Complex Dynamics in Multispecies Communities [and Discussion]

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Complex dynamics in multispecies communities

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SUMMARY

Communities of living organisms have potentially very complex population dynamics. Two components of complexity are considered, the dimensionality of the attractor underlying the persistent dynamics, and the presence of chaos. The dimensionality of real biological communities is unknown while there is great controversy about the presence of chaos in population dynamics. The evidence for chaos, and changes in the popularity of chaos among empirical biologists, is reviewed. Two new techniques developed in the physical sciences, attractor reconstruction and the estimation of the correlation dimension, are described and examples of their use in biology discussed. Although these techniques offer exciting new prospects for investigating community dynamics, there are some major problems in using them in biology. These problems include the length of biological time series, the ubiquity of noise, transient behaviour, Darwinian evolution and problems in interpretation. These problems are discussed and it is concluded that the best prospects of applying these techniques are using data collected in laboratory microcosms.

INTRODUCTION

Biological communities are normally composed of large numbers of interacting species of plants, animals and microorganisms. One consequence of the size of natural communities, and also of the fact that biological systems are subject to time-lags and have spatial extent, is that the dynamics of biological communities are potentially exceedingly complicated. The question of the actual complexity of the dynamics of natural communities is one of the major problems of contemporary population ecology.

It is important to state immediately what is meant by complexity because the word has many different interpretations in the study of large systems. We discuss here two elements of complexity. The persistent behaviour of a system can be described by the properties of the attractor underlying the dynamics. The attractor can be visualized as a geometrical object in a space of appropriate dimensionality determined by the dimensionality of the attractor itself. We take as one element of the complexity of community dynamics the number of dimensions necessary to describe the community attractor. This measure is related to the number of separate equations that are required to describe the persistent behaviour of the system: low dimensionality implies few equations. (Note, however, these equations are not normally the same as the biological equations underpinning the dynamics of individual species.) If the dynamics of the community are chaotic, then the attractor has fractal geometry and, normally, non-integer dimension. We take as our second element of complexity the presence of chaos in the dynamics of a community. The two elements of complexity are potentially orthogonal: chaos may be described by either high- or low-dimensional attractors.

Any answer to the question of community complexity will depend on the scale of investigation. Consider a resource-consumer system where the resource renews itself on a very short timescale compared to that of the dynamics of the consumer. A coarse exploration of the dynamics of the system might just consider the consumer, assuming that the resource instantaneously reaches the equilibrium appropriate to current consumer density. A more detailed exploration of the dynamics might reveal dynamic behaviour caused by short lags in the response of the resource to changes in community abundance. Thus questions of community complexity are inextricably linked to both the scale of investigation and also to problems of model abstraction: the size of the subset of species in the community that need explicit consideration when describing the dynamics of a particular target species.

Throughout the late 1960s and 1970s, the dominant research programme on the dynamics of communities was based on the assumption that all members of the community fluctuated about stable equilibrium population densities. The behaviour of the system in the neighbourhood of the equilibrium could then be studied by linearization about the equilibrium value. The community was characterized by the community matrix, the elements of which, a_{ij}, described the marginal influence of change in the abundance of species i on species j at equilibrium; the matrix included intraspecific density-dependence $(i=j)$ (Levins 1968). Study of linearized community models failed to support the commonly held notion that complex biological systems would automatically be more stable (May 1973) and initiated a continuing debate about whether an association between stability and complexity might be found in biologically realistic community matrices. Studies on the community matrix also examined the question of model abstraction (MacArthur 1972; Levine 1976; Lawlor 1979; Schaffer 1981).

The community matrix approach assumes both that communities have stable equilibria and that the communities exist sufficiently close to the equilibrium that their dynamics may be encapsulated by linearization. It has been known since the work of the founders of population ecology that biological populations are capable of persistent cyclic dynamics and there is little disagreement among empirical biologists that at least some species are cyclic. The discovery that natural populations are potentially chaotic is much more recent, and the question of the existence of chaos in nature far from settled.

In the first section we review the evidence for chaos as an empirical phenomenon in population biology. We then describe a number of new techniques from applied mathematics and the physical sciences that potentially allow the resolution of the problem of the complexity of natural systems. We describe their application to biological data and particular problems that arise in using these techniques in biology.

CHAOS IN ECOLOGICAL SYSTEMS

Chaos was not discovered by mathematicians but by scientists such as meteorologists and biologists working in other disciplines (Gleick 1988). In biology, chaos was discovered through the study of single species population models in discrete generations with self regulation. As the nonlinearities in the self-regulation term increase, the dynamic behaviour of the population changes from a monotonic approach to a stable equilibrium, to an oscillatory approach to equilibrium and then to stable limit cycles which undergo period doubling until chaos ensues. Embedded within the chaotic region of parameter space are small regions where low frequency limit cycles may be observed though these, again through period doubling, merge back into chaos as the strength of the self-regulation is increased (May 1974, 1976; May & Oster 1976). Chaos was also observed in time-lagged, differential equation models of populations (May 1980) and in systems of ordinary differential equation models, though at least three species are required before chaos can be observed (Gilpin 1979).

The possibility that biological populations have chaotic dynamics prompted investigation to see whether the nonlinearities in the dynamics of real populations were sufficient to cause chaos. In what became a very influential paper, Hassell *et al.* (1976) estimated the parameters of a simple single-species, discrete-generation model capable of showing chaos, by using 28 sets of insect population data. The dynamics of the model was characterized by two parameters, one representing fecundity and the second representing the degree of nonlinearity in density dependence. As the nonlinearity increased, the dynamics of the model followed the familiar course of monotonic and oscillatory approaches to equilibrium, limit cycles and chaos. With two exceptions, all the data sets fell within the regions of stable equilibria. The two exceptions were the well-known outbreak pest, the Colorado Beetle (*Leptinotarsus quadrilineata*), which fell in the region of persistent cycles, and Nicholson's laboratory experiments with blowflies which fell within the region of chaos. We shall discuss Nicholson's experiments in more detail below.

In recent years, this study has attracted much criticism as being over simplistic. These criticisms are often unfair as the authors were scrupulous in cataloguing a long list of simplifications and assumptions inherent in their analysis. Perhaps the most important of these simplifications is the assumption that the dynamics of a species embedded in a complex community can be abstracted by fitting the population data to a simple single-species model. The problems of this approach were clearly pointed out by Hassell *et al.* (1976) who noted that their procedure suggested that the Larch Budworm (*Zeiraphera diniana*) should have stable population dynamics whereas there is good evidence that it shows approximately eight-year cycles driven by interactions with its foodplant or a natural enemy (Baltensweiler 1968).

A number of workers looked for evidence of chaos in laboratory systems, again by fitting data to simple population models. In particular, two studies on *Drosophila* (Thomas *et al.* 1980; Mueller & Ayala 1981) failed to find any evidence for chaos. The studies on *Drosophila* prompted speculation that natural selection might be responsible for the absence of chaotic dynamics in nature. Thomas *et al.* suggested that alleles that led to non-chaotic population dynamics might be favoured through group selection. In contrast, Mueller & Ayala showed that, at least under certain circumstances, a population showing non-equilibrium population dynamics could be invaded by alleles that, when common, promoted stable population dynamics.

By the early 1980s, a consensus had arisen among experimental population biologists that chaos was unlikely to be significant in natural populations. The twin planks of this consensus were the failure to predict chaotic dynamics by using models with parameters estimated from real data, and the conjecture that natural selection would promote non-chaotic dynamics. However, we believe a sea-change occurred around the middle of the decade and that in the past five years there has been renewed interest in chaos among empirical ecologists. There are perhaps two reasons for this shift in opinion.

