Estimating population trend and process variation in the presence of sampling error

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Abstract:

Time-series of population abundance estimates often are the only data available for evaluating the prospects for persistence of a species of concern. With such data, it is common to test for a significant trend in the data or to perform a population viability analysis (PVA) with diffusion approximation methods. Sampling error and temporal correlation in the data, however, may detrimentally affect these approaches. We develop a mixed-model method for estimating trend, process variation, and sampling error from a single time-series. The method is based on a discrete geometric model of density independent growth coupled with a model of the sampling process. Transformation of the data yields a conventional linear mixed model, where the variance components are functions of the process variation and sampling error. Simulation results show essentially unbiased estimators of trend, process variation, and sampling error over a range of process variation/sampling error combinations. A test for significant trend that incorporates uncertainty in variance estimators and temporal correlation due to sampling error in the data is developed. The test limits type 1 error rate to nominal levels or smaller under a biologically realistic null hypothesis. This mixed-model method is useful for PVA methods that depend on accurate estimation of process variation.

Keywords

Trend estimation

Population Viability Analysis

Modeling

Process variation

Sampling error

Population growth rate

Mixed linear model

Measurement error

Estimating population trend and process variation in the presence of sampling error.

Introduction

Conservation or management policies generally require assessment of a population's status. Unfortunately, these assessments often must be made with little data. Commonly, the most extensive data available are time-series of count-based data such as population abundance estimates, catch-per-unit effort, or samples of a portion of the life cycle, e.g. spawning redds, nesting adults or mother-cub pairs. Population status often is evaluated from time-series data by a test for significant population trends (Gerrodette 1987, Pechmann et al. 1991, Rieman and Myers 1997) or by a population viability analysis (PVA) (Dennis et al. 1991, Boyce 1992, Morris et al. 2002, Morris and Doak 2002). It is important to realize, however, that the autocorrelation inherent in population dynamics may invalidate these methods. In addition, sampling error may increase uncertainty in results (Ludwig 1999, Maxell 1999).

It is rarely possible to perform a complete census of a population. Population density must be estimated from a sample resulting in an estimator than contains error. In addition to error from only observing a sample of the population, there also is error from not accurately counting individuals in the chosen sampling units. This error is termed observation or measurement error and is likely to increase variation to the data. Error from the estimation process and measurement error combine to form what we refer to in this paper as

sampling error. Note this is not the conventional definition of sampling error, i.e. error due to random sampling.

Common methods of testing for ecological trend ignore both sampling error and correlated variation in population density. Population density estimates are time-series that have temporal autocorrelation. A recent text on population monitoring by Thompson et al. (1998) suggested three methods for testing population trends: standard regression, regression with a randomized or bootstrapped significance test, and the non-parametric Mann-Kendall correlation test. Maxell (1999) showed that type 2 error in a standard regression test for trend increases with increased sampling error. We show that all three of the above methods also have strongly elevated type 1 error rates due to autocorrelation in the data. Dennis et al. (1991) presented a test for significant trend in the presence of process variation but Ludwig (1999) showed that sampling error increases uncertainty in the results.

A count-based PVA using diffusion approximation (DA) methods is useful for analyzing risk to a population. It has been noted, however, that DA methods are vulnerable to sampling error (Ludwig 1999, Fieberg and Ellner 2000). Meir and Fagan (2000) found that estimates of extinction risk are not sensitive to moderate levels of sampling error except when the status of the population is uncertain, precisely the situation when estimates of risk are most crucial. In a PVA, estimates of the growth rate and process variation are used to calculate metrics that describe a population's future. Dennis et al. (1991) described several of these metrics such as the mean time to extinction, distribution of

extinction times, probability of hitting a lower threshold (not necessarily extinction) or the distribution of the population density in the future. These PVA approaches depend on accurate estimates of process variation. Sampling error adds to the variability in the data leading to inflated estimates of process variation.

Holmes (2001) described a method for estimating process variation and sampling error from a single time-series of population estimates based on running sums of the time-series. Holmes' method, however, has little theoretical justification and may have limited applicability. A particularly worrisome feature of the Holmes method is that her estimators of process variation can be biased high or low depending on the subjective choice of the length of the running sum. For longer running sums, the estimator for process variation is biased low and for shorter running sums the estimator is biased high. There is no guideline for choosing the correct length of running sum. Therefore bias in the estimator is unknown in actual applications.

