that the standard error of the estimate is too large to prove a significant difference.

An attempt was made to neutralize the effect of spatial autocorrelation by treating each transect as a single sampling point. Spatially adjusted ANOVA on this relatively crude data set of crabeater seal densities (containing 31 data locations and using the mean seal density within each transect as the dependent variable) indicated that, overall, there was not a significant degree of spatial autocorrelation among the different transects (Table III). However, when these observations were analysed separately within each of the three spatial zones, there was a significant degree of spatial autocorrelation in the zone closest to the fast ice at distances up to 15 n.m. This is largely the result of transect pairs that were separated by a distance of 10 n.m. The overall (nonsignificant) autocorrelation was thus the result of the combination of the data from the inner zone (where significant spatial autocorrelation is present) with those of the outer zones (where there is no spatial autocorrelation). The estimates of the overall mean seal density as well as the differences between seal densities of the three zones were almost identical to those of the analyses that did not treat transects as single data points (Table III). We therefore obtained results that did not differ from those obtained when each compartment was analysed separately. However, the effect of spatial autocorrelation was decreased, although not eliminated by this approach.

**Correlation analysis**

Here we deal with problems involving the correlation of two response variables, e.g. that between seal density and pack ice characteristics. Based on simulations, Cliff & Ord (1981) suggested that the true correlation between two response variables (both with small or moderate but positive spatial autocorrelation) is likely to be a little overestimated using Pearson’s $r$. However, $r$ is likely to be fairly accurate unless the response variables being analysed both have strong spatial autocorrelation. Clifford et al. (1989) and Haining (1991) proposed modifications to Pearson’s $r$ and to Spearman’s rho for application to spatially autocorrelated data. They solve the autocorrelation problem by decreasing the effective number of observations upon which the correlation coefficient is based so that a larger value of $r$ would be required in order to obtain a significant statistical result.

Griffith (1993) offered a different approach by performing nonlinear estimation independently on each of the two variables to be correlated. The residuals of each of these regression analyses represent the un-autocorrelated values of the variables which can, in turn, be analysed by conventional correlation methods.

Figure 2 indicates the relationship between Pearson’s product-moment $r$ and the spatially adjusted $r$, based on ten correlations between seal densities and several pack ice variables. Both types of correlation coefficients are, in turn, strongly correlated. However, the values of the spatially adjusted $r$’s suggest that autocorrelation in the seal density data causes Pearson’s $r$ to overestimate the true correlation by some 25%. This is somewhat more than would have been expected from Cliff & Ord’s (1981) conclusions, based on simulation and suggests that, with the Antarctic pack ice seal data, the autocorrelation in both the response variables is so large that statistical inference using conventional correlation analysis is not reliable.

**The practical implementation of analyses on spatially autocorrelated data**

The estimation of Moran’s $I$ and its statistical significance for spatial data sets has become more frequent since 1990 and several computer programs allow this, including several GIS systems. Two frequently used software packages are SAAP (Wartenberg 1989, Exeter Software Ltd; http://

![Figure 2. Scatterplot of spatially adjusted correlation coefficients against Pearson product-moment correlation coefficients for ten datasets, correlating crabeater seal densities (solid symbols) and Ross seal densities (open symbols) with several pack ice characteristics in the inner pack ice adjacent to the edge of the fast ice. The solid line indicates the expected relationship if both methods yielded identical correlation coefficients. The vertical distance between the observations and the solid line indicates the decrease in Pearson's $r$ required to take the effects of spatial autocorrelation into account.](https://www.cambridge.org/core/core圖像)
programs written in SAS (SAS Institute, Cary, North Carolina) required and it is, consequently, not user friendly. These packages are useful for deriving descriptive autocorrelation statistics for a particular study. They are specifically useful if one wishes to use a non-standard weighting system associated with the observations at different distances from a focal observation in an analysis. However, software for performing inferential tests on spatially autocorrelated data are much more sparse.

The R package (Legendre & Vaudor 1991) comprises several tools, including a spatial analysis of variance based on a random permutation approach. However, its use is limited by two assumptions: firstly, that the data originate from localities on the nodes of a regular lattice and, secondly, that the 'shape parameter' of pseudo-areas generated during each permutation of the data remains the same. Within the context of wildlife surveys dependent on line transects and which do not represent a systematic spatial coverage of the study area, the use of this software is problematic.

Griffith & Layne (1991) and Griffith (1993) presented programs written in SAS (SAS Institute, Cary, North Carolina) for making several types of inferences from spatial data, including correlation, ANOVA and discriminant analysis. Since large parts of the software need to be rewritten for each application, a good understanding of the SAS system is required and it is, consequently, not user friendly.

We have developed a computer program, dubbed SPANOVA (SPAtial aNOVA), which performs several calculations on spatially autocorrelated data. In terms of descriptive statistics, it calculates Moran's I, the pseudo-correlation coefficient (ρ̂) above as well as the true spatial autocorrelation (ρ, using Griffith's approach) for various distance intervals, the statistical significance of the I and ρ̂ as well as an associated sequential Bonferroni correction on these probabilities. In terms of inferential statistics it performs Cliff & Ord's (1981) spatially corrected version of the t-test for two geographic areas, in addition to the spatially adjusted ANOVA for two or more areas as proposed by Griffith (1993). For correlation analyses it calculates the Pearson's correlation coefficient and Clifford et al.'s (1989) modification of this, as well as the spatially adjusted correlation analyses described by Griffith (1993). The software is available from the senior author.

Conclusion

The data on seal densities, as well as some of their environmental characteristics, showed marked spatial autocorrelation. This necessitated the use of methods to take this into account. Griffith's (1978, 1993) approach to include the spatial autocorrelation in an autoregressive structure appears well suited to analyse these data sets. The analyses revealed the well-known characteristics of conventional tests on spatially autocorrelated data sets, including a marked tendency towards type I statistical errors. We hope that our review has helped to shape the methodology for interpreting the huge amount of spatial information that has been collected during the APIS program.

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