CHAOS MEETS DATA IN POPULATION ECOLOGY:
INFERRING THE CAUSES OF POPULATION FLUCTUATIONS

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1. <u>Introduction.</u> The logistic difference equation $x_{t+1} = rx_t(1-x_t)$ with $r=3.7$ produces erratic, chaotically fluctuating values of x_t (Figure 1a). Contemplating this time-series, Solomon (1979) asked, "How could the trajectory of this completely determined process ever be distinguished from the sample path of a stochastic one?" The implication is that there is no way to tell if fluctuations in population abundance are chaotic or random, by any analysis of the time-series data alone.

Fortunately, Solomon's question has a simple answer, shown in Figure 1b. Graphing x_{t+1} vs. x_t, the relationship is seen to be perfectly deterministic, though highly nonlinear. At the time, however, Solomon's opinion was just about every ecologist's opinion: chaotic population dynamics are "indistinguishable from stochastic growth" (Thomas et al. 1980).

In the ecological literature the idea still persists that "for most practical purposes, and certainly for ecologists, the chaotic regime may be regarded as one in which simple and deterministic relationships...give apparently random dynamics" (May 1986). In physics, however, methods for identifying low-dimensional chaos in experimental data (of which Fig. 1 is the simplest example) are widely known and used (Mayer-Kress 1986). The methods have been imported into ecology, and adapted to suit the local conditions, by Schaffer, Kot and coworkers.

In this paper I will briefly review the methods and results of the search for chaos in ecological data, and some related work by economists (Brock 1986, Sayers 1987). I will also present a statistical method, still under development, for estimating a fractal dimension of the dynamics and calculating confidence limits for the estimate. If this dimension is >1 but finite, it indicates aperiodic dynamics which are not just random fluctuations. That's not the same as testing for the presence of chaos, but it's a step in that direction. I have tried to make this paper accessible to ecologists, which means giving intuitive and nonrigorous explanations of some basic terms and concepts.

2. <u>Chaos in ecology, Round 1.</u> When ecologists began to wonder if any real populations behaved chaotically, the only available method was indirect: model the

population dynamics using a difference equation like the logistic, and determine if the underlined model has chaotic dynamics. Data on actual population fluctuations might be used to estimate model parameters, but could not be tested directly for signs of chaos. For this method to be valid, it must be assumed *a priori* that the population dynamics are truly a one-dimensional system, e.g., no predators, competitors, or resources whose dynamics are affected by the population being modeled.

Still, there were no apparent alternatives so it was certainly worth trying, and the results seemed pretty conclusive. Hassell, Lawton and May (1976) analyzed data on 28 populations of seasonally breeding insects with non-overlapping generations, fitting the data to the difference equation $N_{t+1} = \lambda N_t/(1 + aN_t)^b$. The estimated parameters corresponded to a stable equilibrium in the majority of cases, and no natural populations fell in the chaotic region. A follow-up study by Bellows (1981) using the model $N_{t+1} = \lambda N_t/(1 + (aN_t)^b)$ reached the same conclusion. One case had a stable limit cycle, while the remaining 13 had a stable equilibrium.

So chaos was not found in nature; what about the laboratory? Experiments on laboratory populations avoid the problems of unmodeled interactions and an uncontrolled environment. Again, the results were quite uniform. 20 of 25 lines of Drosophila melanogaster raised in the laboratory had stable equilibria for the estimated model parameters (Mueller & Ayala 1981), and in no case could the null hypothesis of a stable equilibrium be rejected. 58 laboratory populations of Drosophila from 27 species were all found to have a globally stable equilibrium (Thomas et al. 1980). Additional data on 10 of those species under a different food regime were fit to the "θ-logistic" model $N_{t+1} = N_t + rN_t(1 - (N_t/K)^\theta)$, and none of the species had parameters in the chaotic region (Phillipi et al. 1987).

In Hassell et al.'s analysis, Nicholson's laboratory blowflies were the only example of parameters in the chaotic region, and they were chaotic also in Brillinger et al.'s (1980) more detailed model. But Nisbet & Gurney (1982) concluded, after their fastidious analysis, that the blowfly oscillations were limit cycles. Thus it was entirely reasonable for Nisbet & Gurney (1982), after surveying all the available evidence, to express the belief that "deterministic stability is the rule rather than the exception, at least with insect populations".

3. Reconstruction. The breakthrough, which made it possible to analyze time-series data directly for evdence of chaos, was Takens' (1981) method of "reconstruction" in time-delay coordinates. Takens' method is simplest for the case of a single-variable time-series. So suppose that the data are one-dimensional, in continuous or discrete

time: $x(t)$, $0 \leq t \leq T$ or $x(t_i)$, $i = 1,2,...,N$. It is assumed that x is one variable out of many, in a deterministic differentiable dynamical system (e.g., a system of ordinary or partial differential equations). From the values of x we create the M-dimensional time-series

$$X(t) = (\ x(t),\ x(t+\tau),\ x(t+2\tau),\ ...\ x(t+(M-1)\tau)\ ).$$

with $\tau > 0$ arbitrary (continuous time) or an arbitrary multiple of the time between measurements (discrete time). M is called the "embedding dimension". For example, if our data are $x(1)$, $x(2)$, $x(3)$,..., and we take $M=3$ and $\tau=2$, then

$$X(1) = (\ x(1), x(3), x(5)\ )$$
$$X(2) = (\ x(2), x(4), x(6)\ )$$
$$X(3) = (\ x(3), x(5), x(7)\ ),$$

and so on. $X(t)$ is then a sequence of points in 3-dimensional space. The same method is used if x is k-dimensional, and the dimension of X is then kM.

Takens proved that for M sufficiently large, the dynamics of $X(t)$ is qualitatively the same as the full system's motion on its "attractor" (technically, the mapping taking the full system to X is generically an embedding of the attractor into Euclidean M-space). Informally, the attractor is where the system winds up if you let it run long enough (assuming such a place exists). Reconstruction lets us see the attractor, if we are content with qualitative information about the dynamics on the attractor (e.g., "is it a limit cycle, or not?"). Quantitative reconstruction is impossible: we can't determine the actual values of the unmeasured state variables. Also, the dynamics off the attractor might not be faithfully reconstructed, in general.