First, the view that chaos only occurs in the presence of biologically unrealistic nonlinearities has been challenged by a series of population models in which chaos occurs with parameters well within the bounds of biological realism. For example, Bellows & Hassell (1988) predicted chaos by using a detailed age-structured host–parasitoid model which they parameterized by using experimental data. Prout & McChesney (1985) found that *Drosophila* females developing in crowded cultures had reduced fecundity as adults. This delayed density-dependence, which can lead to chaotic dynamics, had not been appreciated by earlier workers attempting to assess the likelihood of chaos in laboratory fruitfly systems. These, and similar results, indicated that chaos might become more likely as the number of interacting species, and the complexity of the interaction, increased.

The second factor that has revitalized interest in chaos comes not from biology but from applied mathematics and the physical sciences. A series of new techniques have been developed that allow the analysis of time series data to estimate properties of the attractors underlying dynamic systems. In the next section we review two methods, attractor reconstruction and the estimation of correlation dimensions. The responsibility for bringing these techniques to the attention of biologists, and for pioneering their use on biological data, is largely due to the tireless advocacy of Schaffer and his colleagues (see, for example, Schaffer 1984, 1985; Schaffer & Kot 1985, 1986). We omit discussion of one very new technique, nonlinear forecasting (Sugihara & May 1990*a*), as this is the subject of the next chapter (Sugihara & Grenfell, this symposium).

ANALYSIS OF TIME SERIES

(*a*) *Reconstructing attractors*

Consider data collected on the population densities of a predator and its prey with overlapping generations. The raw data might consist of two parallel time series. It is often more informative to plot the numbers of prey at any particular time against the number of predators at the same time, the resulting plot being known as a phase plot drawn in phase space. Suppose that the interaction between the predator and its prey results in stable equilibria for both species. The phase plot now shows the populations being attracted towards a point in phase space that represents the stable equilibria. If the results from a deterministic model of the interaction was plotted in phase space, the trajectory would approach the single equilibrium and remain there for ever. For real data, the trajectory would be continually displaced from the equilibrium point by stochastic events and the phase plot would resemble a ball of wool centred on the equilibrium value.

The point equilibrium in the above example is an example of a dynamic attractor, in this case a point attractor with zero dimension. Trajectories originating in an area of phase space called the basin of the attractor will flow towards the attractor and, in the absence of perturbation, never leave it. Now suppose that instead of a stable equilibrium, the predator–prey system settles into some regular cycle. When plotted in phase space, the trajectory will, after the transients have died out, converge onto some roughly oval orbit. The equilibrium dynamics is now determined by a periodic attractor, a one-dimensional object plotted in a two dimensional space. More complex periodic cycles can arise by 'period-doublings', leading to figure-of-eights and further twisted structures in phase space.

The above attractors are the standard features of Newtonian dynamics. Chaos is normally produced by objects known as strange attractors. For overlapping generations (ordinary differential equations), a chaotic attractor can only exist in a three-dimensional phase space. So, instead of a simple predator–prey interaction, consider a three-trophic level interaction.† The dynamics of the system may still be described by a classical attractor, either a point attractor for a stable equilibrium, a periodic attractor or even a two-dimensional attractor. However, chaotic behaviour on a strange attractor is now a possibility.

Figure 1 shows a strange attractor in three-dimensional phase space. After any transients have decayed, and again ignoring any stochastic perturbation, all population trajectories originating in the basin of attraction will come to lie on the surface of the attractor. To see why the attractor earns the name strange, consider a cloud of points lying close together on the attractor (see also Schaffer (1984) for a similar explanation). Now follow the fate of the points as they move around the surface of the attractor. This process is exactly analogous to trying to predict the future population densities of several populations that at the present moment have roughly similar population levels. As the cloud of points moves around the surface of the attractor, the cloud is first stretched on the surface of the attractor and then folded over on to itself, a process that happens once for every circuit of the orbit. This continual stretching and folding means that trajectories that started off in close proximity soon become separated. More technically, nearby points become homogenized on the surface of the attractor. The practical consequence of this homogenization is that populations that initially have similar population densities quickly diverge in densities. One of the hallmarks of chaos is extreme sensitivity to initial conditions; present population densities can only be used to predict future densities in the very short term. The pattern of the decay of predictive power with time is further discussed by Sugihara & Grenfell (this symposium).

The attractor in figure 1 appears to be a twisted diaphanous sheet suggesting a two-dimensional structure. However, the apparent two-dimensionality conceals greater complexity. Each time the sheet is folded back on itself, the two halves do not merge but retain their structure such that the sheet consists of an infinite number of separate layers: the ultimate *millefeuille*. The object is in fact a fractal: if a cross section of the flow is taken and examined under increasing magnification, greater and greater detail will be revealed and, in addition, the details will be self repeating. More specifically, the object is a type of Cantor Set, a set of disconnected points that poses problems for traditional

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† The restriction of chaotic attractors in continuous systems to representation in three or more dimensions only partially precludes chaotic dynamics in two-species or even one-species systems. A two-species interaction will always have a zero or one dimensional attractor (and a one-species interaction a zero-dimensional attractor) unless extra degrees of freedom are supplied by the incorporation of a time lag or a spatial component into the interaction. More technically, the dimensionality of the system is equivalent to the number of ordinary differential equations (ODEs) necessary for its specification. A predator–prey interaction described by two differential equations can only display stable or periodic dynamics. However, a time-lagged differential equation, or a partial differential equation (incorporating spatial coordinates) both potentially require an infinite number ODEs for their specification. In practice, the attractors underlying many time-lagged and partial differential equations can be described in low-dimensional phase space.

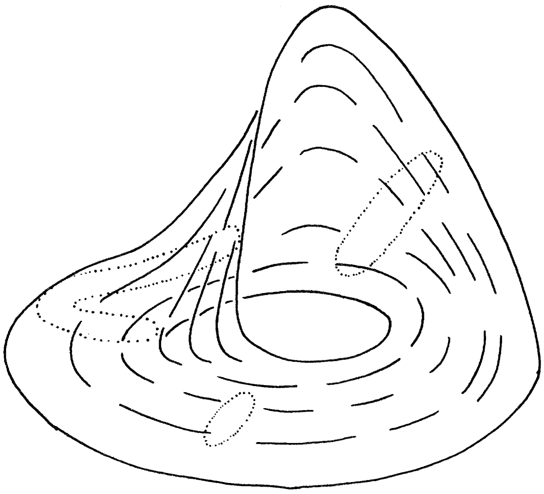

Figure 1. Schematic diagram of a strange attractor (the Rössler attractor). The dotted circle represents a collection of nearby trajectories, which as they orbit the attractor, are initially stretched and then folded over on themselves. As a result, nearby trajectories diverge and prediction is not possible far into the future.

concepts of dimensionality (see Sugihara & May (1990*b*) for a recent discussion of dimensionality and measure theory in biology). Such objects have fractional dimension; for example the object in figure 1 has a dimension of between one and two. It looks like a twisted sheet because it is nearly two-dimensional while the additional complexity of the fractal structure is represented by the fractional part of the dimensionality.