We present a new mixed-model method for estimating trend and variance parameters from a single time-series of population estimates. The data are used to estimate process variation as well as sampling error in a standard linear model framework. The mixed-model method allows essentially unbiased estimation of trend, process variation, and sampling error from time-series of count data or population densities without requiring additional information about sampling error. These estimators are obtained by embedding a model of the sampling process within a model of population growth. Further, we develop a test procedure that

differentiates a true trend in growth from a random walk in the population and limits type 1 error rates to nominal size or smaller.

Methods

The underlying change in population density over time is modeled with a stochastic discrete geometric growth model. This model is used under an assumption of density-independent growth for the population. The population density at time $(t+1)$ is assumed to be

$$N(t+1) = N(t)\exp(g)E(t) \qquad (1)$$

for $t = 1, 2, \ldots, T$; where $N(t)$ represents the actual population density at time (t) and $\exp(g)$ is the mean annual growth rate in population density. If this model is used for abundance estimates, a discrete random variable, as opposed to density, a continuous random variable, then the population abundance should be large enough to justify the continuous approximation with the exponential model. If $g = 0$, then the population is at equilibrium because $\exp(0) = 1$. Natural population growth is not constant from year to year, so a multiplicative term, $E(t)$, is included to represent the process variation or deviation from the long-term trend at time (t). The random variables $E(1)$, $E(2)$, ... are assumed to be independent and identically distributed (iid) as lognormal$(0, \sigma^2_p)$. Dennis et al. (1991) used this model as an approximation of a more complicated demographic population model under the assumption of constant growth (g) and process

variation (σ^2_p) in the absence of density-dependence. The parameters g and σ^2_p are the main quantities of interest when using DA methods for PVA.

The ordinary least squares estimator of the population trend, g, is relatively straightforward to compute and is unbiased. Estimation of the process variation, however, is complicated because observed variability reflects sampling error as well as process variation. In the proposed model, observed data are modeled by embedding the population growth model in (1) into a model that includes sampling error. This is portrayed as

$$O(t) = N(t)Z(t), \tag{2}$$

where $O(t)$ is the observed estimate of population density at time (t) and $Z(t)$ represents error and bias that arises from sampling. The random variables $Z(1)$, $Z(2)$, ... are assumed to be iid lognormal(μ_s, σ^2_s) and independent of $E(t)$. By combining the population growth and sampling models, the observation at time $(t+1)$ is represented as

$$O(t+1) = N(t)\exp(g)E(t)Z(t+1). \tag{3}$$

Define $K(t) = \ln(N(t))$, $\varepsilon(t) = \ln(E(t))$, and $\varphi(t) = \ln(Z(t))$. It is of note that $\varepsilon \sim$ normal($0, \sigma^2_p$) and $\varphi \sim$ normal(μ_s, σ^2_s). Log transformation of the observed values yields:

$$Y(t) = \ln(O(t)) = K(t) + \varphi(t), \text{ and} \tag{4}$$

$$Y(t+1) = K(t) + g + \varepsilon(t) + \varphi(t+1). \tag{5}$$

The differences $W(t) = Y(t+1) - Y(t)$ for $t = 1,2,..,T-1$ give estimates of the growth rate at each individual time step plus error. The mixed model representation of $W(t)$ and $W(t+1)$ are

$$W(t) = g + \varepsilon(t) + \varphi(t+1) - \varphi(t), \text{ and} \qquad (6)$$

$$W(t+1) = g + \varepsilon(t+1) + \varphi(t+2) - \varphi(t+1). \qquad (7)$$

The vector W is the series of the empirical growth at each of the (T-1) one-step time intervals in the time-series of observations. The distribution of W is multivariate-normal($1_{T-1}g, \Sigma$) with Σ representing the (T-1)x(T-1) variance-covariance matrix. The empirical growth observations in W can be expressed as a conventional linear mixed model;

$$W = Xg + v, \qquad (8)$$

where X is a column of ones with length (T-1) and $v \sim (1_{T-1}0, \Sigma)$. Autocorrelation in the time series due to exponential population growth is removed by the differencing step, however, the entries of W are correlated due to sampling error. As can be seen in equations 6 and 7, a single realization of the sampling error, i.e. $\varphi(t+1)$, will be shared by two successive entries of W. This creates a one-step covariance in W. Accordingly, the variance-covariance matrix for W has a banded Toeplitz (2) structure comprised of the variance of individual entries of W on the main diagonal and the one-step covariance on the diagonals above and below the main with zeroes elsewhere. Let σ_1 and σ_2 represent the variance and one-step covariance of W respectively, then;

$$\underset{(T-1)\times(T-1)}{\Sigma} = \begin{bmatrix} \sigma_1 & \sigma_2 & 0 & 0 & . & . & . & 0 \\ \sigma_2 & \sigma_1 & \sigma_2 & 0 & & & & . \\ 0 & \sigma_2 & \sigma_1 & \sigma_2 & 0 & & & . \\ 0 & 0 & \sigma_2 & . & . & . & & . \\ . & & 0 & . & . & . & . & . \\ . & & & . & . & . & . & 0 \\ . & & & & . & . & . & \sigma_2 \\ 0 & . & . & . & . & 0 & \sigma_2 & \sigma_1 \end{bmatrix}. \qquad (9)$$