How large M must be for an accurate reconstruction depends on the attractor dimension, which is generally unknown. In practice, M is increased until $X(t)$ looks well-behaved (smooth trajectories without crossings) and/or the estimated dimension of the reconstructed attractor stops increasing. For mathematical details and rigor, and a review of reconstruction as applied to physical and chemical systems, see the review by Eckmann & Ruelle (1985).

4. <u>Chaos in Ecology, Round 2.</u> This round belongs to Schaffer & Kot, who picked up reconstruction and ran with it, attracting some followers in the process. A small sample of their results is shown in Figure 2 (while Schaffer & Kot have also examined several ecological models, I will discuss here only their analyses of data). In each case the original time-series had dimension 1, and the embedding dimension is 3; the original discrete-time data have been smoothed in some cases, and

interpolated.

Schaffer & Kot (1986) describe these as "some apparent examples of real-world chaos". All of them had been interpreted before as periodic, with superimposed "noise" due to environmental fluctuations (in <u>Thrips</u> the periodicity was seasonal with period 1 year; the others had apparent multi-year periodicities). The reconstructed trajectories appear to trace out an attractor of dimension 2 (or higher, for measles), rather than a 1—dimensional periodic orbit. For measles the case is strengthened by applying the same reconstruction to the time-series of number of infectives produced by an SEIR model with seasonal variation in the disease-transmission rate, and noting the striking similarity to the reconstructed data (Figure 2e). (SEIR models are standard epidemiological models in which the population is classed as Susceptible, Exposed, Infectious, or Removed [dead or immune]; see e.g. Aron & Schwartz 1984). Schaffer (1985) gives the details of the measles reconstruction, and lists 10 population data-sets that are similarly suggestive of chaos (including Nicholson's blowflies).

However, "this looks like chaos to us" may not be quite enough to convince a sceptic, especially a sceptic whose background is in more conventional time-series analysis. Bulmer (1974) observed that the 19th-Century Canadian lynx-cycle had a fairly regular period but irregular amplitude which were "obvious in data on the lynx cycle, and in the correlogram and periodogram calculated from the data". To account for these he proposed the model

$$x_t = \mu + \alpha \sin w(t - \phi) + \beta x_t + e_t$$

where $x_t = \log_{10}$(number of lynx trapped in year t), μ is the mean of x, and the e's are random errors. The sin term accounts for the regular periodicity, while the autoregressive term makes the amplitude fluctuate.

Bulmer gets a better fit (accounting for 86% of the variance) with this model than with models suggested previously by Bartlett and Moran, and judged the residuals to be random. This was taken as confirming the validity of the underlying model, and of the significance level for the periodic component ($\alpha \neq 0$ at P < .001) calculated on the basis of the model. Bulmer (1974) could also point to a biological explanation for the common period of cycles in lynx and 8 other species with α significantly non-zero, namely interactions with the snowshoe hare. Bulmer (1976) developed stochastic models in which the hare follows a noisy limit cycle (conjectured to result from interactions between hare and its food-plants), and the lynx cycle is driven by the hare cycle. The power spectrum of the lynx cycle is found to have the qualitative form predicted by the models, and there are even a

few quantitative agreements.

However, Bulmer "eyeballing" his residuals is no more rigorous than Schaffer & Kot "eyeballing" the same data after reconstruction. Indeed, Finerty's (1980, Fig. 7) reanalysis found evidence of a single dominant cycle with period near 10 years in only 4 of the 10 species for which this was claimed by Bulmer (1974). Their methods of analysis differed only in some apparently minor details, but that was enough to change the results.

Analysis of the infectious disease data raises similar problems. Anderson et al. (1984) performed spectral analyses of measles, mumps, and pertussis incidence. This is a standard statistical method for analyzing time-series, in which the series is expressed as a sum of periodic components (sines & cosines). The "spectral density" is a curve showing the relative importance of the components into which the series was decomposed, as a function of frequency (frequency =1/period, so e.g. a frequency of .5 means a period of 2).

Anderson et al. found consistent peaks in the spectral density at a period of 1 year, and also at multiples of one year: 2 years for measles, 3 years for pertussis and mumps. Figure 3 shows an example of spectral analysis applied to measles incidence. Even in a short time-series, the spectral density has 2 clear peaks, so the hypothesis of purely random fluctuations is soundly rejected. The nonzero spectral density in frequencies outside the peaks can be viewed as random error in the time-series framework, leading to a description of the disease dynamics as a noisy periodic orbit whose period is 2 or 3 years. The multi-year periods observed in the data are roughly in accord with the period of damped oscillations in simple compartment-models for the diseases, and can be interpreted as modes repeatedly kicked into action by the error—noise (Anderson et al. 1984, May 1985).

But when Anderson et al. (1984) "conclude by stressing the regularity of long-term fluctuations in many childhood diseases", they are just reiterating the fact that the spectral densities are overwhelmingly concentrated in 1 or 2 frequencies. They report no consideration of alternate models to critically test their "noisy periodic orbit" description of the dynamics. It has been known for some time that chaotic systems can also have spectral densities with a few clear peaks (e.g., Bunow & Weiss 1979, Smith & Mead 1980), and nonzero spectral density outside the peaks that comes from chaotic (rather than random) aperiodic motion. Thus, spectral analysis by itself can fail to detect chaotic behavior.

To demonstrate the failings of the "noisy periodic orbit" interpretation, the

pro-chaos contingent (Schaffer et al. 1987, Kot et al. 1987) takes a Poincare-section through the reconstructed trajectories and computes the Poincare map. They do this also for a chaotic SEIR model, and for an SEIR model with a limit cycle with some white-noise perturbations. The chaotic model's map looks "noisy" because the attractor has dimension >2, so the section has dimension >1. Visual comparison suggests that the map estimated from the data looks like the map for the chaotic model, while the noisy-limit-cycle model has a "map" that's just mush (Figure 4).

