

## Census error and the detection of density dependence

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### Summary

1. Studies aiming to identify the prevalence and nature of density dependence in ecological populations have often used statistical analysis of ecological time-series of population counts. Such time-series are also being used increasingly to parameterize models that may be used in population management.
2. If time-series contain measurement errors, tests that rely on detecting a negative relationship between log population change and population size are biased and prone to spuriously detecting density dependence (Type I error). This is because the measurement error in density for a given year appears in the corresponding change in population density, with equal magnitude but opposite sign.
3. This effect introduces bias that may invalidate comparisons of ecological data with density-independent time-series. Unless census error can be accounted for, time-series may appear to show strongly density-dependent dynamics, even though the density-dependent signal may in reality be weak or absent.
4. We distinguish two forms of census error, both of which have serious consequences for detecting density dependence.
5. First, estimates of population density are based rarely on exact counts, but on samples. Hence there exists sampling error, with the level of error depending on the method employed and the number of replicates on which the population estimate is based.
6. Secondly, the group of organisms measured is often not a truly self-contained population, but part of a wider ecological population, defined in terms of location or behaviour. Consequently, the subpopulation studied may effectively be a sample of the population and spurious density dependence may be detected in the dynamics of a single subpopulation. In this case, density dependence is detected erroneously, even if numbers within the subpopulation are censused without sampling error.
7. In order to illustrate how process variation and measurement error may be distinguished we review data sets (counts of numbers of birds by single observers) for which both census error and long-term variance in population density can be estimated.
8. Tests for density dependence need to obviate the problem that measured population sizes are typically estimates rather than exact counts. It is possible that in some cases it may be possible to test for density dependence in the presence of unknown levels of census error, for example by uncovering nonlinearities in the density response. However, it seems likely that these may lack power compared with analyses that are able to explicitly include census error and we review some recently developed methods.

*Key-words:* bird population trends, passerines, population dynamics, regulation, state-space model, time-series analysis, waders.

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## Introduction

For years ecologists have lamented the lack of long data sets with which to test basic theoretical ideas (Hassell 1986; Hassell *et al.* 1989; May 1989). More recently such data have become available and are being used to unite theoretical and field ecology in a variety of areas (Gaston & Lawton 1987; Leigh & Johnston 1994; Rees *et al.* 1996; Grenfell *et al.* 1998; Saether *et al.* 2005a,b; Sibly *et al.* 2005). One of the most important applications of such time-series analyses in ecology has been to provide resolution of the long-standing debate concerning the role of regulation in population dynamics (Andrewartha & Birch 1954; Hassell *et al.* 1976; Royama 1981; Hassell 1986; Pollard *et al.* 1987; Stiling 1988; Wolda & Dennis 1993; White 2001, 2004), or to examine the form of density-dependent relationships (Fowler 1981; Sibly *et al.* 2005). Moreover, the problem is not only theoretical, but has practical applications. For example, in population viability analysis it is necessary that the strength of density dependence is estimated (Burgman *et al.* 1992), as in the absence of such information it is not possible to predict accurately population persistence or extinction (Lewontin & Cohen 1969; Foley 1994; Hanski *et al.* 1996). It is necessary to quantify density dependence of models in many applications: for example, to include predictions of the effects of culling on unwanted invaders (Smith *et al.* 2005) and estimating control levels for pests and weeds (Cousens & Mortimer 1995; Watkinson *et al.* 2000). Similarly, it has been recognized that estimating the strength of density dependence is important in understanding the long-term impacts of environmental stress, for example in eco-toxicology (Grant 1998; Sibly *et al.* 2000; Noel *et al.* 2006).

In principle, it should be simple to analyse long-term data to estimate the strength of density-dependent processes, as populations in which density dependence is lacking should exhibit population dynamics that are statistically different from those of populations in which density dependence is strong. For instance, a plot of population change against population density should exhibit a negative relationship in a density-dependent population, but no relationship if density dependence is absent. There are, however, a number of complications (e.g. Benson 1973; Bulmer 1975; Walters & Ludwig 1981; Royama 1992; Rothery 1998).

The foremost problem is that plots of population growth rate against density exhibit a weakly negative slope even for density-independent time-series. For instance, the census point with the highest density almost always yields a negative change (because, unless it is the final census, any ensuing density will be lower), and the point with the lowest density usually yields a positive change (because any subsequent density will be higher unless this is the final census point). When the change in population size is plotted against population density, this means that a negative correlation arises (low densities tend to exhibit positive changes, while

high densities tend to show negative ones). Thus even density-independent time-series may yield apparently weakly density-dependent dynamics. This effect is generally known as 'regression to the mean' (e.g. see Kelly & Price 2005 for a recent review).

An array of statistical techniques have been proposed in the ecological literature, often based on randomization or permutation methods (Manly 1991), have been developed in order to detect density dependence using time-series of census data (Bulmer 1975; Vickery & Nudds 1984; Pollard *et al.* 1987; Dennis & Taper 1994). Individually, tests are not generally reliable (Gaston & Lawton 1987), and for any single time-series a range of methods are often employed (Wolda & Dennis 1993).

One important limitation of tests for density dependence is that time-series rarely consist of exact counts of population numbers, but instead are estimates of population size. If the errors of measurement are large then this may result in tests for density dependence that exhibit high rates of Type I error, i.e. that misleadingly indicate the presence of density dependence. Ecologists have been aware of this problem for some time (Bulmer 1975; Reddingius & den Boer 1989; Dempster *et al.* 1995). To highlight this, Shenk *et al.* (1998) performed a simulation study in which they examined rates of Type I error in commonly employed tests for density dependence. They found that moderate to high levels of measurement error could compromise most commonly used tests, resulting in inflated Type I errors (i.e. incorrectly inferring the existence of density dependence).

Measurement error in population time-series may have a number of sources. In the simplest case this may result from observer error. For example, mistakes in counts are common and may be revealed by simultaneous observations by pairs of observers (e.g. Spearpoint *et al.* 1988). On the other hand, it is impossible to perform exact counts of many populations, and population size has to be estimated using sampling methods. Consequently, depending on the number of samples taken and their variability, the overall mean density will be a more or less accurate estimate of population size, albeit with some sampling error.

A further, potentially important source of error concerns the unit of study. It is usually assumed that the group of organisms studied constitutes a single population. In reality, populations are distributed heterogeneously in space and show differences in behaviour that affect their detectability to census workers. Moreover, censuses consider only part of the wider population. For example, in a bird species populations are frequently distributed across several wintering or breeding sites, or censused as a behaviourally distinct subgroup, such as animals attending breeding colonies, roosts or singing male birds. Biologists are often willing to accept such counts as proxies for the whole population. The proportion of individuals behaving in these ways often varies among time periods because of variation in weather, rates of breeding failure (Green & Hirons

1988), the availability and timing of settlement of potential mates and other factors. This variation is often not recognized and, even if it is, it is usually not possible to estimate its magnitude.

Despite the warning by Shenk *et al.* (1998), many studies continue to employ regressions of population growth rate on population density (directly or indirectly) as the basis for testing for and modelling density dependence. However, only relatively rarely has census error been accounted for (e.g. Solow 1998; Bjørnstad *et al.* 1999; Holmes 2001; Williams *et al.* 2003; Jamieson & Brooks 2004; McNamara & Harding 2004; Viljugrein *et al.* 2005) compared with the huge numbers of analyses of density dependence in ecological populations. Many studies do not account for measurement error, despite previous warnings. In this review we wish to highlight this problem together with recent developments in the literature. We discuss methods that might be employed to circumvent this problem, as well as calling for more attention to be paid to measuring census error.