The parameters in Σ are functions of the process variation and sampling error. The variance of an individual entry of W is $\sigma_1 = 2\sigma^2_s + \sigma^2_p$. The one-step covariance of the entries of W is $\sigma_2 = -\sigma^2_s$. It is now possible to estimate the process variation and sampling error algebraically from the estimates of σ_1 and σ_2 in the covariance matrix.

In simulations, maximum likelihood estimators of g, σ^2_s, and σ^2_p were strongly biased . Biased estimators are a common problem in variance component problems when using maximum likelihood. This bias is overcome by using restricted maximum likelihood (REML) estimation (Searle et al. 1992) in which a transformation of the data is used to eliminate the fixed effect (g) before estimating σ_1 and σ_2. The data transformation used is a one-step difference of the W series;

$$Z(t) = W(t+1) - W(t), \qquad (10)$$

where $Z(t)$ is the transformed data vector of length (T-2). This transformation can be constructed as $Z = U^T W$, where U is a (T-1)x(T-2) contrast matrix with negative 1's on the main diagonal and 1's on the diagonal below the main. The parameters σ_1 and σ_2 are then estimated with maximum likelihood from the transformed data. Because the covariance matrix of Z is related to that of W by the equation $\Theta = U^T \Sigma U$, the covariance matrix Θ also is a function of σ_1 and σ_2. Initial estimates of σ_1 and σ_2 are obtained by the method-of-moments. The values $\hat{\sigma}_1$ and $\hat{\sigma}_2$ that minimize the negative log-likelihood function,

$$L(\sigma_1, \sigma_2 | Z) = \tfrac{1}{2}(T-2)\ln(2\pi) + \tfrac{1}{2}\ln(|\Theta|) + \tfrac{1}{2} Z^T \Theta^{-1} Z, \qquad (11)$$

are then the REML estimates of σ_1 and σ_2. The estimate, **V**, of the covariance matrix, **Σ**, is obtained by inserting $\hat{\sigma}_1$ and $\hat{\sigma}_2$ into equation (9).

To estimate g, a generalized least squares estimator is used. This is an extension of ordinary least squares, e.g. a straight average of the **W**'s, and takes advantage of non-zero covariances in the data. The generalized least squares estimator of the trend is

$$\hat{g} = (\mathbf{X}^T\mathbf{V}^{-1}\mathbf{X})^{-1}\mathbf{X}^T\mathbf{V}^{-1}\mathbf{W}. \tag{12}$$

Kackar and Harville (1984) showed that generalized least squares estimators with estimated weights are unbiased.

If **Σ** is known, then $\hat{g} = (\mathbf{X}^T\mathbf{\Sigma}^{-1}\mathbf{X})^{-1}\mathbf{X}^T\mathbf{\Sigma}^{-1}\mathbf{W}$ and the variance of $\hat{g}$ is exactly $\Phi = Var(\hat{g}) = (\mathbf{X}^T\mathbf{\Sigma}^{-1}\mathbf{X})^{-1}$. Because **Σ** is unknown, the estimated covariance matrix must be used as in (12), resulting in a biased estimator of $Var(\hat{g})$, namely $\hat{\Phi} = (\mathbf{X}^T\mathbf{V}^{-1}\mathbf{X})^{-1}$. Two further adjustments presented in Kenward and Roger (1997) are used that account for the bias in $\hat{\Phi}$ due to uncertainty in **V** and small sample size. We will denote the adjusted estimator as $\hat{\Phi}_A$. The details of the calculation of $\hat{\Phi}_A$ are given in appendix A.