The rate of divergence of nearby trajectories on an attractor is best measured using Lyapunov exponents. Positive Lyapunov exponents indicate divergence in some direction and negative exponents convergence; a strange attractor must have at least one positive Lyapunov exponent. For an essentially two-dimensional attractor such as figure 1, Lyapunov exponents are calculated, as an average over the attractor, (1) in the direction of the flow, (2) perpendicular to the flow in the plane of the attractor and (3) perpendicular to both the flow and the plane of the attractor. In the direction of flow, nearby points are part of the same trajectory and so neither diverge or converge: the Lyapunov exponent is zero. Nearby trajectories in the plane of the attractor diverge (due to stretching and folding) and are associated with positive Lyapunov exponents while those perpendicular to the plane of the attractor, and which are pulled down onto the surface of the attractor, converge and are associated with a negative Lyapunov exponent. A strange attractor that exists in three-dimensional space must have one positive and one negative Lyapunov exponent. Higher dimensional strange attractors may have different combinations of positive and negative Lyapunov exponents and this provides a partial taxonomy of the attractors.

The characteristic shape of strange attractors suggests a way of identifying chaos in time series. Plot the time series in phase space and then examine the flow on the attractor to look for stretching and folding. However, to construct the phase plot one needs to know the population densities for each species in the system. A biologist typically does not have this data and frequently does not even know the number of species for which data is required. A solution to this problem was provided by Packard *et al.* (1980) and Takens (1981) who proved that the properties of the attractor governing the system can be obtained from a single time series by plotting trajectories in a phase space constructed from lagged coordinates. For example, a three-dimensional plot might be obtained by giving each point $s(t)$ in the series the coordinates (x, y, z), where $x = s(t)$, $y = s(t-\tau)$ and $z = s(t-2\tau)$ where τ is a suitably chosen time lag.

An immediate question is the number of dimensions that are necessary in order to draw the attractor. Takens (1981) and Packard *et al.* (1980) proved that for a system of m equations, a sufficient number of dimensions is $2m+1$. This provides rather cold comfort, especially for high m. However, examination of physical systems suggests that the dynamics of at least some complex systems are governed by low dimensional attractors. For example, a famous non-equilibrium chemical reaction, the Belousov–Zhabotinskii reaction, involving possibly over 25 chemical compounds, has been shown to be described by an attractor with a dimension near two (Roux *et al.* 1983). If complex systems of interacting species also have low-dimensional attractors, and if sufficient data is at hand, plotting time series in lagged coordinate space should reveal the shape of the attractor.

Supposing the structure of the attractor has been convincingly recreated in phase space, further analysis is possible by associating the dynamics on the attractor with a one-dimensional return map. Return maps are most familiar in biology as a means of analysing populations with discrete generations. The size of the population in generation $t+1$ is plotted against the size of the population in generation t, the resulting line is often called a Moran curve or Ricker curve. Return maps are also useful for visualizing the onset of chaos in populations with discrete generations (May & Oster 1976). Return maps can be generated from smooth flows by sectioning the attractor in a plane perpendicular to the flow (in general, the intersection of a multidimensional flow with a lower dimensional object perpendicular to the flow is known as a Poincaré section). In the case of a nearly two dimensional object such as the attractor in figure 1, the Poincaré section is taken using a plane and the intersection of the plane with the attractor is a set of points that almost form a line (figure 2). The next stage is actually to fit a line to the series of points and to measure the distance of each point along the line. Each time the population completes a whole circuit of the attractor, it will intersect the Poincaré section once. Thus each point on the line is associated with a position in the time series. A return map is constructed by plotting the position of each point along the line against the point that preceded it.

An examination of the one-dimensional return map can reveal much about the behaviour of the whole attractor. For example, suppose the return map is

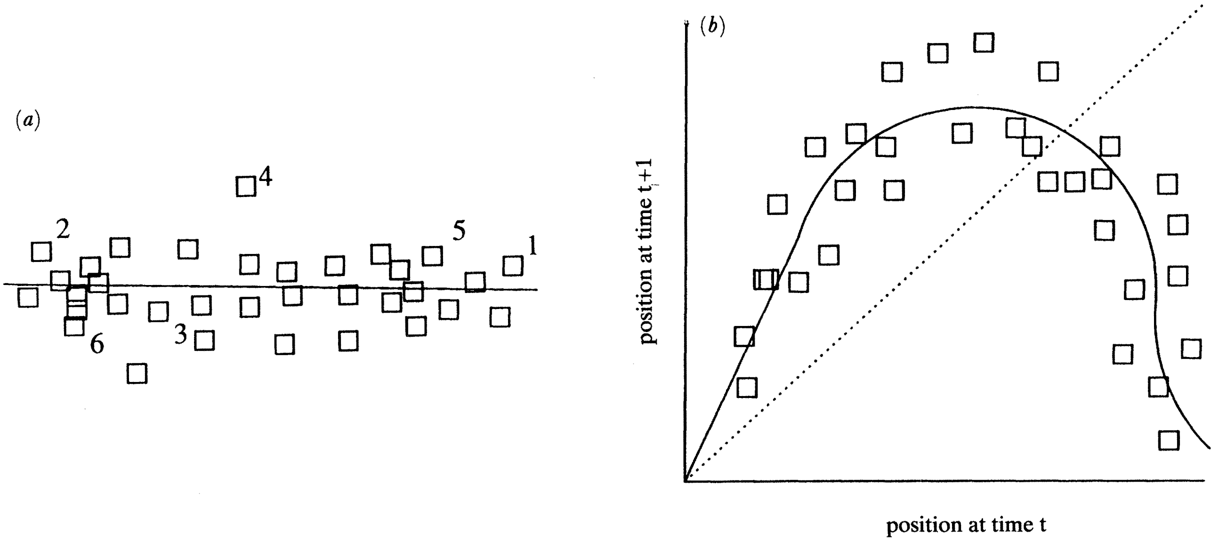

Figure 2. The intersection of a strange attractor, such as that in figure 1, and a plane perpendicular to the flow is a Poincaré section. As explained in the text, the Poincaré section is approximately a straight line (*a*). Successive intersections of the orbit with the section (numbered) can be used to construct a one-dimensional return map (*b*).

unimodal, an examination of the shape of the curve will show whether the population will behave chaotically and also reveal the way chaos arises through a series of bifurcations leading to period doubling. Note, an examination of a Ricker curve reveals exactly the same thing for a single-species population in discrete generations. In addition, the map can be used to estimate Lyapunov exponents.

Finally, we point out that chaotic attractors arise in a number of ways apart from through period doubling (Schaffer *et al.* 1988). If interacting populations are affected by some external cyclic influence, for example daily or annual environmental influences, the attractor may appear like the surface of a hollow doughnut or torus. Here, instead of stretching or folding, clouds of nearby points are stretched and then overlain on each other as they move around the torus. If the attractor is drawn in phase space (as above) and then a Poincaré section taken, the intersection is a circle rather than a line, a circular map rather than a one-dimensional map is then studied. Various complications arise in the presence of environmental forcing. For example, the dynamics may become phase-locked: exhibiting fluctuations of the same frequency as the environmental fluctuations, or of a harmonic of that frequency.

(*b*) *Estimating dimensions*

Ideally, one would like to be able to measure the number and magnitude of Lyapunov exponents directly from the data. This would provide information both on the dimensionality of the attractor and also on the presence of chaos. In practice, estimating Lyapunov exponents is computationally difficult and demanding of data, especially when the number of Lyapunov exponents is unknown. An alternative to the calculation of Lyapunov exponents is the estimation of entropy measures which provide some of the same information.