### Components of measured population dynamics

Population dynamics may be decomposed into two components, namely stochastic and deterministic changes in population numbers. Stochastic changes result, for example, from the impacts of weather on mortality or fecundity, and the relative effect of such processes does not depend on population size. If changes in population size are determined by only this type of process then population dynamics follow a random walk. Deterministic (density-dependent) dynamics, in contrast, result from systematic reductions in population growth with increasing densities owing, for example, to food shortages, lack of suitable breeding sites or the effects of predators.

Because most long-term censuses are based on estimates of density rather than exact counts of the total number of individuals within a population, sampling error is present in almost all data. Measurement or sampling error acts in addition to process variation and is a property of the data that have been collected, rather than some ecological property of the population.

### MODELS FOR POPULATION DYNAMICS

The distinction between stochastic noise, census errors and density dependence can be used to set up some simple null models for population dynamics. For a range of tests for density dependence (e.g. Bulmer 1975; Vickery & Nudds 1984; Pollard *et al.* 1987; Dennis & Taper 1994) the starting point is a null model based on a population growing in a density-independent manner in a stochastic environment. In this case only the stochastic component is included in the model. The dynamics of the system are then given by:

$$N_{t+1} = e^{r_t} N_t \quad \text{eqn 1}$$

The change in population size ( $N$ ) from time  $t$  to  $t + 1$  is determined by  $r$ , the intrinsic rate of increase of the population. The subscripts in eqn 1, by convention, denote the time-dependency of the various components of the model. In particular, stochasticity is included through year-to-year variability in  $r_t$ , which is assumed to be distributed with mean  $\bar{r}$  and variance  $\text{var}(r)$  with successive values being uncorrelated. To simplify the analysis, we let  $n \equiv \ln N$  and analyse the model in the linearized form:

$$n_{t+1} = r_t + n_t \quad \text{eqn 2}$$

Because there is no density-dependent element in eqn 2,  $n$  follows a random walk (e.g. Bartlett 1966).

A further source of stochasticity is demographic stochasticity. We ignore demographic stochasticity in the rest of this paper. However, this can often be an important source of stochasticity in population dynamics (Lande *et al.* 2003). The results we present in this section would not be altered substantially by including demographic stochasticity. However, because demographic stochasticity can lead to systematic changes in the variance of  $r$  with density, the performance of statistical tests that assume the variance of  $r$  to be constant would very probably be compromised.

Density-dependent population change may be included by introducing some function  $f$  that is a function of density or log density, i.e.

$$n_{t+1} = r_t + n_t - f(N_t) \quad \text{eqn 3}$$

A range of forms of  $f()$  have been adopted, including logistic and hyperbolic first-order density dependence (Hassell 1975; Watkinson 1980; Lande *et al.* 2003; Sibly *et al.* 2005), or forms that include lags or complex density dependence (e.g. Royama 1996; Lindström *et al.* 1999; Clark & Bjørnstad 2004).

### TESTING FOR DENSITY DEPENDENCE

The difference between eqns 2 and 3 would appear to suggest some simple tests for density dependence. Specifically, if population dynamics are density-dependent the per capita rate of population change (measured as  $N_{t+1}/N_t$  or  $n_{t+1} - n_t$ ) should decline with increasing density, whereas if population dynamics are density-independent they should be independent of density and there should on average be a simple linear relationship between population sizes in successive time periods (e.g. Maelzer 1970; Slade 1977; Walters & Ludwig 1981; Hilburn & Walters 1992; Harms *et al.* 2000).

As noted above, the problem with implementing such procedures is that tests based on simple correlative approaches are likely to be biased (Maelzer 1970; St Amant 1970; Kuno 1971; Itô 1972). The statistical nature of the autocorrelation within populations may be complex, hence the need to develop a range of tests (Turchin 1995; Elkinton 2000).

## INCLUDING MEASUREMENT ERROR

Eqn 2 can also be used as the basis for looking at the consequences of census errors for the statistical properties of population time-series. When census error exists the actual population dynamics are given by eqn 2, but the dynamics we observe are given by:

$$\begin{aligned} n_{t+1} &= r_t + n_t \\ n_{t+1}^{est} &= \varepsilon_{t+1} + n_{t+1} \end{aligned} \quad \text{eqn 4}$$

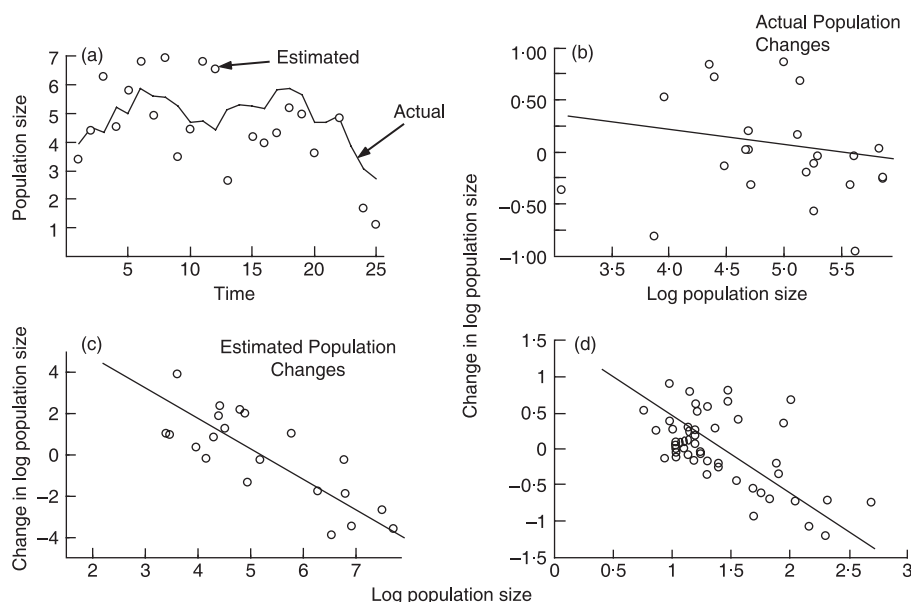
The superscripts in eqn 4 denote that measured densities are estimates of those in eqn 2, i.e. they include measurement errors. In particular, there is a measurement error  $\varepsilon$  associated with each estimate of density such that  $n^{est} = [n + \varepsilon]$ . If the measurements are unbiased the mean value of  $\varepsilon$  is zero. It is important to note that  $n$  and  $\varepsilon$  can not be dissociated as, by definition, we cannot estimate  $n$  without error. Although it has been stated that both measurement errors may be combined into a single error term (Ruesink 2000), this is incorrect as we never observe  $n$  on its own.

The dynamics of such time-series differ from density-independent time-series in a number of respects. For example, a characteristic feature of density-independent random walks is that their time-series are non-stationary (i.e. the variance expected in population size increases over time; Chatfield 1996). Because of census error density-independent time-series may appear stationary when they contain large amounts of measurement error.