The correlation in **W** from sampling error affects the sampling distribution of the test statistic fro testing H_0: $g = 0$. This results in a liberal significance test for trend when using the t distribution with T-4 degrees of freedom. The quantity T-4 is correct only if independence among the **W** entries is satisfied. The method presented in Kenward and Roger (1997) to estimate degrees of freedom based on the data is used to produce an adjusted sampling distribution. The details of

the calculations for the adjusted degrees of freedom, denoted as m, are given in appendix A. The test statistic for a non-zero growth rate is: $t = \hat{g}\sqrt{\hat{\Phi}_A}^{-1}$ and is approximately distributed as a t with m degrees of freedom. This is a standard test for significance except it uses the modified estimates of $Var(\hat{g})$ and modified degrees of freedom. To construct confidence intervals, critical values from a t distribution with m degrees of freedom are used. An approximate $(1-\alpha)100\%$ confidence interval is constructed as: $\hat{g} \pm t_{(\alpha/2,m)}\sqrt{\hat{\Phi}_A}$.

Simulation Analysis

The behavior of the mixed-model procedure was explored with analysis of simulated time-series data at nine process variation and sampling error combinations. For each simulation, 2000 time-series of length 50 were generated by first simulating the actual population growth with process variation and then 'observing' the population densities with sampling error. Process variation and sampling error were each set at three levels: $L = 0.09$, $M = 0.0225$, and $S = 0.0025$. For each of the nine variation combinations, simulations with and without a true underlying trend were analyzed. The simulations with no trend, random walks, consisted of population growth that had random fluctuations due to process variation only. Simulations with a true trend had a long-term average decline in total population density of 5% per year.

Results

Table 1 displays the rates at which the null hypothesis was rejected for methods presented in Thompson et al. (1998) as well as for the mixed-model significance test with adjusted degrees of freedom for simulations of a random walk population. The size of the test (rejection rate of true null hypothesis) is over eight times the nominal size of 0.10 for the standard regression, regression with randomization test, and the Kendall correlation test for trend. In contrast, the mixed-model method has a type 1 error rate slightly less than α. The type 1 error rates of the mixed-model test with adjusted degrees of freedom are compared with the mixed-model test with unadjusted (T-4) degrees of freedom in Table 2. In all simulations, the Type 1 error rate of the adjusted test was less than or not significantly larger than the nominal test size of $\alpha = 0.10$. In situations where the sampling error was much larger than the process variation, the adjusted test size could be considerably less than α. In contrast, the unadjusted test consistently had type 1 error rates greater than α. In cases where the adjusted test size was zero due to high sampling error, the unadjusted test size was over double the nominal size of $\alpha = 0.10$.

In simulations, the mixed-model method provided an unbiased estimator of trend and estimators for variance components that are only slightly biased. Figure 1 shows the distribution of trend estimates for simulations with a true average decline of 5% per year. The variation in the estimates of trend depends mainly on the process variation. Sampling error appears to have little effect on the variability of the trend estimate though it will affect the estimated variance of the trend estimate due to increased variability in the data.

Estimators of process variation and sampling error behaved similarly for simulations with and without a true underlying trend therefore only the results from simulations with an average 5% per year decline are given. Figure 2 shows the distribution of process variation estimates. Overall, the estimator for process variation shows very little bias. Occasionally estimates of process variation are extremely high in the presence of high sampling error, especially when the actual process variation is low. The high process variation estimates can be seen in Figure 2 as groups of extreme estimates for the LL, ML, SL, and SM simulations. These high estimates correspond to sampling error estimates near or equal to zero. Figure 3 gives the estimates of sampling error.

Observed power of the adjusted test to detect the decline also varied with the relationship of process variation to sampling error. Table 3 gives the observed power of the adjusted test compared to the test presented in Dennis et al (1991) in which Σ is assumed to be the identity matrix. The power of the adjusted mixed-model test was reduced at high levels of sampling error, most strikingly at low levels of process variation where the difference between process variation and sampling error is greatest. The Dennis test, however, generally showed lower power than the adjusted mixed-model test.

Discussion

The mixed-model method provides an unbiased estimator of trend and nearly unbiased estimators of process variation and sampling error from a single time-series with no additional information about sampling error. Generalized least squares, an extension of ordinary least squares, permits estimating the mean observed growth rate while incorporating information from the one time-step correlation in the data due to sampling error. The precision of the trend estimator is improved by including this temporal correlation into the modeling and estimation procedure. As presented, the method cannot incorporate unequal sampling intervals; the data therefore need to be gathered on uniform time intervals with no missing observations. This method will be extended to application to time-series with non-uniform sampling intervals in a future paper.

In some instances, the distribution of process variation estimates for the mixed-model method has an isolated group of estimates at extremely high values. This typically happens when the sampling error is equal to or larger than the process variation. The estimates of process variation with extreme values comprising these groups correspond directly to estimates of sampling error that are close to or equal to zero. It is unreasonable to have zero sampling error in an actual application. Therefore a near-zero estimate of sampling error in practice would serve as a warning that the process variation estimate could be biased high.