This seems to eliminate one noisy-limit-cycle model, but there are many more. To my knowledge there has not been a critical examination of how easily reconstruction techniques can be fooled by stochasticity, aside from small white-noise-ish perturbations. If the stochastic factors have correlation times comparable to the intrinsic period of the system, or to the period of damped oscillations about a limit cycle, it would seem that the interactions could be complicated. Some spadework still remains to be done, before we can feel completely confident about taking results like Figures 2 and 4 at face value.

5. <u>Invariants</u> <u>in</u> <u>ecology?</u> Population-dynamics data are almost invariably so flawed (short, inaccurate, etc.) that more or less equally good fits to it can often be made by different investigators predisposed to different sorts of models. That (in unfair caricature) is the situation described in the last section, for chaotic vs. stochastic explanations of population fluctuations. "Goodness of fit" criteria can be used for model-choice in a parametric or nested-models framework, but they make less sense if completely different qualitative descriptions of the data are being compared. Each modeler can pay some more attention to details, and improve the fit.

Dynamical systems theory has identified some numerical quantities, called "invariants", which characterize qualitative aspects of dynamics (e.g., is it chaotic?). The most widely used invariants are various "dimensions", the "entropy", and the "Lyapunov exponents", all of which can be estimated directly from the reconstructed dynamics of the full system. Since reconstruction made the estimates possible, invariants have been very useful in characterizing the dynamics of physical and chemical experimental systems (Mayer-Kress 1986). If these quantities could be estimated from population abundance time-series, they might allow us to choose among alternate classes of descriptions for the dynamics. This point isn't original: it's the reason for the popularity of invariants in physics and chemistry, and the most recent work by Schaffer and colleagues on disease dynamics has involved serious efforts at estimating invariants.

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In the following sections, I will outline one possible approach to estimating the attractor dimension of an ecological time-series. For ecologists, I should first address two questions: what is a dimension, and why is it worth estimating?

Attractor dimensions are worth estimating because they can be used to distinguish among qualitativdly different classes of dynamic behavior. [In contrast, the embedding dimension M is chosen by the data analyst (within constraints), so it's not very informative]. If the system has a stable equilibrium, the attractor consists of a single point. For example, in the logistic equation $\frac{dx}{dt} = rx(1-(x/K))$, the attractor is the point x=K. In this case, the system is moving in one dimension, but the attractor is zero—dimensional. In a two-species predator/prey model with a limit cycle, the system is moving in the plane, which is two-dimensional, but its attractor is a curve. Locally (i.e., looking at it one small piece at a time) the attractor looks like a slightly bent line, so we can regard the attractor as being one-dimensional.

Thus, if we can establish that the attractor's dimension is not 0 or 1, we can conclude that the system is neither sitting at an equilibrium, nor following a periodic orbit.

To put these observations to use, our intuitive idea of dimension has to be generalized, so that the complicated attractors of chaotic systems will have well-defined dimensions (and so that a line still has dimension=1, a plane still has dimension=2, etc.) It happens that there are many sensible ways to define a "fractal" dimension that can handle most chaotic attractors, and the choice among them is mostly a matter of convenience. Experience to date suggests that estimation of the "correlation dimension" D_2 (defined below) requires less data than any of the known alternatives, so D_2 is the most practically useful and most commonly used dimension. (The notation D_2 comes from Renyi (1970), who introduced an infinite family of dimensions {D_q, $q \geq 0$}).

D_2 has the useful property that if the data are a series of independent continuous random variables (e.g., normally distributed) then D_2 equals the embedding dimension M. Thus, D_2 can in principle distinguish between deterministic and random fluctuations. If the estimated D_2 increases without bound as M is increased, then the fluctuations are random; if it doesn't, but $D_2 > 1$, then the dynamics are aperiodic but nonrandom. Integer attractor dimensions > 1 (e.g., an attractor that looks like the surface of a smooth donut) can be produced by linear systems with several periods whose ratio is irrational. But if D_2 is >1 and not an integer, then the dynamics (although not necessarily chaotic) could not be produced by any linear system.

For ecological applications, the problem is to estimate the dimension and other invariants from short, noisy data sets. A physicist can feel that a series of 500 values is very "short" (Abraham et al. 1986). An ecologist or economist (Brock 1986) usually has less data, with larger measurement errors and an uncontrolled, time-varying environment. Applied to such data, sometimes the physicists' methods work and sometimes they don't. When they do work, it may not be clear how the results should be interpreted; for example, would an estimated dimension of 1.25 suggest that you have a periodic orbit (since $1.25 \approx 1$), or that you don't (since $1.25 > 1$)? Unlike the physicist, we need reliable confidence intervals to go along with our estimates of invariants.

6. <u>Estimating</u> $\underline{D_2}$. To define D_2, let δ be the distance between 2 random points chosen independently from the invariant measure on the attractor (the invariant measure is the probability distribution that describes the relative amounts of time the system spends in different parts of the attractor). Let F be the cumulative distribution function of δ, i.e. $F(r) = P(\delta \leq r)$. If $F(r) \sim r^d$ as $r \downarrow 0$, then $D_2 = d$.

Grassberger & Procaccia (1983) proposed estimating D_2 from a time-series of observations $x_1, x_2,...x_N$ by computing

$$\hat{F}(r) = \frac{\#\{ \text{ pairs } x_i, x_j \text{ with } i \neq j, \ \| x_i - x_j \| \leq r \}}{N(N-1)}$$

(actually, assuming N would always be very large they used N^2 rather than $N(N-1)$ in the denominator). Plotting $\log \hat{F}(r)$ vs. $\log r$, D_2 is the slope at small values of r. This implicitly assumes that $\log \hat{F}(r) = a + D_2 \log r$ for $r \approx 0$, which is not always true, but experience so far suggests that the linear approximation is adequate in practice for experimental data analysis.

Eckmann and Ruelle (1985) note that this procedure is "not entirely justified mathematically, but nevertheless quite sound". However, they were summarizing physicists' experience with experimental data and with output from computer simulations. With small, noisy time-series there are problems. At "large" values of r, approaching the diameter of the attractor, the slope of $\log \hat{F}$ decreases to 0. At "small" values of r there are distortions due to noise (e.g., measurement error or roundoff error) and due to finite-sample effects (e.g., $\hat{F} = 0$ for $r <$ smallest interpoint distance in the time-series). The linear approximation for $\log \hat{F}$ therefore holds only on a finite "scaling region" $\gamma_0 \leq r \leq \gamma_1$. In practice, the scaling region shrinks and

eventually may vanish as the embedding dimension is increased, making it difficult to determine if the embedding dimension is large enough for successful reconstruction.