The modelling framework in eqn 4 is termed a state-space model (e.g. Harvey 1989; see below). Writing the model for population dynamics in this way is important, because the consequences of variance in  $r$  and variance in  $\varepsilon$  for the analysis of census data are different, as we illustrate in the next section. We return to the state-space modelling framework later, as this has formed the basis for recent modelling studies.

## Census error generates spurious density dependence

Sampling error may generate measured population changes that are apparently density-dependent, even though the underlying dynamics are not. In this section we outline why this may happen. Figure 1a shows a hypothetical time-series (line) that is generated by a simple density-independent model (eqn 1). The only source of variability in this time-series is the density-independent year-to-year stochastic variations in rates of population change. It was then assumed that the population size was estimated each year with an error. The open points in Fig. 1a show these estimates. For the time-series of estimates, there are two sources of variability: the variance in the actual numbers of animals, plus variability resulting from the measurement errors. Based on the actual population numbers there is only a weak correlation between rate of population change and population density (Fig. 1b; see above for why the expected correlation is negative). However, the estimates of population density suggest that there is a strong



**Fig. 1.** (a) Census error leads to spurious detection of density dependence. The actual population time-series is shown as a line. The points indicate the estimated population sizes, i.e. the actual population multiplied by a random error. (b) In this example there is no evidence for density dependence in the actual patterns of population change. (c) Based on the estimated population sizes, the change in population size appears to be density-dependent. (d) An example of the spurious detection of density dependence as a consequence of measurement error. Fifty individuals were asked at 2-min intervals to estimate the population size of the UK Royal Family through the question 'how many direct descendents of the Queen Mother are there?'. No individual was able to give the exact answer to the question, hence the variation in the time-series of estimates is almost entirely composed entirely of census error. The patterns of change in successive estimates of population size showed strong evidence for density dependence.

correlation (Fig. 1c) and consequently that there is strong density dependence.

The reason for the spurious relationship shown in Fig. 1c is that it was assumed that census errors were large; indeed, so large that they dominated estimates of population size. As a result the estimates of population size in Fig. 1b bear little relation to the actual population densities. Consequently, a high estimate of population density one year (i.e. resulting from an overestimate of population numbers) is likely to be followed by a lower population estimate the next year, as we are unlikely to over-estimate population numbers to the same high degree for two years running; a low estimate (resulting from an under-estimate of population size), on the other hand, is likely to be followed by an overestimate the next year, this time because we are unlikely to under-estimate population numbers to the same degree for two years in succession. In contrast, for a (random walk) time-series, in which population changes do not depend on density, the probability of observing an increase or decrease in population size from one year to the next is, by definition, unaffected by the previous years' population size.

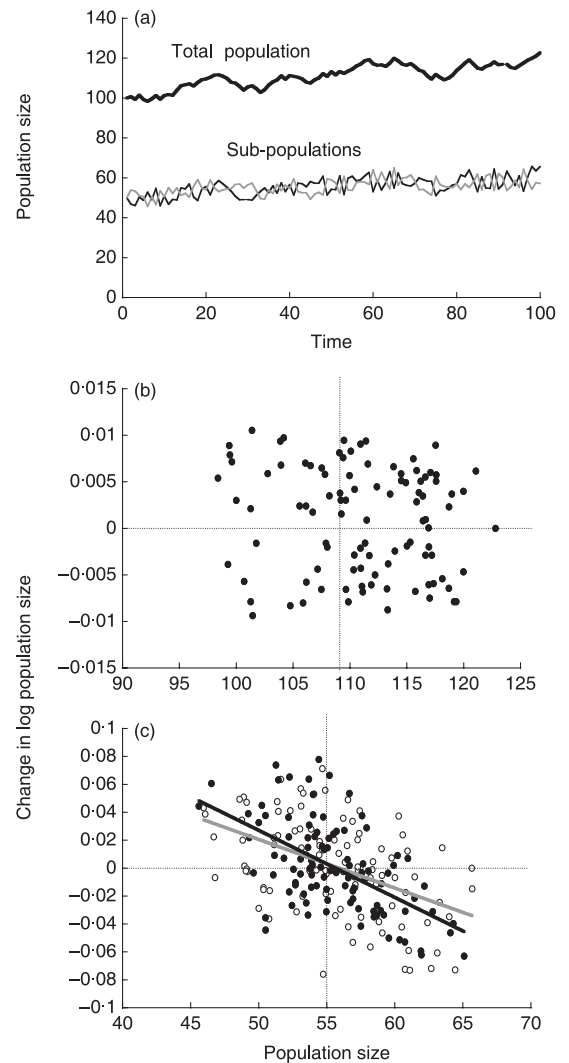
The phenomenon outlined in Fig. 1 is generalized readily using a simple analytical framework. The expected change in population size from a given measured population size is:

$$E\{n_{t+1}^{est} - n_t^{est}; n_t^{est}\} = E\{[n_{t+1} + \varepsilon_{t+1}] - n_t^{est}; n_t^{est}\}$$

where  $\bar{n}$  is the mean population size and  $E\{; n_t\}$  denotes mathematical expectation for a given population size at time  $t$ . Using the linear properties of expectations, we find:

$$E\{[n_{t+1} + \varepsilon_{t+1}] - n_t^{est}; n_t^{est}\} = E\{[n_{t+1} + \varepsilon_{t+1}]\} - n_t^{est} \quad \text{eqn 5} \\ = \bar{n} - [n_t + \varepsilon_t]$$

When measurement error exists, the measurement error in density for a given year therefore appears in the ensuing estimated change in population density, with equal magnitude but opposite sign. This generates patterns of population change that are apparently density-dependent, as in Fig. 1c. The covariance between population change and population size is biased by the presence of measurement error and in the extreme case that measurement error is very large, to the extent that all meaningful variation in population size is swamped, then the correlation between population change and population density approaches a value of  $-1/\sqrt{2} = -0.707$  (Royama 1992). While appreciable correlations between population change and population density may exist for short density-independent time-series with no measurement error, these decay as the time-series becomes longer. The potential for the existence of dynamics such as those shown in Fig. 1 has been recognized for a long time. Eberhardt (1970), for example, noted that a sequence of uncorrelated random numbers tends to follow a pattern consistent with density dependence.



**Fig. 2.** An illustration of artefactual density dependence in a spatially divided population. (a) One population is split into two subpopulations; for example, as happens when a population has several breeding populations. It is assumed that, on average 50% of the whole population is in either of the subpopulations, with the exact proportion varying from year-to-year. (b) In the population as a whole there is no density dependence. (c) However, when either of the subpopulations are considered, density dependence appears to be strong.

Figure 2 shows a second hypothetical example. The solid line in Fig. 2a shows the dynamics of the population, which is growing very slowly and exhibits no density dependence (Fig. 2b). It is assumed that the population is distributed across two sites and that on average 50% of the overall population locates at each site. However, the exact fraction at one site or the other was assumed to vary uniformly each year between 45% and 55%, because of a small fraction of individuals moving between the two sites. This is intended to mimic a situation such as a set of communal roosting or overwintering sites which are used by a fraction of a population and between which individuals sometimes move. Censuses of individuals at such locations are used frequently as proxies for the total population size.