Diffusion approximation methods will benefit by more accurate estimation of process variation in the presence of sampling error, but there are other

assumptions inherent in DA methods that need to be addressed. The mixed-model method helps rectify a major liability in DA methods by decreasing bias and increasing precision in risk predictions through more accurate estimation of process variation. However, DA methods assume there is no density dependence in population growth, no extreme environmental perturbations, e.g. catastrophes or bonanzas, and that the environmental variation is uncorrelated (Morris and Doak 2002). These factors also disrupt the mixed-model method in the current form. In the near future, the mixed-model method will be extended to include density dependence, correlated environmental variation, and external information on sampling error.

The Holmes method (Holmes 2001) allows estimation of process variation in the presence of sampling error but it suffers from limited applicability and bias issues. In addition, it currently has no method for testing for a significant trend and was described by Morris and Doak (2002) as best suited for analyzing populations with short, well-known life spans consisting of adults that reproduce only once.

Bias in the Holmes method depends on two subjective parameters and the unknown relationship of process variation to sampling error. For the Holmes method, a running sum of length L of observations is used rather than the individual observations. For example if $L = 3$, the first, second, and third observations are added; then the second, third, and fourth observations are added and so on. For a time-series of observations of length T, this creates a series of running sums of length $(T - L + 1)$. Denote the series of running sums

as R. Once R is calculated, the log population growth rate over time intervals of length $i = 1,2,...,i_{max}$ is calculated by $\log(R(t+i)/R(t))$ with $R(t)$ being the running sum beginning at time t. The slope of a linear regression of the means and variances of the $\log(R(t+i)/R(t))$ values against i are the estimators of the growth rate (g) and process variation (σ^2_p) respectively. The regression estimator for process variation is biased depending on the length of the running sum (L) and the largest time interval used in the regression (i_{max}) (Morris and Doak 2002). The running sum serves to filter out sampling error from the observations, however, it also filters out the process variation to an unknown degree depending of the length of the running sum (L). For small L, the estimates of process variation are likely biased high, while for large L the estimates are likely biased low. There are no clear guidelines on how long the running sum should be as it depends on the unknown relationship between the process variation and sampling error. The maximum time interval for the regression (i_{max}) can also affect the bias in the estimator although not as much as the length of the running sum. In application, the appropriate L and i_{max} are unknown leading to an unknown bias in the estimates derived from the Holmes method.

Common methods for testing for significant trend are invalidated by temporal correlations in the data inherent in population growth. Population densities are directly related to previous population density through the growth of the population. Therefore the deviation from the long-term growth at time t will be correlated with the deviation at time $t+1$. The covariance for successive population densities is given in appendix B. This correlated error violates a

fundamental assumption in standard regression techniques and changes the distribution of the test statistic leading to type 1 error rates up to eight times the nominal rate. Non-parametric tests such as the randomization significance test for regression and Kendall's correlation procedure have apparent type 1 error rates much higher than nominal if they are used to test for a trend in the population growth. When used to test for a trend, the alternative hypothesis is assumed to be that the population has a non-zero growth rate. The null hypothesis, however, for these tests is that no relationship exists between successive population observations, or in other words, that the observed population density is an independent random variable at each time step. Rejection of this null hypothesis only implies there is some relationship between the observed population densities; precisely what one would expect due to the nature of the population growth itself. Rejection of the null hypothesis then does not imply a trend in the observed population densities as this is not the only possible alternative hypothesis. A random walk population will tend to show a significant result, i.e. rejection of the null hypothesis, for these tests even though there is no actual long-term trend in the growth.

The mixed-model method incorporates sampling error and temporal correlation in the data due to sampling error into a testing framework that limits type 1 error rates to less than or equal to the nominal rate. Further development of the degrees of freedom approximation is needed for more consistent type 1 error rates for various levels of process variation and sampling error. Because it is testing for a non-zero growth rate, the mixed-model method uses a more

biologically realistic null hypothesis of a random walk in the population growth over time. Rejection of this null implies that there is actually a non-zero population growth rate. The mixed-model method partitions process variation from sampling error in a single time-series allowing more precise estimates of the trend as well as larger power to detect a true trend compared to the Dennis test for a non-zero growth rate.