Error estimation is also a problem. The usual approach is to calculate $\log \hat{F}$ at several values in the scaling region, and do a standard linear regression. The slope of the regression line is the estimate of D_2, and the standard error of the slope is the reported error estimate. However, the basic linear regression assumption of independent, normally distributed errors isn't satisfied in this case, so the supposed "standard error of the slope" is invalid. As Caswell & Yorke (1986) note (regarding estimation of a different dimension), error estimates obtained by standard linear regression can be orders of magnitude smaller than the actual difference between the estimate and the true dimension. The "reference point" procedure suggested by Holfuss & Mayer-Kress (1986) also ignores the actual error structure of an empirical cumulative distribution function, and uses an inappropriate weighted-least-squares method.

The actual distribution of $\hat{F}$ could be used as the basis of valid error-estimation for the Grassberger-Procaccia procedure, and this approach is being investigated (Sayers 1987). Takens (1984) suggested using maximum likelihood rather than least-squares estimation, and gave confidence intervals for the case of $\gamma_0 = 0$ and a large number of observations. I have extended the method to allow $\gamma_0 > 0$ and a small number of observations, and it seems to work well if the scaling region is well-defined. Interpoint distances δ larger than γ_1 are discarded; for $\delta < \gamma_1$ define

$$\rho = \min \{ \ T, \ \ln(\gamma_1/\delta) \ \}, \quad \text{where} \quad T = \ln(\gamma_1/\gamma_0).$$

If $F(r) = a + D_2 \ln r$ for $\gamma_0 < r < \gamma_1$, then the distribution of ρ is easily shown to be a right-censored exponential, with smooth density $f(\rho) = D_2 \exp(-\rho D_2)$ on $0 < \rho < T$, and a point-mass at $\rho = T$ holding the probability from the truncated tail.

Parameter estimation for this distribution is a problem with a long history in reliability theory, since it corresponds to mean-lifetime estimation with a constant failure rate and fixed experiment duration T. Given values $\rho_1, \rho_2, \ldots, \rho_n$, the maximum likelihood estimator of D_2 is

$$\hat{D} = R / \sum_{i=1}^{n} \rho_i, \quad \text{where} \quad R = \#\{ \ \rho_i < T\}. \tag{1}$$

(Deemer & Votaw 1955). Approximate confidence intervals can be set by the "percentile" method, using the asymptotic normality of the relative error as the

sample size increases, and the asymptotic relative error variance (Deemer & Votaw 1955). The approximate $100(1-\alpha)\%$ confidence interval is

$$\hat{D} \; \pm \; Z_{\alpha/2}\hat{D}/\sqrt{n \; (1-(\gamma_0/\gamma_1)^{\hat{D}})} \qquad (2)$$

where Z_α is the probability-α critical value of the standard normal distribution.

To leading order (2) is the same as the asymptotic confidence intervals suggested in the literature (Bartlett 1953; Deemer & Votaw 1955; Bartholomew 1963). It is the simplest (too simple to have been published?) since it doesn't require iterative solution of nonlinear equations, and it was also the most accurate in Monte Carlo simulations with $20-100$ distances and $.5 \leq D_2 \leq 3$. Barlow et al. (1968) give an implicit formula for exact confidence intervals, but for >35 values the approximate intervals were much more accurate than numerical evaluation of the "exact" intervals (in double-precision IMSL). While (2) is only exact as $n \rightarrow \infty$, it is acceptably accurate for $n \geq 50$: in Monte Carlo simulations with pseudorandom values having right-censored exponential distributions, nominal 95% confidence intervals had coverage frequencies .945 to .952 (2-sided) and .938 to .969 (1-sided), with standard errors $\leq$ .005. For the procedure described below, this means that there must be 100 or more values in the time-series.

7. <u>Does</u> <u>it</u> <u>work?</u> In the intended application, the data consists of points $x_1, x_2, \ldots, x_N$. The apparent scaling region was identified by calculating local slopes at 100-125 values of r (evenly spaced on the logarithmic scale) using linear regression of $\ln \hat{F}$ on $\ln r$ through 5 adjacent values of r. Since the x's are presumably measured with some error, there are at most $N/2$ independent distances (i.e., $N/2$ independent draws of a ρ) that can be obtained. Therefore $n = N/2$ was used in equation (1), by choosing at random n interpoint distances $\leq \gamma_1$. To reduce the effects of sampling variablitity on the calculated $\hat{D}$, this procedure was repeated m times ($m = 10$ to 25) and the average $\hat{D}$ was used. Having done that it is tempting to divide the confidence interval width by $\sqrt{m}$, but that doesn't work because the replicates of $\hat{D}$ are not independent. For now, I set conservative confidence intervals by using $n = N/2$ in equation (2).

Table 1 summarizes the results on two time-honored test cases: the "critical" logistic map at the onset of chaos, and the Henon map. The estimates of D_2 are fairly good and the confidence intervals are generally conservative, as expected. However these are easy targets: there is no noise aside from roundoff error, the

Table 1. Estimation of D_2 for time-series produced by chaotic dynamical systems: the Henon map with a=1.4, b=0.3, and the "critical" logistic map with r=3.5699456. N = length of the time-series. In all cases n=N/2 was used in equation (2) to compute nominal 95% confidence intervals. Values were obtained by 2000 Monte-Carlo simulations with randomly chosen initial conditions and 250 iterations prior to generating the time-series used in estimating the dimension. ( )= standard error of estimate. "Power" is the frequency of 2-sided confidence intervals that contained no integer values.