The consequence for tests of density dependence of the variation in numbers resulting from movements of individuals between sites is shown in Fig. 2c. The two subpopulations apparently exhibit very strong density dependence, even though the overall population is not subject to density dependence. Importantly, in Fig. 2c it is assumed that the numbers at each site are monitored without any sampling error. Hence, if a study were performed at a single site, it would perhaps be assumed erroneously that population censuses were very accurate. In fact, only a very small amount of movement between populations in such a system is required in order to generate strong apparent density dependence.

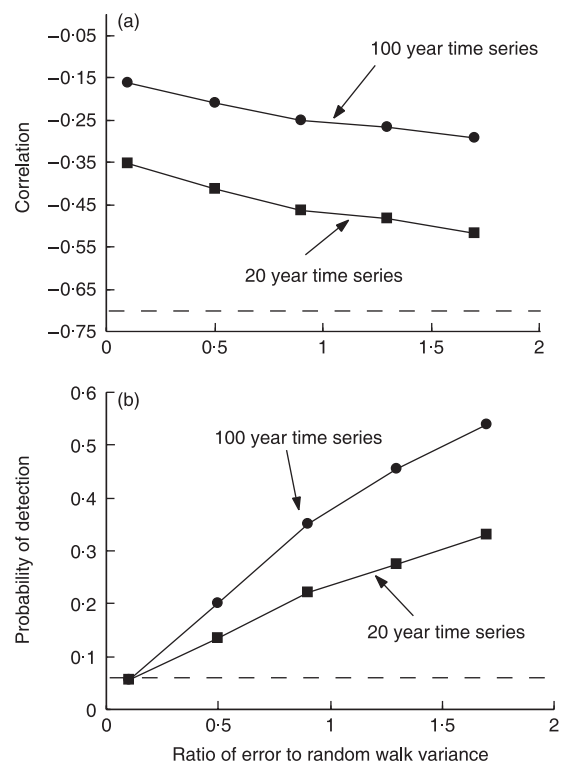
The situation illustrated in Fig. 2 is one in which each subpopulation constitutes a variably sized sample from the whole population. If the two subpopulations were unlinked, and both responded in the same way to a common stochastic variable, then each would fluctuate in the same manner as the whole population and density dependence would not be detected. In terms of eqn 5, the error is the degree to which each subpopulation differs from the number that would be predicted given the average proportion in each site and total population size. If this difference varies randomly from year to year, as does the error in eqn 5, then the subpopulations will show apparent density dependence.

The dynamics of spatially linked populations may differ qualitatively from those of isolated populations, and the consequences of spatial divisions for population and community dynamics are potentially profound (e.g. Ives *et al.* 2004). However, the case envisaged here is one in which the division of the population has no consequence for population dynamics. For example, the division may represent differing night-time roosts of a single population that feeds on a common resource during the daytime.

### How severe can the problem be?

Given that many existing analyses of population dynamics do not control for measurement error, it is necessary to estimate the probable severity of the problem. Shenk *et al.* (1998) provide a detailed survey of the effects of incorporating census error on the performance of a range of tests for density dependence, specifically highlighting Type I errors, i.e. the spurious detection of density dependence.

Figure 3 shows the rate of Type I error as a function of the relative level of measurement error for simple correlations between population growth rates and density. Comparatively small amounts of census error can lead to increasingly strong correlations between population change and population size (Fig. 3a). This means that the probability of detection of density dependence (by comparing 5000 density-independent time-series incorporating measurement error with 5000 simulated random walk time-series that contained no measurement error) in density-independent



**Fig. 3.** An illustration of how much census error is required to generate high levels of spurious density dependence. (a) Random (density-independent) time-series were generated in which the ratio of the variance in the census error to variance in the random walk parameter was varied and the mean correlation between the change in log-population size and log-population size was recorded. (b) Correspondingly, increasing census error increases the probability of detection of density dependence in time-series that are density-independent (i.e. Type I error rates); and the level of Type I error increases with the length of the time-series. The test for density dependence employed was the test of Pollard *et al.* (1987).

time-series (Type I error) increases rapidly to statistically unacceptable levels (Fig. 3b). Importantly, the effects of census error on the level of Type I error become stronger as the time-series become longer. In Fig. 3, the probability of detecting density dependence in a 100 years density-independent time-series is almost double the probability of detecting density dependence in a 20-year time-series (see also Royama 1992; Rothery 1998). In analyses that assume no census error, the power to detect density dependence increases as the length of the time-series becomes longer (Hassell, Latto & May 1989; Solow & Steele 1990). It would usually be assumed that evidence or not for density dependence in a longer time-series would be more robust than from a shorter time-series. However, as is clear from Fig. 3, this is not the case when the time-series contains census error.

Shenk *et al.* (1998) detailed how census error leads to high Type I error rates in the tests developed by Bulmer (1975), Pollard *et al.* (1987) and Dennis & Taper (1994). Bulmer (1975) proposed a test, the  $R^*$  test, that is designed to deal with data subject to measurement



error. Shenk *et al.* (1998), however, demonstrate that the test lacks power to detect density dependence.

### Assessing the degree of measurement error

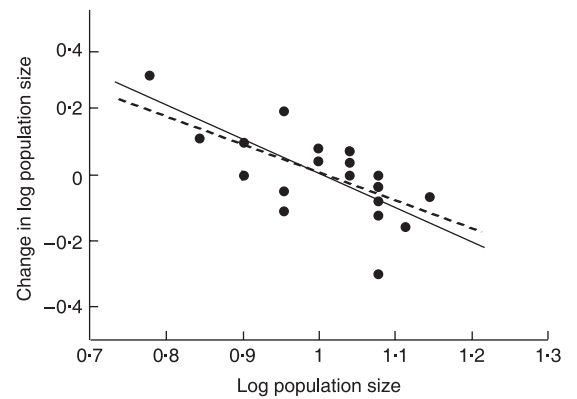
Clearly, robust tests for density dependence using time-series data are impossible in the absence of information on the degree of census error. To try to assess the degree to which census errors could affect the results of tests for density dependence, we have analysed two data sets for which long-term variability in numbers, as well as the level of census error, has been assessed.

#### LONG-TERM BIRD CENSUS DATA

The first case we explore involves a census technique for which census error has been quantified, and which has been used separately to study variation in population size over time. A 22-year time-series of estimated densities of five species of woodland birds (Beven 1976) was collected according to the methods of the UK Common Bird Census (abbreviated to CBC; Williamson 1964). A single individual oversaw the mapping of bird territories and the analysis of these to generate estimates of population numbers.

The methods used in the CBC have been evaluated statistically and, in particular, two sources of census error have been quantified in detail (O'Connor & Marchant 1981). These are the variance in estimates of density that can be attributed to variations between observers (who map observations of birds) and the variation that can be attributed to analysts (who interpret these maps). The estimates of these sources of variance that we report below represent the maximum levels of variance that would be expected to be encountered using these census techniques and can be used to analyse the maximum, or worst-case, impacts of census errors on tests for density dependence.

A simple way to explore data to determine the impact of census error is to examine how much of the variation in population size results from census error and how much variation is 'left over' and hence can be considered to be meaningful variation in population size. We performed this by comparing the observed variance in estimated log-population changes with estimates of variance resulting from census error. If the former is much greater than the latter, then census error plays only a minor role in determining year-to-year variations in population sizes, whereas if the two values are the same the year-to-year variations in actual population size and census errors cannot be disentangled. We measured the difference between these using an *F*-ratio (observed variance divided by error variance; an *F*-ratio was used as both variances were estimates). A value of the *F*-ratio of unity indicates that the observed variance in population sizes is indistinguishable from census error of whatever form; a value much greater than unity indicates that there exists meaningful measured variation in densities that can be analysed.