Consider an arbitrarily small box in the phase space containing an attractor. In two dimensions, the box is a square; in three dimensions a cube and in higher dimensions a hypercube. An entropy or information measure gives a value for the uncertainty of the future behaviour of the system, based on the knowledge of the box containing the system trajectory at the present time.

The uncertainty can be partitioned into different components corresponding to the dimensions of phase space. For example, consider the strange attractor shown in figure 1. Knowledge of the presence of the trajectory at a particular point gives us different information about the future position of the system (1) in the direction perpendicular to the plane of the attractor, no information, (2) along the flow of the trajectory, perfect information, and (3) across the fractal surface of the attractor, an intermediate amount of information, the quality depending on the rate of trajectory divergence. Adding up the partial dimensions in each direction provides an overall information dimension that is related to the fractal dimension of the attractor (Grassberger 1986*a*).

The calculation of information measures poses many of the same problems as the calculation of Lyapunov exponents. However, it is usually simpler to calculate an overall information dimension. A number of different dimensions may be calculated depending on the particular definition of entropy employed. A useful family of entropies is the order-α generalized Renyi information.

$$S^{(\alpha)}(\epsilon) = \frac{1}{1-\alpha}\log\left[\sum_i p_i^{\alpha}\right]. \qquad (1)$$

Where α is a parameter, and p_i is the probability that the i^{th} box of side ϵ contains a trajectory, summed over the non-empty boxes. As the p_i are in a sense the 'weights' of each box, $S^{(\alpha)}(\epsilon)$ is related to the mass distribution of trajectories over the attractor, at resolution ϵ. The information dimensions $D^{(\alpha)}$ are calculated from

$$D^{(\alpha)} = \lim_{\epsilon \to 0} \left[\frac{S^{(\alpha)}(\epsilon)}{\log(1/\epsilon)} \right]. \quad (2)$$

The sequence $D^{(\alpha)}$ is always a decreasing function for increasing alpha. There is considerable confusion in the terminology applied to these dimensions, which we will try not to add to here. $D^{(0)}$ is the fractal dimension, as $S^{(0)}(\epsilon)$ is the log of the number of non-empty ϵ-boxes. $D^{(1)}$ (the limit as $\alpha \to 1$) is confusingly called the information dimension, as $S^{(1)}(\epsilon)$ reduces to the more familiar Shannon information measure for entropy. $D^{(2)}$ is known as the correlation dimension or exponent, and as Grassberger (1986*a*, p. 305) says, '[it] is the easiest generalized dimension to estimate, even if it is not the most interesting'. Most practical calculations of 'dimension' of an attractor have involved $D^{(2)}$, either as a quantity in its own right, or as a lower bound to the fractal dimension $D^{(0)}$.

To calculate the correlation dimensions from experimental data, one embeds a time series in spaces of different dimensions using lagged coordinates (see previous section). Then, in each dimension, one calculates the correlation integral, $C(x)$, the proportion of points that are separated by a distance less than a threshold, x. When x is very small, all, or nearly all, points will be separated by a distance greater than x and the value of $C(x)$ will be around zero. When x is very large, all points will be separated by a distance less than x and consequently $C(x) = 1$. Grassberger & Procaccia (1983*a*, *b*) showed that for intermediate values of x,

$$C(x) \approx x^{d_C}, \quad (3)$$

or equivalently

$$\ln(C(x)) \approx d_C \ln(x). \quad (4)$$

The value of d_C calculated using this method asymptotes at the value of the correlation dimension $D^{(2)}$ as the embedding dimension increases.

The size of the interval on x for which equation (3) holds (the scaling region) depends both on the embedding dimension and on the noisiness of the data. The scaling region decreases in size as the embedding dimension increases setting an upper limit on the dimensionality of the attractor that can be detected for finite data sets. Noise also reduces the size of the scaling region, typically by obscuring the correlation for low values of x.

We show the calculation of correlation dimensions by using an example from a model with chaotic behaviour. Hochberg *et al.* (1990) studied the three-species interaction between an insect and its specific parasitoid and pathogen. The pathogen is contracted by eating infected food and also exists in a protected stage that allows persistence of the disease in the temporary absence of the host. Parasitoid attack is independent of the presence of the disease and may be either random or clumped. For different parameter values, host-pathogen, host-parasitoid or three species interactions may be stable. The model is phrased as a

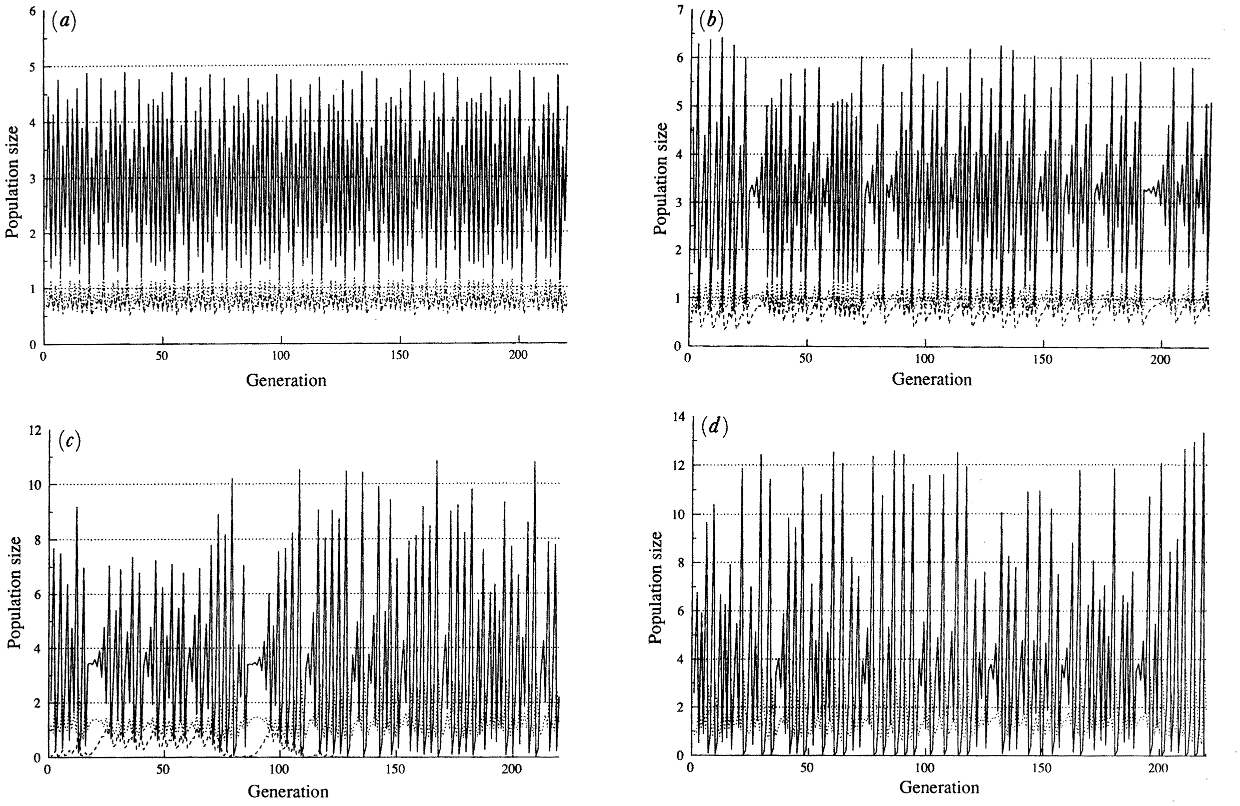

Figure 3. An example of host–parasitoid–pathogen dynamics from a model of Hochberg, Hassell & May (1990). All parameters are constant except host fecundity. Unbroken line, the host; dashed line, the parasitoid; dotted line, the pathogen. (*a*) Fecundity = 6; (*b*) fecundity = 8; (*c*) fecundity = 10; (*d*) fecundity = 12.

system of three difference equations with a time step equal to the host and parasitoid generation times. Each host generation, a pathogen epidemic occurs that determines the number of infectious particles in the next generation.