	Henon N=500	Henon N=100	Logistic N=500	Logistic N=100
Coverage frequency				
2-sided	1.0 (0)	.998 (.001)	.997 (.001)	.998 (.001)
lower	1.0 (0)	1.0 (0)	.964 (.004)	.918 (.006)
upper	.999 (.001)	.997 (.001)	1.0 (0)	1.0 (0)
Relative error in $\hat{D}_2$				
mean	.001 (.001)	.03 (.003)	.085 (.002)	.224 (.001)
standard deviation	.03	.081	.026	.058
Power	.984 (.003)	.044 (.005)	1.0 (0)	1.0 (0)

Table 2. Estimates of D_2 for disease incidence. N=length of the time-series. Values in parentheses are the 95% confidence interval from equation (2) with n=N/2.

Embedding Dimension	SEIR model N=2400	Baltimore measles 1928-1963, N=432	Milwaukee Chickenpox 1926-1965, N=480
3	2.16 (2.09, 2.24)	2.17 (1.98, 2.36)	3.55 (3.19, 3.92)
4	2.24 (2.15, 2.32)	2.50 (2.27, 2.72)	4.03 (3.60, 4.47)
5	2.23 (2.13, 2.35)	2.38 (2.15, 2.61)	4.50 (3.98, 5.02)
6	2.23 (2.12, 2.34)	2.57 (2.32, 2.82)	4.31 (3.83, 4.78)

minimal embedding dimension is known, and the scaling regions in $\hat{F}$ are fairly unambiguous (Figure 5; the wiggles in the logistic $\hat{F}$ are real, an example in which the linear approximation is not exact).

A less tame and more realistic test-case was provided by W.M. Schaffer, 2400 monthly values of the number of infectives from a chaotic SEIR model (Figure 6). Because the model output (like the measles data) has such spiky seasonal variability, the best results are obtained by treating each month separately and looking at 12 Poincare sections through the attractor (Schaffer et al. 1987). For each embedding dimension the 12 monthly time-series were rescaled either to have mean value $=1$ or to have maximum interpoint distance $=1$ (whichever gave the more well-defined scaling region). The intramonth distances were computed and then combined into a single distance distribution from which $\hat{F}$, $\hat{D}$, etc. were computed. The dimension of the full attractor is obtained by adding 1 to the section dimension. This procedure is valid in theory: the true dimensions of the attractor sections are identical (since they are diffeomorphic images of each other), are 1 less than the attractor dimension, and are not affected by a linear rescaling. This method gives a reasonably good scaling region (Figure 6) and consistent results as the embedding dimension is increased (Table 2); the confidence interval width increases in higher embedding dimensions because (γ_0/γ_1) increases. The bound $D_2 \leq D_1 = 2.39$ is consistent with the Table 2 results, and confirms that the qualitative nature of the attractor has been identified correctly (i.e., fractal with $2 < D < 3$; D_1 was computed by the Kaplan—Yorke formula from the Lyapunov exponents for the model, W.M. Schaffer, *pers. comm.*).

The same procedure was applied to measles incidence in Baltimore, 1928-1963, and to chickenpox in Milwaukee, 1926-1965 (Table 2; data provided by W.M. Schaffer). Identifying the scaling region is rather subjective for these data-sets, so that the values obtained are certainly not definitive. Nonetheless, they seem to be informative. Firstly, there is an appreciable difference between the values for measles and chickenpox. For measles the estimates indicate an attractor with $2 < D_2 < 3$. The chickenpox data suggest an higher-dimensional attractor, or else stronger effects of noise. For a periodic orbit with white-noise perturbations in embedding dimension M, we should theoretically get an apparent dimension of 1, or M, or both 1 and M in two different scaling regions (Ben-Mizrachi et al. 1984, Brock 1986). In practice with white-noise data, the dimension-estimates may continue to increase as the embedding dimension increases, but with the estimated $D_2 < M$ (Holzfuss and Mayer-Kress 1986). In any event, the dimension calculations clearly

suggest that the measles and chickenpox dynamics are in fact qualitatively different.

8. <u>Conclusions</u> It should be apparent that much work remains to be done on error-estimation for D_2. The results are good for perfectly accurate data and a clean scaling region, even with realistically short time-series for ecological applications. However real-world data require *ad hoc* pre-treatments to extract a scaling region, with ill-defined limits and some legitimate doubt still as to whether it's real or imaginary. A good deal of subjective choice on these matters preceded the calculations on disease incidences. This problem is not unique to D_2. For example, in the more familiar application of fractal dimensions to spatial data (e.g., the dimension of a coastline or leaf surface) the fractal structure is absent at lengths larger than the region being studied, and at molecular length-scales. I am working on an apparently better method for choosing the scaling region, which uses small windows from the order-statistics of the interpoint distances (rather than $\hat{F}$) as the basis for ML estimation of the "local slope". But for now, the best I can say for highly "spiky" data is that the estimates are fairly robust ($\pm 10 - 20\%$) over several different sensible ways of combining the 12 monthly data-sets (e.g., cf. Table 2 with the estimates of Schaffer et al. 1987).

For comparing models with data, or comparing different populations, all of $\hat{F}$ may be relevant, not just the apparent scaling regions. Significant differences in the $\hat{F}$'s could indicate qualitative differences in the dynamics, even if it isn't feasible to estimate the invariants accurately. Econometricians have recently tested for model-misspecification in traditional time-series models (e.g. AR or ARMA models), using methods based on Brock's (1986) "Residual Test Theorem": if a finite-order autoregressive model

$$x_t = \sum_{j=1}^{m} a_j x_{t-j} + \epsilon_t$$

is fit to the data, the residuals $\{\epsilon_t\}$ will generically have the same invariants as the original time-series $\{x_t\}$. After fitting a model, the residuals are tested for departures from white noise, by comparing the $\hat{F}$'s of (a) the residuals, (b) random reshufflings of the residuals, and (c) pseudorandom Gaussian sequences with the same mean, variance, and length. While an adequate statistical theory for these methods has not yet been developed, the numerical results can give striking evidence for inadequacy of an autoregressive model (Sayers 1986).

At present, it seems that dimensions can be estimated from quite <u>short</u> data-

sets, but that dealing with noisy data remains problematic. Research is currently quite active on how one can best extract a chaotic "signal" from "noisy" interference (Abraham et al. 1986; Albano et al. 1986, 1987, *pers. comm.*; Broomhead & King 1986). That work essentially stops at the point where γ_0 and γ_1 have been estimated (and uses the standard point-estimate of D_2), so it is complementary to research on error-estimation methods. Dimension estimation consequently poses some well-defined open statistical problems, whose solutions would be of immediate interest to biologists, economists, and even some physicists whose experimental systems can't be kept stationary for long (Albano et al 1986).