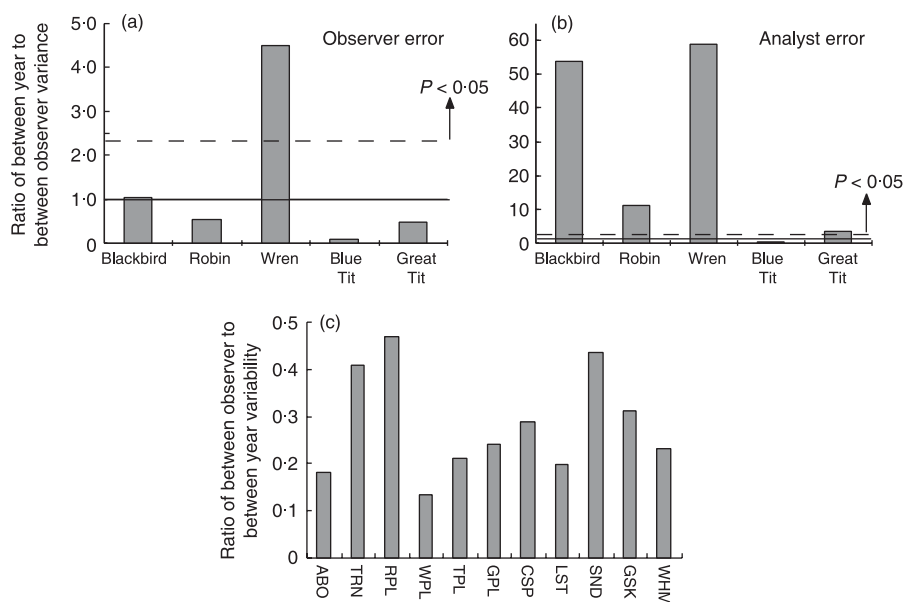


**Fig. 4.** An analysis of one of the time-series explored used in the text, illustrating the need to know the degree of census error. The change in log population size of blackbirds is plotted as a function of log population size. The solid line shows the predicted relationship between the two either if (i) all meaningful variability in the data results from measurement errors; or (ii) there is no measurement error, but populations are fluctuating randomly about a fixed equilibrium with density dependence being perfectly compensating. In both cases the correlation between change in log population size and log population size is predicted to be 0.707, compared with an observed value of 0.69. In this case the counts are thought to be extremely accurate and hence it is very likely that the relationship does actually reveal density dependence.

In these worst-case scenarios, census error can dominate the estimates of population change and thus impact severely on tests for density dependence (e.g. see Fig. 4 for an example from this dataset that could be consistent with either strong density dependence or pure error if no information on the accuracy of the census method were available). When compared with the degree of census error between observers, it is clear that in four of five cases all variation in population changes could be attributed to census error (Fig. 5a). That is not to say that there would be no variation in actual density or that density dependence did not exist – rather, census error would mask the genuine variations. In contrast, if all census error resulted from variations between analysts, then in four of five cases the observed variation is significantly higher than the census error (Fig. 5b). If this were the case it would be possible to control for census error in the null model and hence perform a robust test for density dependence. Because the time-series was in reality generated by multiple observers under the supervision of a single individual, we would expect that the variance in densities owing to census errors would be considerably lower than when estimated by a number of observers. Gaston & Blackburn (2000), for example, show that the time-series changed enormously when the original coordinator retired. The lesson from this analysis is that, wherever possible, measures of error should be built into census protocols.

#### REPLICATED OBSERVATIONS

Few studies have estimated simultaneously the effects of between-observer and between-year variability. The



**Fig. 5.** An assessment of the maximum impact of measurement error on the variance in population changes? We used data on five species of woodland birds (blackbird: *Turdus merula*; robin: *Erithacus rubecula*; wren: *Troglodytes troglodytes*; blue tit: *Parus caeruleus*; great tit: *Parus major*) for which data were available on both the variance in numbers over time as well as potential levels of census error (see text for details). We compared the observed variance in log-population changes with error variation between (a) observers and (b) analysts using an *F*-ratio test. The solid line indicates  $F = 1$  (i.e. no difference), while the dashed line shows the *F*-value required for statistical significance, i.e. the observed variance in log-population sizes is significantly greater than that from census error. (c) Comparison of the degree of variation between observers with year-to-year variation in numbers of 11 species of waders (ABO: African black oystercatcher (*Haematopus moquini*); TRN: turnstone (*Arenaria interpres*); RPL: ringed plover (*Charadrius hiaticula*); WPL: white-fronted plover (*Charadrius marginatus*); TPL: three-banded plover (*Charadrius tricollaris*); GPL: grey plover (*Pluvialis squatarola*); CSP: curlew sandpiper (*Caladris ferruginea*); LST: little stint (*Caladris minuta*); SND: sanderling (*Caladris alba*); GSK: greenshank (*Tringa nebularia*); WHM: whimbrel (*Numerius phaeopus*)).

second example we have analysed is a study on variation in numbers of shorebirds. Spearpoint, Every & Underhill (1988) estimated the variability in counts between two observers measuring the same populations simultaneously, as well as long-term (1981–88) variability in numbers. Variability was measured as the deviation from the median level of abundance and, as shown in Fig. 5c, the variability between the pair of observers ranged from 0.15 to 0.45 of the year-to-year variations in numbers. This indicates that counts of individuals of these species taken by single observers are extremely variable, and could add a significant additional variance to population census estimates. Interestingly, the level of between observer variability is correlated negatively with the logarithm of bird body size (mean individual weight; Spearpoint *et al.* 1988) for these species ( $r = -0.678$ ;  $n = 11$ ;  $P < 0.02$ ), i.e. the difference between observers is lower for larger species. This may reflect differences in detectability between species.

Detailed analysis of variability between observers as a source of measurement error in population counts has been performed by Cunningham *et al.* (1999), who analysed replicated censuses of 65 species of Australian woodland birds. For some groups of birds they found that between-observer error would increase confidence intervals for estimated mean population sizes by around 40%. Furthermore, the degree of between observer variability was, in some cases, found to be related to the nature of the area being sampled (type of

forest) or to the method being used. Importantly, their analysis showed that taking the average of counts of pairs of observers would compensate for much of the variability introduced into estimates of population sizes owing to observer heterogeneity.

### Statistical methods

In the previous section we outlined examples of how it might be possible to use information from replicated observations of the same system in order to infer the relative levels of process and census error in long-term sets of data. In this section we review methods by which it may be possible to control for census errors in analyses of time-series.

#### ADAPTING EXISTING METHODS

The  $R^*$  test of Bulmer (1975) offers one option in the face of unknown levels of census error. It is unclear, however, for which levels of error it is valid, and it may lack power when density dependence is occurring (Shenk *et al.* 1998). However, comparison of results using the unmodified  $R$  with those from calculating  $R^*$  may provide an indication of whether an impact of census error may be likely: if both tests yield a significant result then the result may be considered more robust.