The dynamic behaviour of the system is strongly influenced by host fecundity. For one particular parameter set, we chart the change in system dynamics as host fecundity increases from 2 to 12. When the fecundity is two, a stable three species equilibrium is found. As fecundity increases stable limit cycles are found which increase in period until the system becomes chaotic. As fecundity is further increased within the chaotic region, the apparent 'randomness' of the population trajectories also increases (figure 3). At a fecundity of about 10, the parasitoid becomes extinct though the remaining host–pathogen interaction is also chaotic.

We ran the model for 500 generations, which appeared to eliminate transient behaviour and then used the results for another 500 generations to estimate the correlation dimension of the attractor in the chaotic region. Stable equilibria (zero-dimensional) and periodic behaviour (one-dimensional) give way to dynamic behaviour governed by attractors of between 1 and 1.5 (figure 4). When the parasitoid drops out of the interaction, the correlation dimension falls from about 1.4 to 1.1 though the non-integer dimensionality confirms that the interaction is still chaotic.

EXAMPLES OF USE

(*a*) *Laboratory data: Nicholson's blowflies*

During the 1950s the Australian entomologist A. J. Nicholson performed a series of cage experiments using populations of the sheep blowfly *Lucilia cuprina* (Wied.), under a variety of food-supply regimes, to investigate the process of density dependence in population dynamics (Nicholson 1954, 1957). In one of these experiments, Nicholson (1957) produced a striking pattern of variation in adult blowfly numbers with time (Figure 5), starting with irregular cyclic behaviour, and changing after about one year to a pattern of large and erratic fluctuations superimposed upon an increasing average population size.

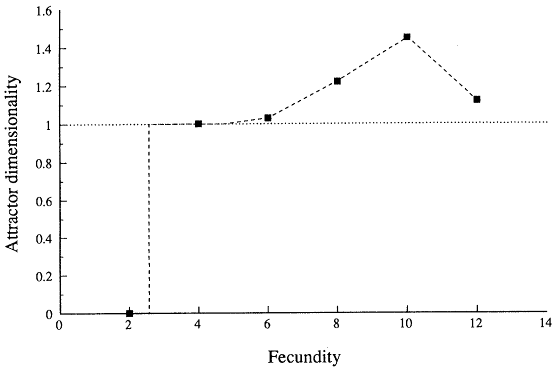

Figure 4. The dimension of the attractor underlying the host–parasitoid–pathogen dynamics illustrated in figure 3 for different values of the fecundity of the host.

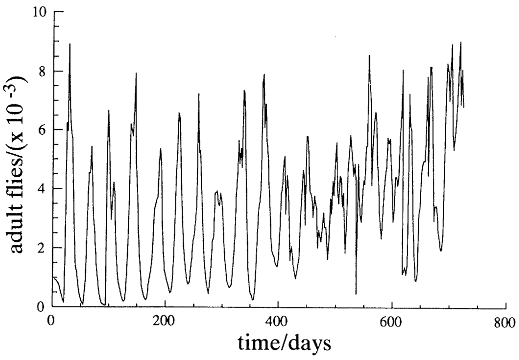

Figure 5. Changes in blowfly numbers in Nicholson's long-term laboratory cage experiment.

There has been much debate on the population dynamics underlying Nicholson's results. As mentioned above, Hassall *et al.* (1976) suggested that the dynamics were chaotic after using the data to estimate the parameters of a single-species population model in discrete generations. More detailed stage-structured models have been fitted to the same experimental data by a number of groups (Oster & Takahashi 1974; Gurney *et al.* 1980; Readshaw & Cuff 1980; Brillinger *et al.* 1980; Stokes *et al.* 1988). There is general agreement that at least the earlier part of the data can be explained by perturbed limit cycles (rather than quasi-cycles, see below). However, there is disagreement about whether the perturbed limit cycles might better be explained by a model with a chaotic component, and whether the data set becomes chaotic latterly.

The results of the estimated correlation dimension for this data set are shown in figure 6 (Blythe & Stokes 1988). The correlation dimension increases with the embedding dimension; though there is some suggestion that the correlation dimension is beginning to stabilize at a value of around 5, there is only weak evidence of a low-dimensional attractor. Two possible explanations for the poor performance of the technique are the relatively small data set, and the possibility that the system was subject to natural selection over the course of the experiment. We return to this last point below.

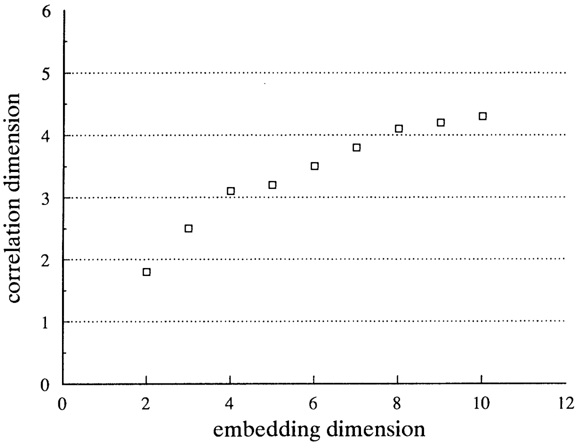

Figure 6. Estimating the correlation dimension for the blowfly population in Figure 5. The graph shows the estimated value of the correlation dimension, d_c, as a function of the embedding dimension.

(*b*) *Field data: lynx and measles attractors*

The technique of reconstructing an attractor from a lagged time series, followed by inspection of the form of the attractor for the presence of stretching and folding, has been applied to data on the Canadian Lynx and on measles epidemics by Schaffer (1984) and Schaffer & Kot (1985), respectively. In both cases the time series are strongly cyclic, in the case of the lynx with a period of approximately 9–10 years and in the case of the measles epidemics with a period of 2–3 years.

The data on lynx populations was obtained indirectly from the returns of fur trappers in the Canadian arctic between 1735 and 1934. This famous data set was first studied by Elton & Nicholson (1942) and by many subsequent workers. Schaffer analysed data from 1821 to 1913, a period of sustained 9–10 year oscillations. By using a time lag of three years and an embedding dimension of three, the attractor appeared as an essentially two-dimensional sheet, twisted into a cone. Poincaré sections were nearly one-dimensional and revealed some evidence of stretching and folding. The sections appeared to be describable by a unimodal map though the data was not of sufficient quality for the dynamic properties of the whole system to be precisely reconstructed from the map. Schaffer concludes that the most likely explanations for the data are that they are twice periodic or slightly chaotic, the chaos possibly caused by an interaction between an underlying twice-periodic orbit and noise.