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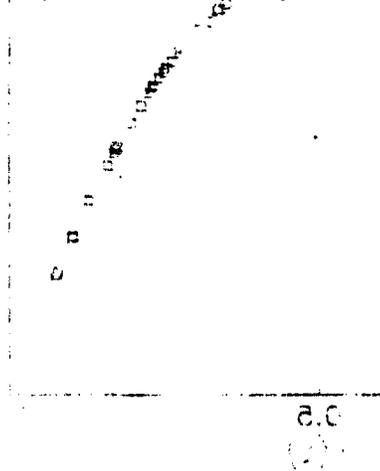
Figure 1. (a) The chaotic time-series x_t produced by the logistic difference equation with $r=3.7$, $x_0=0.5$. (b) The time-series is seen to be deterministic, by plotting the values as ordered pairs (x_t, x_{t+1}).
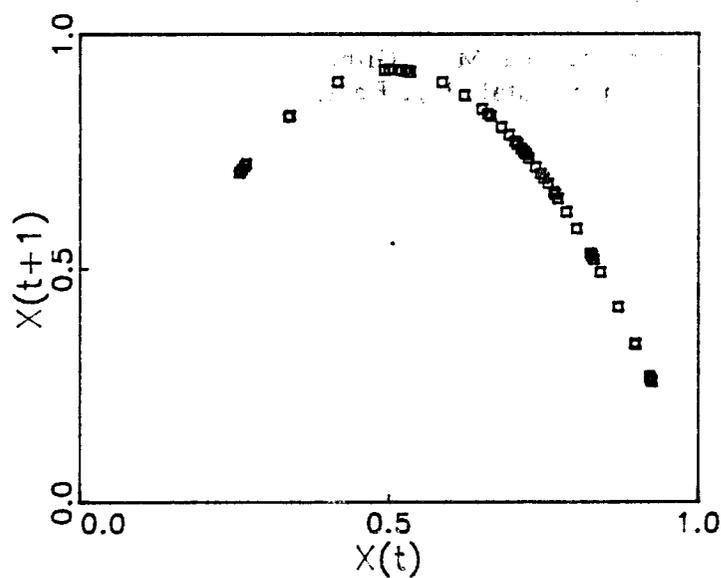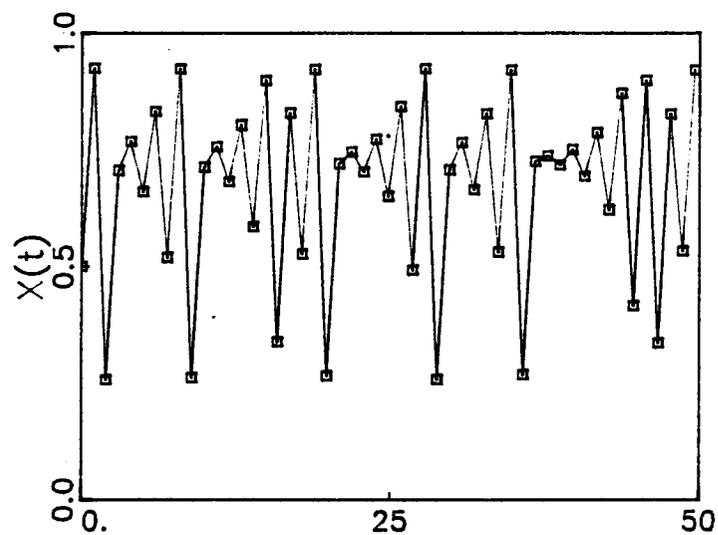
Figure 2. Examples of population fluctuations reconstructed in time-delay coordinates by Schaffer & Kot. (a) the lynx cycle in Canada; (b) outbreaks of the insect *Thrips imaginis*; (c) a microtine rodent cycle (d) measles incidence in Baltimore, 1900-1927; (e) an SEIR model with chaotic dynamics