An alternative to this approach is to fit a model including no density dependence and ask retrospectively

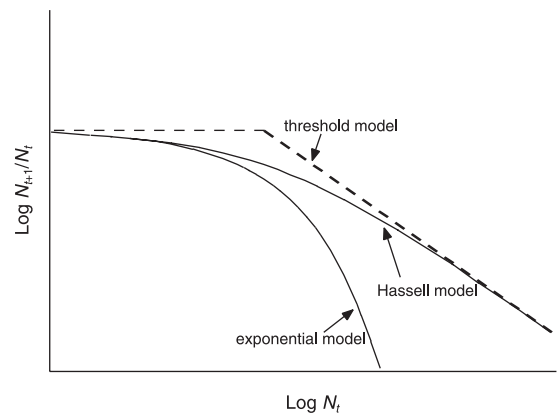


how much census error would have been required in order to produce the observed levels of density dependence. If it appears that only small amounts of census error are necessary to yield the observed amount of density dependence then the pattern could be attributed easily to spurious density dependence arising from census error. By contrast, if the amount of census error required to produce spurious density dependence is large, then the results might be considered more robust. In the example shown in Fig. 4, for example, almost all variation in numbers would have to result from census error in order for a density-independent time-series to appear density-dependent. Hence one might conclude that the pattern is robust to the effects of census error. Along these lines, Turchin & Ellner (2000) were able to argue persuasively that the role of census error was minimal across most of the range of densities observed in their time-series (see also Hanski *et al.* 1994).

More sophisticated approaches have also been developed based on existing statistical frameworks. For instance, maximum likelihood methods that have been developed for fitting population models to error-free data (e.g. Dennis *et al.* 1991) can be adapted to include the presence of measurement errors (Holmes 2001; Staples *et al.* 2004). This requires that a distribution can be specified for the errors. The problem with this approach is that it is necessary to integrate the likelihood function across all possible densities at all monitoring points. For a time-series of length  $T$  this leads to a  $T$ -dimensional integral that is computationally difficult to evaluate. To solve this problem, Lele (2006) has developed a method based on composite-likelihood, which is an approximation of much lower dimension. Lele (2006) shows that this method is considerably less intensive than full likelihood methods, and would therefore be appropriate for large data sets.

#### NON-LINEARITY

Not all tests for density dependence are necessarily subject to the problems outlined above. As shown in Fig. 6, analyses that demonstrate nonlinearity in relationships between log-population change and log-population density (Fig. 6) can be argued to be valid, even when the degree of census error has not been quantified. This is because the spurious relationship that results from census error is strictly linear on the log-log scale (Eberhardt 1970), whereas a number of traditional ecological models, such as exponential and hyperbolic models (e.g. Maynard Smith & Slatkin 1973; Hassell 1975), yield nonlinear relationships (Fig. 6). The test developed by Dennis & Taper (1994), which is based on a logistic model, could be modified readily to include an explicit test for linearity. The response surface methodology employed by Lindström *et al.* (1999), for example, includes explicit tests for deviations from linearity. In addition, statistical models that pick out thresholds defining changes in correlations between log-population

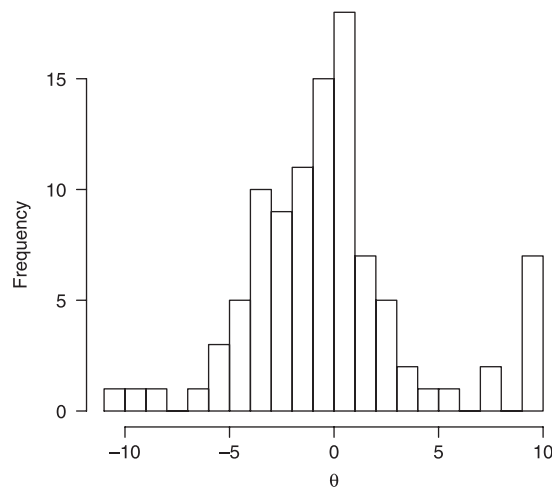


**Fig. 6.** Systematic trends in plots of log population growth rate against log population size that are not consistent with spurious trends owing to census error. The relationship between log population change and log population size that results from census error is basically linear. Irrespective of whether unquantified census error exists in the data set, systematic deviations from a linear pattern could therefore be taken as evidence for density dependence. The three examples illustrated are the Hassell (hyperbolic-logistic) model, exponential model and a threshold model (dashed line). It is clear that all three show considerable deviation from linearity when a large enough range of densities are available.

change and log-population size (Grenfell *et al.* 1998) should be robust to census error, and may be related to more traditional ecological models (Stenseth & Chan 1998). Similarly, Bjørnstad *et al.* (1999) developed a technique for detecting nonlinearity in population growth trajectories that was shown to be moderately robust to low levels of census error (measurement error less than 10% of mean abundance), but which nevertheless showed high Type I error rates when large (> 10% of mean abundance) measurement errors exist.

A related observation is that the relationship between log population growth rate and log density should have a slope of  $-1$  for a pure error model, or between 0 and  $-1$  for a density-independent random walk with added measurement error. However, if the measured relationship has a slope steeper than  $-1$ , then it may be safe to conclude that density dependence exists. In fact, for populations with very strong density dependence (i.e. slopes of density-dependent relationships with slopes steeper than  $-1$ ) the effect of measurement error could be to weaken the apparent effect of density dependence. Such populations might include those with nonlinear dynamics, including cycles, limit cycles and chaos. The presence of large amounts of measurement error would lead therefore to underestimation of the degree to which populations may show unstable dynamics.

Although in principle analyses that utilize nonlinearity appear potentially robust to census error, such methods need to be developed cautiously. Recently there has been a great deal of interest in the  $\theta$ -logistic model (Saether *et al.* 2000, 2003, 2004; Lande *et al.* 2003; Sibly *et al.* 2005), which is a modified version of the logistic



**Fig. 7.** An illustration of the problem of estimating nonlinearity in density dependence in systems with measurement error. Nonlinearity in population growth rates is estimated by  $\theta$  of the  $\theta$ -logistic model. Data are generated from a density-independent model with measurement error, in which the process variance and error variance are equal. A wide range of  $\theta$ -values are possible.

model. Whereas the logistic model assumes that the relationship between log population growth rate and density is linear, the  $\theta$ -logistic includes a parameter  $\theta$  which allows the nonlinearity of the relationship to be varied. Values of  $\theta > 1$  indicate convex relationships,  $\theta = 1$  indicates a linear relationship, while  $\theta < 1$  yields a concave relationship. A value of  $\theta = 0$  indicates that the relationship between log population growth rate and log density is linear, as would be expected for a density-independent series including measurement error. In principle this statistic would appear to offer the potential to distinguish varying degrees of nonlinearity and hence diagnose population dynamic patterns distinct from those that result from measurement error. However, this is not the case: as shown in Fig. 7 some caution is required. The data in Fig. 7 summarize the values of  $\theta$  estimated from a density-independent time-series with added measurement error. It is clear that a wide distribution of values of  $\theta$  are possible, and that without careful analysis the value of  $\theta$  cannot be interpreted safely as diagnosing lack of measurement error.