The mixed-model method fills a serious deficiency in variance estimation and can be extended to address other problems inherent in analysis of count-based data. It uses established linear model theory that allows the incorporation of differing variance/covariance structures. Through the covariance structure the method can be extended to include other features such as correlated process variation, non-uniform sampling intervals, and density dependence in population growth. Unfortunately, variance estimation from a single time-series is an inherently difficult problem, especially in real-life situations where long time-series are rarely available and sampling error is usually large. Good statistical methods can only go so far; accurate evaluations of a population's risk will likely necessitate more information than a single time-series of population estimates such as replicate time-series and direct measurements of demographic parameters.

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Appendix A

Calculations for adjusted Var($\hat{g}$) estimator ($\hat{\Phi}_A$)

Partition the variance of $\hat{g}$ into two components;

$$\hat{\Phi}_A = \hat{\Phi} + 2\Lambda, \quad \text{where}$$

$$\hat{\Phi} = (\mathbf{X}^T\mathbf{V}^{-1}\mathbf{X})^{-1}$$

is the conventional estimator for the variance of $\hat{g}$ and

$$\Lambda = 2\hat{\Phi}\left\{\sum_{i=1}^{2}\sum_{j=1}^{2}\mathbf{M}_{ij}(\mathbf{Q}_{ij} - \mathbf{P}_i\Phi\mathbf{P}_j)\right\}\hat{\Phi}$$

represents the amount to which the conventional estimator underestimates the variance of $\hat{g}$. Quantities in the underestimated portion are defined as

$$\mathbf{Q}_{ij} = \mathbf{X}^T\mathbf{V}^{-1}\frac{\delta\mathbf{V}}{\delta\sigma_i}\mathbf{V}^{-1}\frac{\delta\mathbf{V}}{\delta\sigma_j}\mathbf{V}^{-1}\mathbf{X} \quad \text{and}$$

$$\mathbf{P}_i = \mathbf{X}^T(-\mathbf{V}^{-1})\frac{\delta\mathbf{V}}{\delta\sigma_i}\mathbf{V}^{-1}\mathbf{X}$$

where $\dfrac{\delta\mathbf{V}}{\delta\sigma_1}$ is an identity matrix of size T-1 and $\dfrac{\delta\mathbf{V}}{\delta\sigma_2}$ is a (T-1)x(T-1) matrix with

ones on the diagonals above and below the main and zeros elsewhere.

$\mathbf{M} = \{\mathbf{I}_E\}^{-1}$ is the variance-covariance matrix of $\hat{\sigma}_1$ and $\hat{\sigma}_2$ which is derived from

the expected information matrix:

$$\{\mathbf{I}_E\}_{ij} = \frac{1}{2}\left\{trace\left(\mathbf{V}^{-1}\frac{\delta\mathbf{V}}{\delta\sigma_i}\mathbf{V}^{-1}\frac{\delta\mathbf{V}}{\delta\sigma_j}\right) - trace\left(2\hat{\Phi}\mathbf{Q}_{ij} - \hat{\Phi}\mathbf{P}_i\hat{\Phi}\mathbf{P}_j\right)\right\}.$$

Calculations for adjusted degrees of freedom (m)

This calculation is based on estimating the mean and variance of the test statistic from the data and using these estimated moments to calculate the degrees of freedom. Note these calculations are based on a F distribution, which is the square of the test statistic given in the text. The estimated of the mean is

$$E = (1 - A_2)^{-1} \quad \text{where}$$

$$A_2 = \sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{M}_{ij} trace(\mathbf{P}_i \widehat{\Phi} \mathbf{P}_j \widehat{\Phi}).$$

The estimated variance is given by

$$V = 2\left(\frac{1 + c_1 B}{(1 - c_2 B)^2 (1 - c_3 B)} \right) \quad \text{where}$$

$$c_1 = \frac{d}{3 + 2(1-d)}, \quad c_2 = \frac{1-d}{3 + 2(1-d)}, \quad c_3 = \frac{3-d}{3 + 2(1-d)}, \text{ and } d = \frac{2A_1 - 5A_2}{3A_2}$$

The quantity B is defined as

$$B = \frac{1}{2}(A_1 + 6A_2) \quad \text{where}$$

$$A_1 = \sum_{i=1}^{2} \sum_{j=1}^{2} \mathbf{M}_{ij} trace(\mathbf{P}_i \widehat{\Phi}) trace(\mathbf{P}_j \widehat{\Phi}).$$

Then the degrees of freedom, m, is calculated as

$$m = 4 + \frac{3}{\rho - 1} \quad \text{where}$$

$$\rho = \frac{V}{2E^2}.$$

Appendix B.