due to seasonal variation in the transmission rate; note the similarity to (d). Reproduced from Schaffer & Kot (1986).
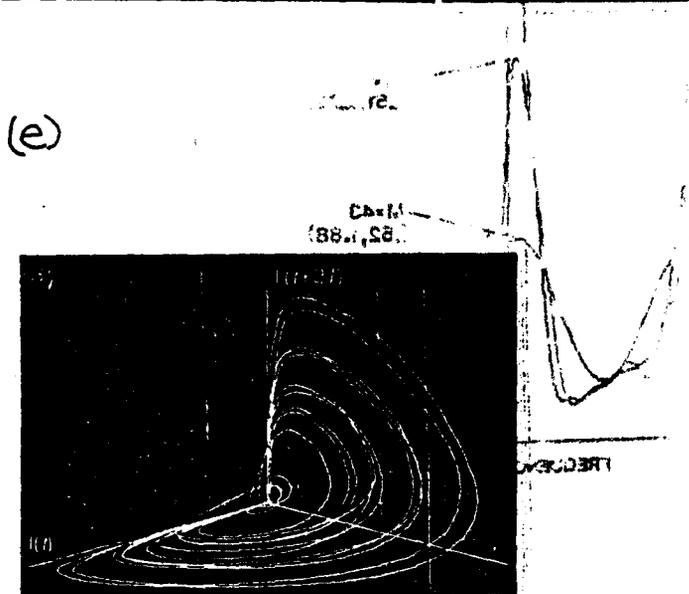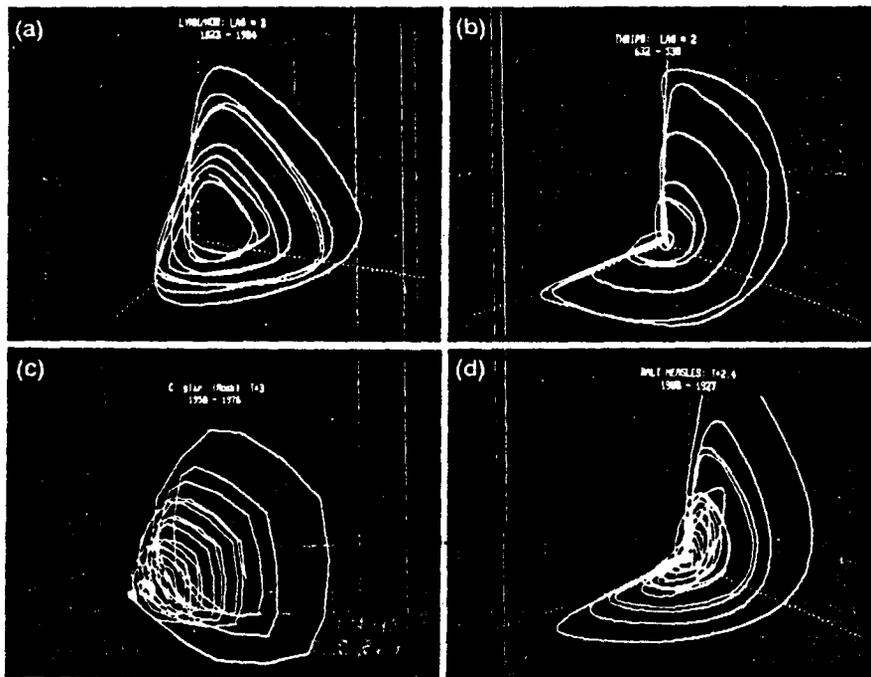
Figure 3. Conventional time-series analysis of measles-incidence in Baltimore 1928-1963. Reproduced from Kot et al. (1987).
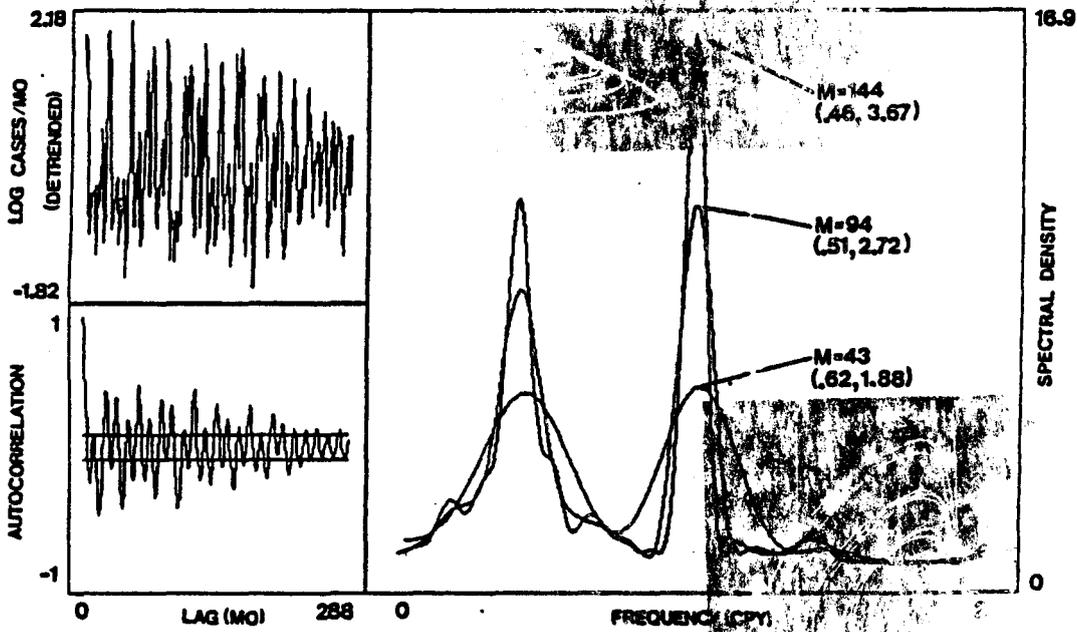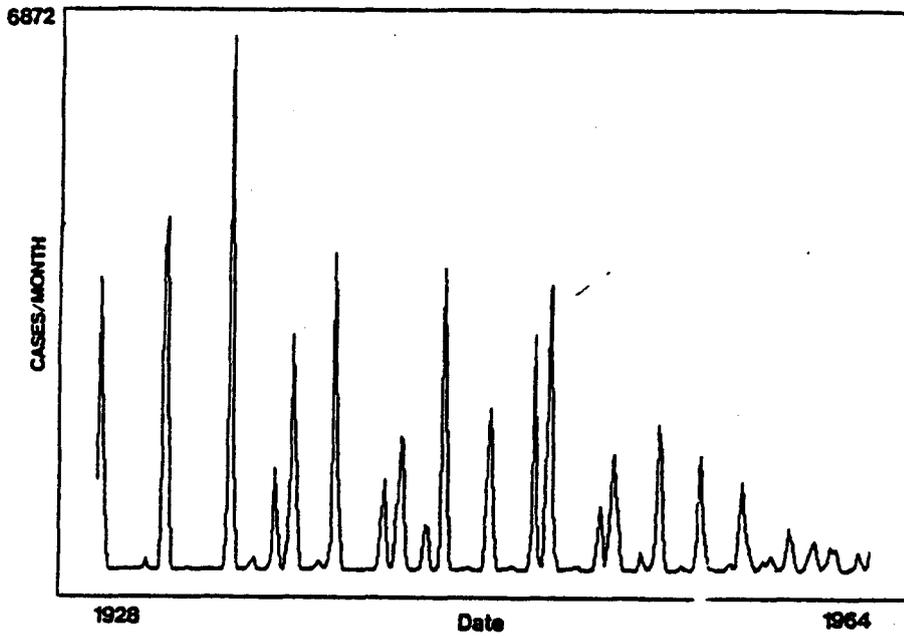
Figure 4. Poincare "maps". Clockwise from top left (a) chaotic SEIR model for measles; (b) SEIR model with a limit cycle, and small white-noise perturbations; (c) measles incidence in Baltimore 1928-1963. Reproduced from Kot et al. (1987).