#### ESTIMATION OF MODEL PARAMETERS

The problem of measurement error has been viewed typically in terms of Type I error rates in tests for the existence or not of density dependence. However, census data may also be used in order to parameterize models for population dynamics that are used in a predictive manner, for example in population viability analysis, harvesting or pest control applications (e.g. Bayliss 1989; Burgman *et al.* 1992; Freckleton *et al.* 2000; Freckleton & Watkinson 2001). The technique of regressing log population changes on log population size has actually been recommended for detecting and

modelling density dependence (Burgmann *et al.* 1992). However, it is important to be aware that, as well as over-estimating the strength of density dependence, census error will bias parameter estimates. Specifically, the maximal rate of population increase at low densities ( $r$ ) will be over-estimated, because the estimated rate of population change will increase with decreasing density, even if there is no or only weak density dependence.

The bias in the estimate of  $r$  is particularly important because this parameter is used to generate, among other things, estimates of extinction probabilities on its own or together with  $K$  (Lewontin & Cohen 1969; Foley 1994), predicting the off-take from populations that may be harvested (Usher 1966, 1969; Enright & Ogden 1979; Freckleton *et al.* 2003) or the long-term outcome of culling strategies (Smith *et al.* 2005).

Recently, McNamara & Harding (2004) noted that estimates of extinction risk using diffusion approximations (e.g. Lande & Orzack 1988) would not be affected by census error, so long as the correlation structure of the time-series were accounted for in estimating the variance in population growth rate. They noted that census error would introduce negative serial autocorrelations into time-series of population growth rates. This is because, as outlined above, a high over-estimate of population size in year  $t$  will lead to an over-estimate of population growth rate in year  $t$ , and an under-estimate in year  $t + 1$ . This negative autocorrelation in population growth rates cancels out the inflation in variance in population growth rate owing to measurement error in density, as long as the variance is calculated controlling for autocorrelations in density. As a consequence, diffusion approximations unexpectedly yield the correct probability of extinction. The complication, however, arises when the source of negative autocorrelation is unknown (e.g. when it is not known whether this is the consequence of true density dependence or census error). For this reason, McNamara & Harding (2004) recommend that their result is treated with caution and census error estimated where possible.

A counterpart to the ecological problem of detecting density dependence from census data containing error has been analysed in studies of stock-recruitment relationships in fisheries. Walters & Ludwig (1981), for example, developed techniques for the analysis of relationships between numbers of new recruits and breeding population size in which gross measurement error obliterates clear relationships between the two variables. In the examples they employ, the number of recruits is a simple linear function of the number of spawners (i.e. the per capita rate of recruitment is density-independent). When measurement errors are introduced, however, the linear relationship is obscured, with the consequence that the number of recruits appears to be independent of the number of spawning fish (i.e. the per capita rate of recruitment declines with increasing density). This is the same phenomenon as outlined in Fig. 1: the per capita rate of recruitment (the number of recruits divided by the

number of spawning fish) declines spuriously with density (Hilburn & Walters 1992).

Ellner *et al.* (2002) apply a technique that attempts to reduce or remove bias in parameters or functional forms of density relationships resulting from measurement errors. The technique they use is SIMEX bias reduction (Cook & Stefanski 1994; Carroll *et al.* 1995; Stefanski & Cook 1995). In simple terms this method works by using a model of measurement error to simulate the effects of varying levels of error variance on parameter estimates. By extrapolating back to zero error variance, it is possible to control for bias in the estimates of model parameters.

As an example of this, assume we have a series of (log) density estimates ( $n$ ), that the error for each estimate  $n^{est}$  is given by an additive model  $n^{est} = [n + \varepsilon]$  in which  $\varepsilon$  is normally distributed with zero mean and its error variance is known to be  $\sigma_\varepsilon^2$ . The SIMEX procedure defines a parameter  $\lambda$ , and generates a simulated series of density estimates according to:

$$n_i^* = n_i^{est} + \lambda^{1/2} \sigma_\varepsilon z_i \quad \text{eqn 6}$$

in which  $z$  is a standard normal random variate. Increasing  $\lambda$  increases the variance of the measurement error in the estimates of density from  $\sigma_\varepsilon^2$  to  $\sigma_\varepsilon^2(1 + \lambda)$ . For parameters biased by measurement error, increasing  $\lambda$  should therefore increase bias. The method works by estimating parameters on simulated data sets with enhanced variance. Plots of parameter estimates against  $\lambda$  can then be constructed and, by extrapolating the plot (linearly or nonlinearly as appropriate) to estimate the value of the parameter at a value of  $\lambda = -1$ , the effects of measurement error can be removed.

Ellner *et al.* (2002) show that this method is effective in some cases, although less effective in others. The methodology described by Ellner *et al.* (2002) is particularly interesting as it allows, through non-parametric regression, the effects of measurement error on the shape of inferred density responses to be inferred and thus allows not only measurement error to be controlled for, but also uncertainty in the precise shape of the density response.

#### NUMERICALLY INTENSIVE METHODS

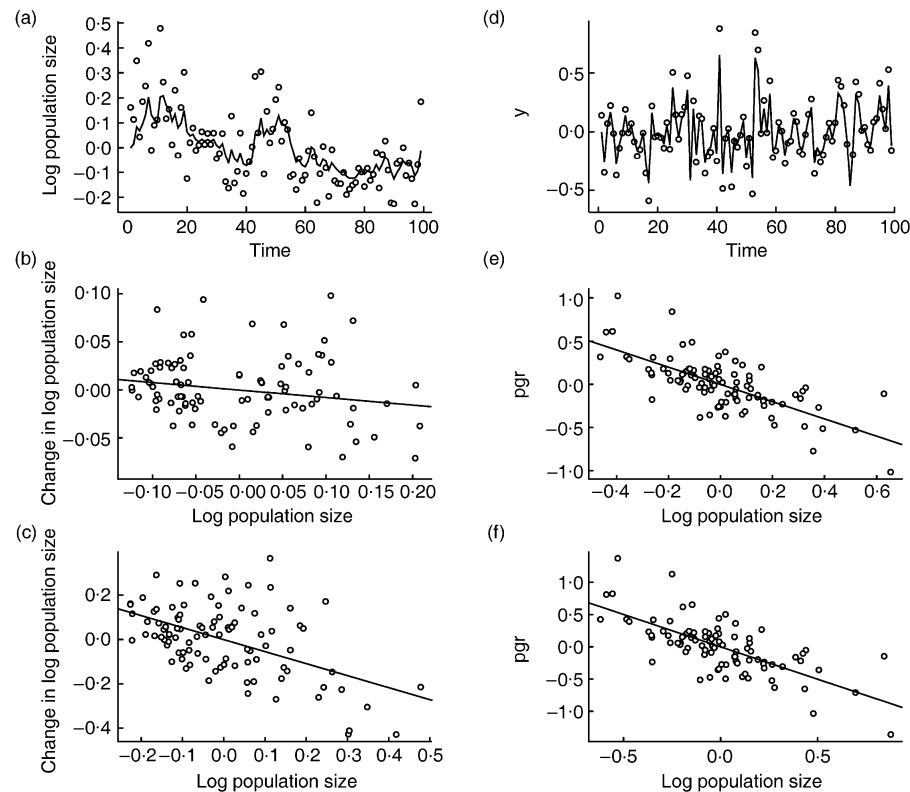
The SIMEX approach is one of a number of numerically intensive methods that have been used to account for measurement errors; it might be expected that simulation may provide a general and robust approach (Manly 1991; Dempster *et al.* 1995; Rothery 1998; Bjørnstad *et al.* 1999) to control for inflated Type I error rates. If it is possible to specify an error distribution for the census errors, then maximum likelihood approaches may be used to account for measurement errors (e.g. Carroll *et al.* 1995). This approach has been applied, for example, by Fromentin *et al.* (2001), who found that including census error had marked effects on estimates of the strength of density dependence in cod populations.