Data on measles was obtained from medical health records from New York & Baltimore spanning the period 1928 until the advent of vaccination in 1963. Explanations for the presence of recurrent measles epidemics involve seasonal differences in the rate of transmission or random events leading to temporary extinction of the disease (see, for example, May & Anderson 1979). Schaffer & Kot reconstructed the attractor in three dimensions using a three month lag. Again the attractor appeared cone-like; essentially a two-dimensional object in three-dimensional space. Poincaré sectioning suggested stretching and folding while the properties of a one-dimensional return map constructed from the sections also suggested chaos (for example, a positive Lyapunov exponent was calculated from the return map). Finally, the correlation dimension was non-integer (fractal), again suggesting chaos. Sugihara & May (1990*a*; see also Sugihara & Grenfell, this symposium) also analyse this data set and conclude that there is evidence of chaos.

(*c*) *Field data: dimension of plankton dynamics*

We have attempted to apply the correlation dimension technique to a classic long-term data set, the Continuous Plankton Record (H. C. J. Godfray *et al.* unpublished data). Since 1948, regular monthly surveys of plankton have been carried out by using continuous plankton recorders towed behind merchant ships and weather ships in the North Sea and Atlantic (Colebrook 1960, 1975). Plankton are collected at a standard depth of 10 m and identified to as low a taxonomic level as possible. Each data point represents the estimated density for a particular group of plankton in an area of sea.

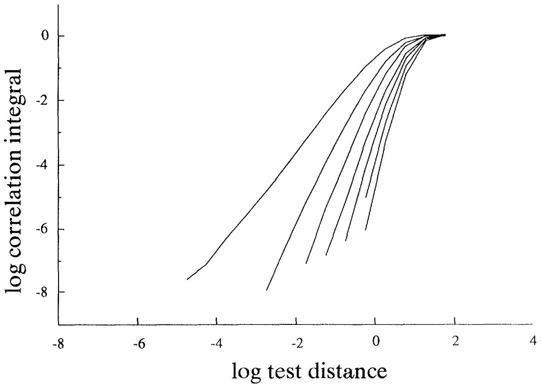

Figure 7. An attempt to estimate d_c from plankton data collected as part of the Continuous Plankton Record (the copepod *Calanus finmarchicus* from area C2 in the North Sea, see Colebrook, 1960). The slope of the graph of the correlation integral plotted against the test distance fails to asymptote as the embedding dimension increases.

From the large number of possible data sets, we selected 20 time series using as criteria those data sets with the smallest numbers of missing values and real zeros. When missing values occurred (not more than 10 in any data set), we estimated replacement values using linear interpolation. The data sets we used were chiefly groupings of copepods and euphausiaceans from the southern part of the North Sea (see H. C. J. Godfray *et al.* (unpublished data) for full details of data and localities). There is evidence of a long-term decline in the abundance of plankton in the area (see, for example, Colebrook 1978) and we have used the logarithm of the monthly differences as our raw data. In embedding the time series using lagged coordinates, we used a lag of seven months (for some data sets we explored other lags though our results were identical). Initially, we explored the data sets using traditional time series analysis. The majority (though not all) of the data sets showed annual cycles while four-yearly and four-monthly cycles were observed in some sets.

An example of the relation between the correlation integral and the test distance for the plankton data is shown in figure 7. The correlation integral increases with the test distance and there is no scaling interval that allows the estimation of the correlation dimension for any but the lowest embedding dimension. This result is typical of all the 20 data sets we explored. Thus there may be no low-dimensional attractor underlying the dynamics of these North Sea plankton. However, it is also possible that even the (relatively) outstanding quality of data of the Continuous Plankton Record is insufficient to allow the application of this technique.

BIOLOGICAL PROBLEMS

The techniques discussed above were chiefly developed with applications in the physical sciences in mind. Using these techniques in the biological sciences presents a number of problems, some peculiar to, and some exacerbated by, the need to work with living organisms.

(*a*) *Size of data base*

Attempts to reconstruct the shape of attractors and to estimate correlation dimensions demand long time series of data. Very few biological data sets are sufficiently long for these purposes. The exact length requirement will obviously depend on the quality of the data though little information about the structure of a strange attractor is likely to be obtained without information on 20 orbits, at the very least.

The lack of long term data on long-lived plants and animals is not surprising; few biologists embark on studies destined to occupy a substantial fraction of their own lives. It is perhaps more surprising that there is so little data on short-lived animals such as plankton that can be easily cultured in the laboratory for many generations.

The problem of small data sets is, of course, not unique to the biological sciences. The search for a global climatic attractor provides a cautionary tale about the dangers of over-interpreting short data sets. It has been suggested that the ratio of oxygen isotopes in cores from the seabed are correlated with climatic conditions at the time of sediment deposition. Nicolis & Nicolis (1984) examined a time-series of 184 oxygen-isotope data points. Unfortunately, the 184 data points were unevenly spaced over time, which presents obvious difficulties if the data set is to be embedded by using lagged coordinates. The solution adopted by Nicolis & Nicolis was to interpolate the data, increasing the length to just under 500 data points. Application of the Grassberger & Procaccia algorithm suggested an attractor with a dimension of 3.1. However, as was pointed out by Grassberger (1986*b*; see also Schaffer *et al.* (1988)), the process of interpolation introduces spurious correlation between data points and artefactually low estimates of attractor dimensionality. Unfortunately, the length of the data set is too short either to make a strong positive or negative statement about a potential attractor.

(*b*) *Noise*

Biologically data is typically much more noisy than data from the physical sciences and this can obfuscate underlying deterministic patterns. The effect of noise can be explored in model systems by artificially generating variability in parameters and observing the consequences on the detection of chaos and estimation of dimensionality (see, for example, Schaffer 1984). Most such experiments have involved uncorrelated, or white noise. Typically, longer data sets are required to overcome moderate levels of noise. A more serious problem, that has received less attention, is correlated or coloured noise. This is a greater problem as it results in correlation between data points that may influence the estimation of dimensionality.

Several workers have pointed out that moderate amounts of noise may actually help reveal underlying dynamics (Nisbet & Gurney 1982; Schaffer 1985). Consider a deterministic system whose dynamics are described by a unimodal return map. If the system has a point attractor then the addition of noise will result in a cloud of points about the stable point. However, if the system has a periodic solution then the addition of noise will lead to the system wondering over the surface of the map, revealing its structure in more detail. Of course, a chaotic system reveals its own map and extra noise is unlikely to increase the resolution.

Periodic attractors can also be transformed into strange attractors by the addition of noise. For example, the logistic map is said to become chaotic when the fecundity exceeds a certain value. In fact, the chaotic region contains an infinite number of periodic solutions. However, even the presence of very small amounts of noise results in most of the region being chaotic.

(*c*) *Transients*

The structure of an attractor can only be reconstructed if the trajectory of the system through phase space lies on the attractor. If the study is initiated when the system is some way from the attractor, the estimation of attractor properties will be impeded by the presence of transients. This problem is of course present in many dynamical experiments, but it may be particularly acute in population dynamics: laboratory populations and communities are frequently set up with little knowledge of the consequences of different starting conditions.

Blythe & Stokes (1988) examined some of the consequences of initial transients using a second-order ordinary differential equation,

$$\mathrm{d}^2x/\mathrm{d}t^2+2b\,\mathrm{d}x/\mathrm{d}t+\omega^2x=0, \quad x|_{t=0}=1, \quad \mathrm{d}x/\mathrm{d}t|_{t=0}=0. \tag{5}$$

This has a stable equilibrium at $x = 0$, approached via damped oscillations when $\omega^2 > b^2$ (figure 8*a*). The system thus has a point attractor with zero dimensions. However, if the correlation dimension technique is applied to data collected during the period of oscillatory transience, a dimension of about 0.9 is estimated. Thus an uncritical reading of the results would suggest a periodic attractor rather than a point attractor, possibly with a slight chaotic component.