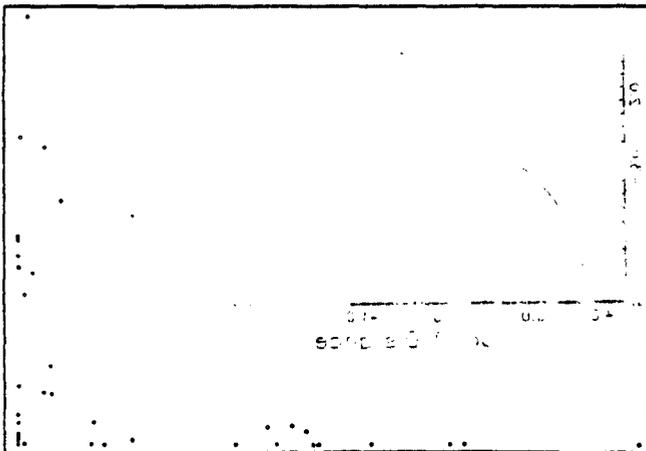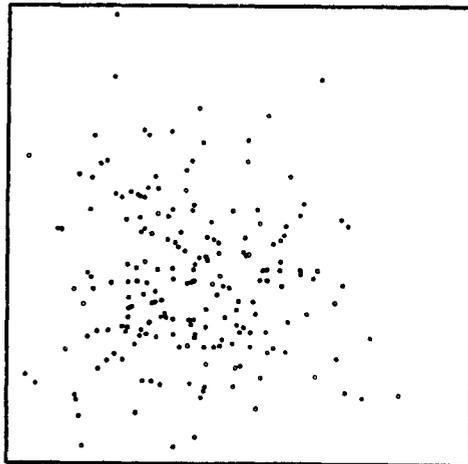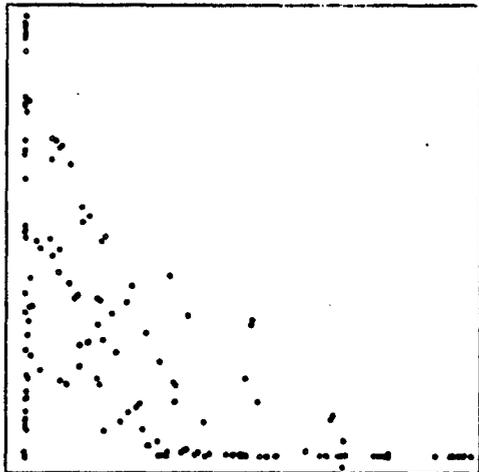
Figure 5. Grassberger-Procaccia plots (log F vs. log r), N=length of
the time-series. Clockwise from upper left: (a) the Henon map with
a=1.4, b=0.3, N=100; (b) the logistic map with r=3.5699456, N=500;
(c) a chaotic SEIR model, N=2400; (d) measles incidence in Baltimore,
1928-1963, N=432; the solid line shows the "scaling region" used for
the dimension estimate. The embedding dimensions for reconstruction
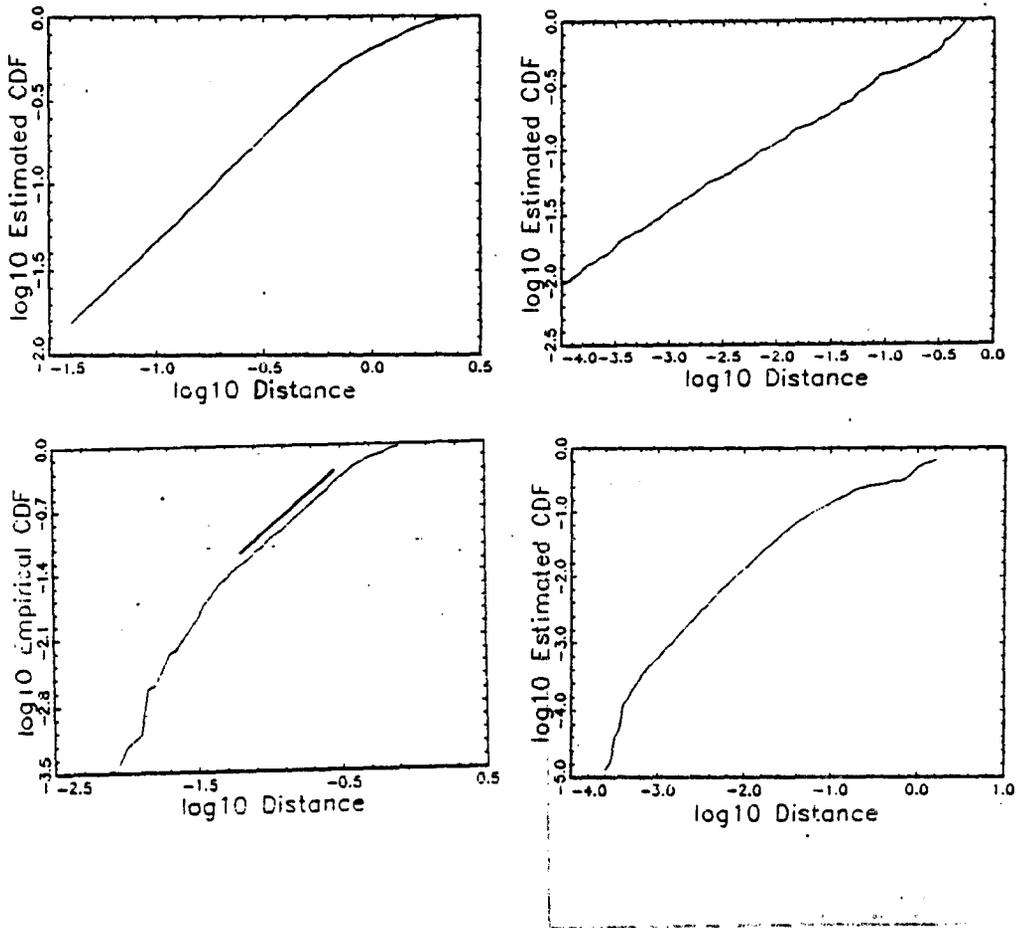were 2, 1, 4, and 4 respectively.

Figure 6. Log number of infectives vs. time (in units of 10 years) for the chaotic SEIR model of Figure 5(c) and Table 2.