de Valpine & Hastings (2002), de Valpine (2003) Williams *et al.* (2003) and Viljugrein *et al.* (2005) have employed a more direct method, based on fitting state-space models of the form of eqn 4. The model fitted is split into two components, the dynamics of the actual population and that of the measured data. To be able to fit such a model an estimate of the error variance is usually required, although as outlined below, Dennis *et al.* (in press) show how this type of model can be fitted in the absence of such estimates. As shown in Fig. 8 this approach is potentially very powerful and can distinguish time-series which are genuinely density-dependent from those that are not. Viljugrein *et al.* (2005) have performed simulations showing that the technique performs well in reducing bias, at least for the data set they used, although more extensive simulation studies are needed to examine how the techniques cope in the face of varying forms of density dependence and error. Moreover, de Valpine & Hastings (2002) have considered how state-space models may be fitted to nonlinear systems when errors are non-normally distributed, greatly extending the utility of this approach. As an application of this to real data, a recent study by Wang *et al.* (2006) show how the state-space model may be adapted to explore problems in spatio-temporal dynamics.

As noted above, Dennis *et al.* (in press) have shown that state-space models may be adapted to estimate eqn 4 even when an estimate of the measurement error is not available. Their approach relies on the observation that in first order density-dependent models, there should be no temporal autocorrelation of residuals. Measurement error, however, will lead to autocorrelation in the residuals, the strength of this autocorrelation being a function of the degree of error. They use this autocorrelation to estimate measurement error along with process variation and the strength of density dependence.

Another area of recent development has been in the application of Bayesian methodology (e.g. Clark & Bjørnstad 2004; Jamieson & Brooks 2004; Carroll *et al.* 2006). Bayesian methods may be used as an alternative computational method for fitting the state-space model, in which parameters are treated as being drawn from a prior distribution (Clark & Bjørnstad 2004). Framed in this way, the posterior parameter distribution can be estimated using a simulation scheme for numerical integration such as a Markov chain Monte Carlo (MCMC) approach (e.g. Gelfand & Smith 1990; Gammelman 1997). The computational advantage is that the numerical integration circumvents the complex problem of combining the distributions for different parameters in the model. Consequently, multiple sources of error can be included that would otherwise be analytically difficult to deal with. The power of the approach is then that it is possible to create complex models including uncertainty in multiple parameters and predictors, including census error.

In summary, techniques exist that allow the effects of census error to be accounted for and dealt with.



**Fig. 8.** State-space models applied to simulated data. (a–c), data from a density-independent time-series; (d–f) are from a density-dependent time-series. In both cases the data are simulated with measurement error (for instance, as illustrated in Fig. 1). (a and d) Time-series (points), together with the fitted state-space models (lines). (b and c) Relationship between change in log population size and log population size having accounted for measurement error. The relationship is identified correctly as being weak for the density-independent series (b) and strong for the density-dependent series (e). This contrasts with the strong patterns exhibited in the raw data (c and f), which is incorrect and arises from measurement error in (f).

Although simulations will probably be required in order to validate techniques for specific data sets and models, it appears that the technical background for dealing with census error is developing quickly. What is particularly notable is that methods of analyses are moving away from statistical tests for the existence or not of density dependence, towards fitting population models that estimate the functional form of density dependence as well as the relevant population parameters.

#### SPATIAL AND BEHAVIOURAL DIVISIONS

No analysis to date has looked at how spatial or behavioural divisions of populations may influence the detection of density dependence. This is despite the enormous current interest in large scale spatio-temporal dynamics (Grenfell *et al.* 1998; Hanski 1999; Lande *et al.* 2003; Ives *et al.* 2004). In the absence of estimates of the degree of flux of individuals amongst spatial and behaviourally defined sub-groups of populations and the extent to which these sub-groups differ in detectability to the census workers, it would seem difficult to estimate the degree to which this is likely to be an issue in estimating the strength of density dependence. In many cases the migration pattern varies between years according to the weather (Wernham *et al.* 2002), although this would usually be impractical. However, our

experience is that the counting of sub-populations, both behaviourally and spatially defined, is an extremely common feature of long-term census data. We also believe that quantifying variation among census periods in the proportion of the wider population in the countable component is difficult and rarely attempted. Clearly, approaches that only evaluate variation among observers do not tackle this problem. Dealing with this analytically will prove to be a major challenge.

#### Concluding remarks

Most techniques for that test for density dependence do not account for census error. Those studies that present enough information indicate that censuses of the sort employed in long-term population monitoring may contain significant census error. For instance, Dennis *et al.* (in press) estimated that up to 70% of variance in density in the time-series they examined resulted from census error. In extreme cases, data may be entirely consistent with either strong density dependence leading to random fluctuations around a fixed equilibrium or large measurement errors causing negative correlations between the two variables. Although sophisticated tests for density dependence are available when such information is available, this situation is relatively unusual.

Only rarely are numbers or densities based on error-free exact counts of individuals. This situation has arisen from time to time in the analysis of the role of density dependence in annual plants, which are relatively easy to census accurately, and in some cases each individual within the population is mapped accurately (Pacala & Silander 1990; Rees *et al.* 1996; Watkinson, Freckleton & Forrester 2000; Freckleton & Watkinson 2001). Manipulations of densities provide another effective method for detecting density dependence in plants (Watkinson & Harper 1978), although may fail when applied to plant mixtures (Freckleton & Watkinson 2000). Manipulations, while effective, are impractical for most animal populations, the data sets analysed above being cases in point. On the other hand, behavioural modelling allows density dependence to be characterized from first principles (Sutherland 1996), while detailed analysis of the components of the life-cycle circumvents some of the statistical problems outlined above (Newton 1998).

In the above we have assumed that census error has resulted from the measurement process. Thus, by increasing the number of observations on which an estimate is based, or by providing information on the level of error, it should be possible to assess the potential severity of the problem. However, it is important to be aware that there exist situations in which it may well be impossible to account for census error. For instance, imagine that a population of birds is censused at one time of year, for example at a given over-wintering site. If only a proportion of the population over-winters at that site, and that proportion varies from year to year, then this will introduce an error into estimates of population size that cannot be accounted for by replicated observations at the same site. Similarly, if populations are swelled periodically by immigrants, as happens frequently in over-wintering birds, and the proportion of immigrants varies from year to year, then this will also generate a census error that cannot be accounted for by replicated observations.

There exists a large body of work, the validity and utility of which is called into question. Until the role of census error is clearly elucidated, the scale of the problem is not certain, and attempts to demonstrate the role of density dependence in population dynamics from time-series data will be thwarted. One straightforward and invaluable approach is for individuals to carry out repeat censuses as one way of estimating error. However, the problem of censuses that cover only a variable sub-population of the wider population is one which cannot be solved in this way.

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