Covariance between two successive population densities. This ignores sampling error as this is assumed to be iid throughout the time-series.

Following from equations (1) and (5) the log of population size at time t is

$$K(t) = K(o) + tg + \sum_{i=1}^{t} \varepsilon(i) \qquad (B1)$$

where $K(o)$ is the initial population density (or the first data point in the time-series. Similarly, the population density at time $t+1$ is given by

$$K(t+1) = K(o) + (t+1)g + \sum_{i=1}^{t} \varepsilon(i) + \varepsilon(t+1) \qquad (B2)$$

Then the $\mathrm{Cov}[K(t),K(t+1)] = E[K(t)*K(t+1)] - E[K(t)]E[K(t+1)]$

$$= E[\sum_{i=1}^{t} \varepsilon(i)] = \mathrm{Var}[\sum_{i=1}^{t} \varepsilon(i)]$$

$$= \sum_{i=1}^{t} \mathrm{Var}[\varepsilon(i)] = t\,\sigma^2_p$$

Table 1

Observed size of significance tests for trend

	Observed Size
Adjusted Mixed-Model Method	0.081
Standard Regression	0.829
Regression w/ Randomization	0.865
Kendall Correlation	0.814

Rate of Type 1 error (rejecting true null hypothesis) for mixed-model method and various other common tests. Data generated by random walk population observed with error. True $g = 0$, $\sigma^2_p = 0.0225$, $\sigma^2_s = 0.0225$, 2000 repetitions, $\alpha = 0.10$.

Table 2

Type 1 error rates for significance tests with and without adjusted degrees of
freedom

Error Structure	Adjusted df	T-4 df
LL	0.076	0.120
LM	0.103	0.128
LS	0.104	0.122
ML	0.052	0.199
MM	0.081	0.134
MS	0.111	0.126
SL	0	0.238
SM	0.010	0.213
SS	0.099	0.148

Observed type 1 error rate of the mixed-model method significance test with
adjusted degrees of freedom and a two-sided t-test with T-4 df. LL, LM, ..., SS
represent respectively the level of process variance and sampling variance used
in the simulation. True g = 0, α = 0.10.

Table 3

Observed power to detect –0.05 trend

Error Structure	Mixed-Model	Dennis test
LL	0.248	0.039
LM	0.296	0.203
LS	0.348	0.326
ML	0.493	0.014
MM	0.654	0.286
MS	0.720	0.680
SL	0.388	0
SM	0.812	0.402
SS	1	1

Power of mixed model with adjusted degrees of freedom and an ordinary t-test to detect trend. Results from 2000 simulations of length 50 with a –0.05 trend at various levels of process variation/sampling error combinations.

Figure 1. Distribution of trend estimates for 2000 simulations of length 50. LL,LM,...,SS represent the process variation and sampling error levels respectively. True trend = -0.05 is marked by the dashed line.

Figure 2.　　Estimates of process variation in standard deviations. True values of the parameters are given by an asterisk (*). LL, LM, ..., SS represent respectively the level of process variance and sampling variance used in the simulation.