When analysing data from the field, or from long-term laboratory experiments, any initial transients may be expected to be absent or at least to die away. However, a system that displays an oscillatory approach to equilibrium, and that is continually subject to external stochastic perturbations, may show a mixture of apparently cyclic and noisy dynamic behaviour that appears superficially very similar to chaos. Such behaviour has been called quasi-cycles by Nisbet *et al.* (1977) and we digress slightly to discuss how quasi-cycles may be characterized (see also Nisbet & Gurney (1982)).

Quasi-cycles can be described by a quantity the coherence number n_c, the number of cycles taken for the amplitude of the oscillation to decay by a factor e^{-1}. The coherence number equals $\omega/(2\pi\mu)$ where ω is the angular frequency of the oscillatory transients which decay at a rate proportional to $\mathrm{e}^{-\mu t}$. Quasi-cycles are typically characterized by bursts of approximately $3n_c$ rough cycles, interspersed by noise. Quasi-cycles can be

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

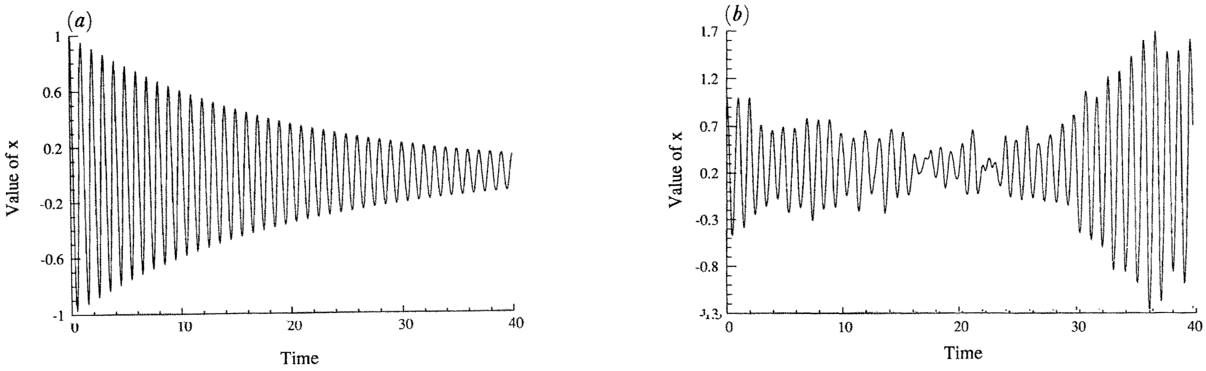

Figure 8. (*a*) The oscillatory approach (to a stable equilibrium) of equation (5); (*b*) quasi-cycles around a stable equilibrium of equation (7). In both cases $w = 2\pi$.

generated by random (white) noise when the transfer function $T(f)$ of the system has a sharp peak. The transfer function relates the amplitude of an external perturbation, at frequency f, to the consequent fluctuations at the same frequency in the population under study. If a population has a 'flat' transfer function then all external perturbations are faithfully mirrored by the population. If the transfer function has a sharp peak, say at frequency $\hat{f}$, then only perturbations of that frequency cause oscillations in the population. White noise contains fluctuations of all frequencies, including $\hat{f}$, and is thus able to cause well-characterized cycles in populations with a sharp transfer function. In general, if the range of frequencies present in the external noise is described by the spectral density s_n, the equivalent variance in the population fluctuations is

$$\sigma_x^2 = s_n \int_{-\infty}^{+\infty} |T(f)|^2 \, df. \tag{6}$$

The quantity within the integral is the modulus of the transfer function (in general a complex number) and represents the ratio of the amplitude of the environmental fluctuation and the response of the population.

To explore the influence of quasi-cycles on the calculation of dimensions, consider first a non-homogenous extension of equation (5)

$$d^2x/dt^2 + 2b\,dx/dt + \omega^2 x = \gamma(t), \quad x|_{t=0} = 1, \quad dx/dt|_{t=0} = 0. \tag{7}$$

Where $\gamma(t)$ is a source of Gaussian random noise with zero mean and spectral density s_n. Solutions of equation (7) exhibit coherent quasi-cycles (figure 8*b*). Blythe & Stokes (1988) calculated the correlation dimension for such a trajectory, embedding the time series in 2–11-dimensional space. No convergent scaling regions were found and so no estimate of attractor dimensionality was possible. Thus the quasi-cycles obscure the presence of a simple point attractor though the correlation dimension distinguishes quasi-cycles from, at least, low-dimensional chaos.

It may easily be shown that the variance in the fluctuations of equation (7), σ_x^2, is

$$\sigma_x^2 \approx s_n / 2b\omega^2. \tag{8}$$

As $\omega = 2\pi$ in the example in figure 8, we would expect to need a large spectral density s_n in order to produce significant variance in the population fluctuations. Also, for that example, $n_c \approx 20$, so that bursts of up to 60 reasonably well-formed cycles would be expected during the coherent phase.

A second, and biologically more plausible, example of quasi-cycles can be obtained from the time-delayed logistic equation with a randomly perturbed parameter. Here, the coherence number is lower and the sensitivity of population variance to noise spectral density somewhat greater. In scaled (dimensionless) form with X the population variable, the time-delayed logistic is

$$\frac{dX_t}{dt} = aX_t[1-(1+\gamma(t))\,X_{t-1}], \quad x_t|_{t\leqslant 0} = 1, \tag{9}$$

where a is scaled fecundity. The scaled carrying capacity = 1 and we assume is subject to environmental perturbation described by $\gamma(t)$ with mean = 0 and variance s_n. When $\gamma(t) = 0$ ($S_n = 0$), equation (9) has a stable point for $a < \frac{1}{2}\pi$, and regular cycles (period initially ≈ 4) if $a > \frac{1}{2}\pi$. We assume that the population is at carrying capacity as an arbitrary initial history.

The quasi-cycle behaviour of equation (7) was examined by Nisbet *et al.* (1977) and Nisbet & Gurney (1982). If we choose a value of $a = 1.4$, then we have $n_c \approx 2.8$, and a sharp peak in the transfer function at scaled angular frequency 1.70, so that we might expect up to 8 or 9 rough cycles per coherent burst. The relation between s_n and σ_x^2 (equation 4) is approximately linear, with a proportionality constant of order unity (Nisbet *et al.* 1977), so that we may expect much less regularity in the population fluctuations obtained from equation (7) in comparison with equation (5) (figure 9). The pattern of irregular quasi-cyclic bursts is not atypical of population data, and it is certainly not clear, upon inspection only, whether we are seeing chaos, noisy limit cycles, or quasi-cycles.

We attempted to estimate the attractor dimension of the data in figure 9 by embedding the time series in embedding dimensions of 2–8 (we used a longer data run than that illustrated in the figure). We found no evidence for the gradient reaching a limiting value as the embedding dimension increases. If the dimension

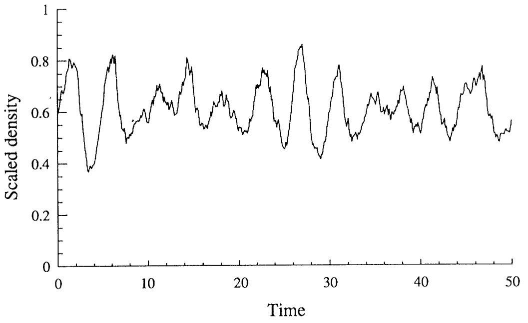

Figure 9. The dynamics of the time-delayed logistic equation with stochastic variation in carrying capacity (equation 9), $a = 1.4$, spectral density = 1.5.

were all the information available to us, we would be inclined to regard the data in figure 9 as essentially random. But spectral analysis of the data reveals a very strong periodic elements, clearly contradicting the notion of a noise process.