Figure 3.　　Estimates of sampling error in standard deviations. True values of the parameters are given by an asterisk (*). LL, LM, ..., SS represent respectively the level of process variance and sampling variance used in the simulation.
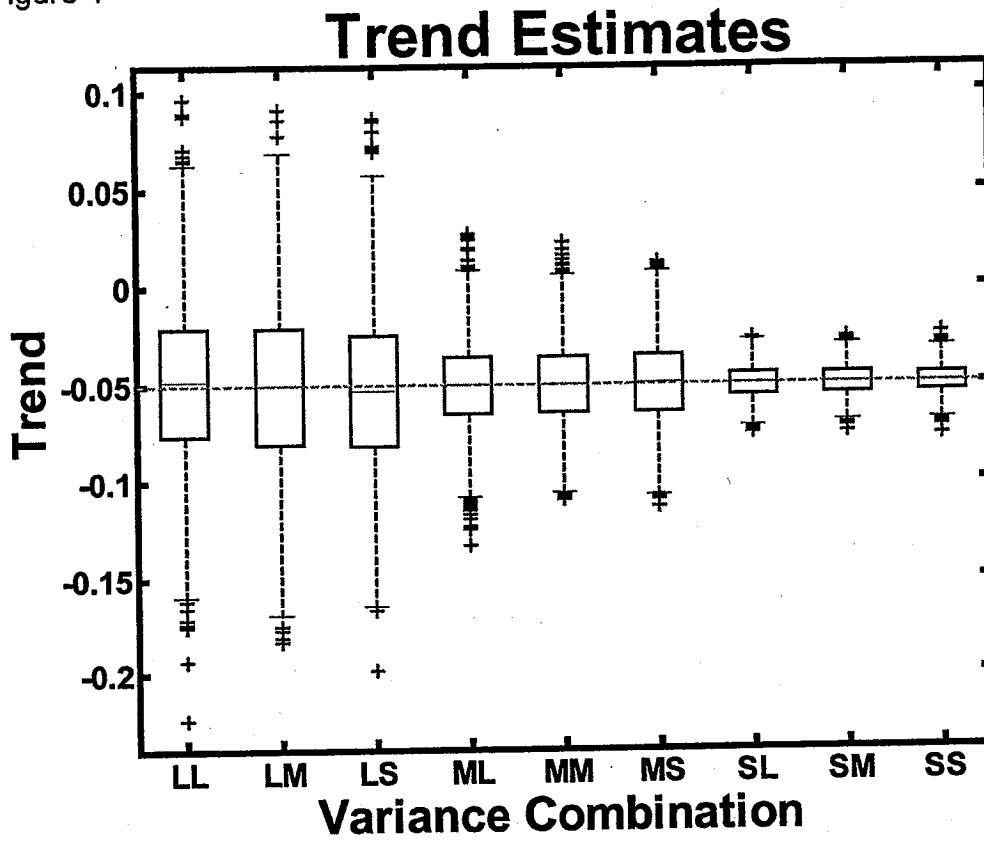
Figure 1

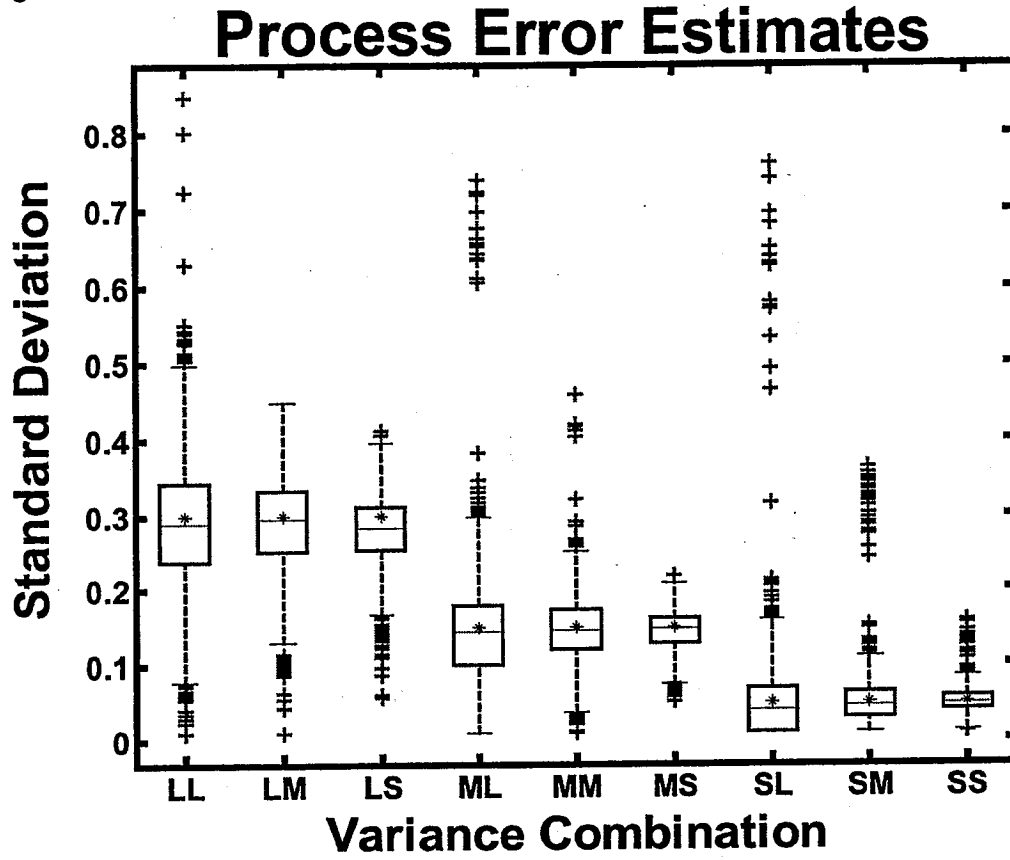# Trend Estimates

Figure 2

Process Error Estimates

Figure 3

Sampling Error Estimates