In conclusion, the calculation of correlation dimensions is fraught with difficulty in the presence of noise and transients, sometimes giving false positives, as in the case of a simple transient from initial conditions, and sometimes giving false negatives, as in the case of coherent quasi-cycles.

(*d*) *Evolution*

One view of organic evolution is that animals and plants spend most of their time at evolutionary equilibrium. From time to time they are confronted by new challenges, either from the biotic or abiotic environments, which cause relatively fast shifts to new equilibria through the action of natural selection. The alternative view is symbolized by van Valen's Red Queen Hypothesis (1973). Just as Lewis Carroll's Red Queen had to keep running to remain still, so all organisms have to continually evolve in the face of ever changing selection pressures. In van Valen's view, selection resulting in change in one organism in a community alters the selection experienced by other organisms, which in turn feeds back to cause more change in the first organism.

A more concrete example of possible red queen evolution has been suggested by Hamilton (1980) to occur between parasites and their hosts. If certain host genotypes are more susceptible to certain parasite genotypes then, under certain circumstances frequency dependent selection can lead to persistent cycles in host and parasite gene frequencies. The maintenance of such cycles requires continual, often quite heavy, mortality from disease in the host. As was pointed out by May & Anderson (1983), the genetic interactions between host and parasite will have important consequences on the population dynamics.

How might evolution affect the detection of dimensionality and chaos? If individuals from wild populations are introduced into laboratory microcosms, the novel conditions they experience may lead to selection on life history parameters (Blythe & Stokes 1988). As a result, the dynamic properties of the system may change. The Nicholson blowfly experiments (see above) are a plausible example of evolution occurring over the course of a laboratory experiment. In a sense, this form of evolutionary change is analogous to a transient as after the population has adapted to the new conditions in the laboratory, the dynamic behaviour should be unaffected by evolution. However, when interpreting results from the asymptoting dynamics, it must be borne in mind that the observed dynamics in the laboratory may differ from those in the field. It is also possible that the invariable simplicity of laboratory ecosystems in comparison with their natural counterparts might lead to consistent biases in the estimation of such properties as dimensionality.

Red Queen evolution may have a number of consequences for the population dynamics of a system. First, if the course of evolution was relatively slow compared to the length of the time series available for analysis, the form of an attractor may change over the course of the sampling period. If the shape of the attractor was reconstructed by embedding, then early and later trajectories might be physically separated in phase space. Similarly, such changes in the properties of an attractor would complicate estimation of dimensionality. A more interesting consequence occurs if the rate of evolution is relatively fast compared to the length of the time series. In these circumstances, population densities and gene frequencies may change on similar time scales and a reconstruction of the dynamics of the system would incorporate both population and genetic variables. The dimensionality of the system would be influenced by the degree of independence of population dynamics and population genetics.

(*e*) *Interpretation*

The attempts both to reconstruct attractors, and to estimate correlation dimensions, involve a degree of subjective pattern recognition. For example, the identification of regions of stretching and folding has to be made by eye. Taking Poincaré sections and estimating one-dimensional return maps increases objectivity though fitting curves to one-dimensional return maps with few data points results in large standard errors on parameters and consequent ambiguity in predicted dynamics. Similarly, when estimating correlation dimensions, the size of the scaling region has to be chosen subjectively.

Biologists, brought up on a diet of strict hypothesis testing, are typically more suspicious than physical scientists of conclusions drawn from the visual inspection of geometrical objects. Thus Berryman & Millstein (1989), unfairly in our view, dismiss the attempts of Schaffer and his colleagues to reconstruct attractors as providing evidence for chaos that is 'more illusory than scientific': the case for at least a chaotic measles attractor is now very strong (Schaffer 1985; Sugihara & May 1990*a*). In part, the problems of subjectivity can only be resolved through the use of better data. However, we also believe that biologists should adopt a more robust approach to scientific hypothesis testing.

CONCLUSIONS

The new techniques from applied mathematics and the physical sciences offer very exciting prospects of new approaches to some of the most interesting questions in population and community ecology. Nevertheless, there are formidable problems in applying these techniques in ecology: very few data sets are of sufficient quality and length to be analysed in this way. Further effort is needed by applied mathematicians to develop techniques better suited to the biological, as opposed to the physical sciences.

We believe that the best prospects of investigating community dynamics in biology lie with the study of experimental microcosms of short-lived organisms, for example, freshwater zoo-plankton. Obviously, the study of experimental communities is second-best to the study of natural communities. However, if it is not possible to understand the dynamics of a simplified community, under controlled conditions, there is very little prospect of understanding the dynamics of real communities. We strongly agree with a recent remark of Kareiva's (1989) 'ecologists gave up bottle experiments too soon'.

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Discussion

M. Williamson (*Department of Biology, University of York, U.K.*). When testing time series of biotic entities for chaos is there not a possibly confusing factor? It is one of the triumphs of nonlinear science to show that there is chaos in the physical environment on a variety of timescales from days (as in the weather) to millions of years (as in planetary orbits). If Dr Godfray shows chaos in a biological time series, may he not merely be showing chaos in the physical environment affecting the biological entity? Is he not trying to determine whether there is chaos in the population dynamics of that entity?

H. C. J. Godfray. One of the key issues here is the relative scales of the physical and biological processes. When experimentally studying biological populations, one is not normally concerned with climatic attractors or planetary motion with characteristic periods of very many generations. However, meteorological and tidal patterns may be of a scale likely to influence experimental results. Normally, it is far easier to measure the physical rather than the biological dynamics and so identification of the 'driving chaos' may be far simpler than the identification of chaos in the population dynamics. Of course, microcosm studies have the advantage of being able to control for external physical processes.

S. P. Blythe. Additional insight into this problem may be gained by modelling: consideration of forcing functions may be a good way forward in this area, as the study of complicated dynamics in these circumstances dates back to Cartwright (1948, *Journal of the Institute of Electrical Engineers* **95**, pp. 223) and many results are available. Note also that a chaotic forcing term is not needed to induce chaos: a periodic function will often do the trick (see, for example, Marcus *et al.* (1984), *FEBS Letters* 172, pp. 235). There is much scope (and need) for analysis in this area.

J. N. Perry (*Institute of Arable Crops Research, Statistics Department, Rothamsted Experimental Station, Harpendon, Herts. U.K.*). Dr Godfray refers to the study of Hassell *et al.* (1976) where an intrinsic growth parameter, λ, and a density-dependence parameter, β, were estimated from data. Since λ is calculated after allowing for all density-independent mortality, and since we now know that density dependence may often be present but undetected (and therefore underestimated), these estimates of λ may be biased downwards, i.e. underestimates. However, λ and β are clearly positively correlated; hence calculated β values may consequently also be underestimates. Therefore some data points in the figure might require amendment by a shift away from the origin, towards the chaotic region. I wonder to what extent some populations would exhibit chaos under Hassell *et al.*'s model, were all the density-dependence allowed for?

H. C. J. Godfray. This is an interesting additional caveat to the Hassell *et al.* study. However, my feeling is that 15 years on from this study we need more sophisticated techniques for detecting chaos: either more realistic underlying models, or techniques that do not make *a priori* assumptions about underlying mechanisms.