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Chaotic behaviour in simulated planktonic successions, I: Discrete temporal maps*

JORDI BASCOMPTE[1], RICARD V. SOLÉ[2] and JOAQUIM VALLS[2]

[1]Departament d'Ecologia, Universitat de Barcelona.
Diagonal 645, 08028 Barcelona, Spain.
[2]Departament de Física i Enginyeria Nuclear, Universitat Politècnica de Catalunya.
Pau Gargallo 5, 08028 Barcelona, Spain.

SUMMARY: Planktonic successions are short ones, truncated by inputs of external energy. Thus, long-term data can involve different stages with different interaction rules. Any model used to describe planktonic dynamics must take this variation in growth and interaction rates into account. In this paper we study a simple two-dimensional discrete map of predator-prey interaction and explore how the variation of parameters can affect the dimensionality of the system. Implications for the characterization of real planktonic time series in the light of dynamical systems theory are also discussed.

Key words: Deterministic chaos, ecological models, time series, planktonic succession, fractal dimension.

RESUMEN: COMPORTAMIENTO CAÓTICO EN SUCESIONES PLANCTÓNICAS SIMULADAS, I: APLICACIONES DISCRETAS. — Las sucesiones planctónicas son cortas y se ven a menudo interrumpidas por entradas de energía externa. De este modo, series temporales largas pueden superponer diferentes estadios de la sucesión con diferentes reglas de interacción. Cualquier modelo utilizado para describir la dinámica del plancton debe considerar esta variación en las tasas de crecimiento e interacción. En este artículo se estudia una aplicación sencilla del tipo presa-depredador y se explora como la variación de los parámetros puede afectar a la dimensionalidad del sistema. Asimismo, se discuten las implicaciones para la caracterización de series temporales planctónicas reales bajo la luz de la teoría de los sistemas dinámicos.

Palabras clave: Caos determinista, modelos ecológicos, series temporales, sucesión planctónica, dimensión fractal.

INTRODUCTION

Nonlinear phenomena and chaos have received increasing attention in the last few years (STEWART, 1989). The study of discrete maps of population dynamics was one of the pioneering fields in which deterministic chaos theory was developed (MAY, 1976; FEIGENBAUM, 1979). It was shown that even the simplest models could give an unexpected richness of dy-

$$X_{n+1} = F_\mu(X_n)$$

i.e., the X-value in the next time step is a function of its present value. F_μ is often a nonlinear map, μ being the so-called bifurcation parameter, that is, a parameter that drive the system through different kinds of dynamics (stationary, periodic and chaotic) when its numerical value is increased.

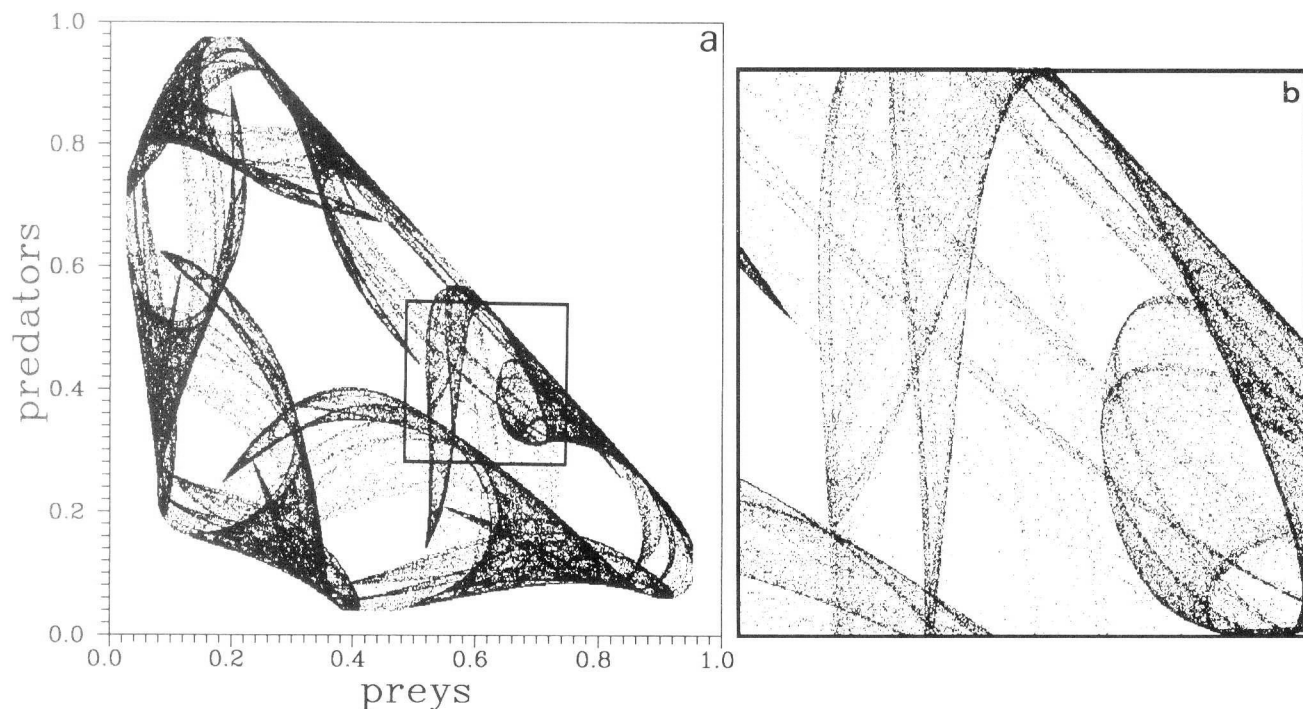Thus, the utilization of discrete (difference) maps

FIG. 1. — Strange attractor of model (1). In spite of being temporal series (Fig. 3c) noise-like, chaos has an underlying order as can be seen in this plot of phase space. $\mu = 3.45$. A large enough number of iterations were discarded in order to prevent transient behaviour. Right: a magnification of a detail of the attractor.

objection is especially evident when we model ecological systems linked with a high degree of enviromental variability. In such a situation, the parameter values are expected to change with time. A planktonic ecosystem is the best example. Its physical constrains determine a high turnover to compensate for short, truncated successions that are governed by inputs of external energy. These "reset" successions involve a change in the interaction rules. Thus, variation of the parameters can lead the system to different dynamical behaviour, including a chaotic domain, in different segments of the ecological history (MARGALEF, 1986).

The study of planktonic time series in the light of dynamical systems theory has shown opposite results. In first place, the study by SUGIHARA and MAY (1990) of a weekly record of marine planktonic diatoms gathered at San Diego, by means of nonlinear forecasting, shows that the time series is chaotic with an embedding dimension about 3 (low-dimensional chaos). On the other hand, GODFRAY and BLYTHE (1990) apply the correlation dimension technique (see following sections) to a plankton record data from the North Sea. As it is shown, the correlation sum fails to converge as the embedding dimension increases. This lack of convergence is characteristic of noise and indicates that there is no low-dimensional attractor underlying the dynamics. However, as

GODFRAY and BLYTHE point out, the data quality of the plankton record may not be good enough to allow the application of this technique. In fact, GODFRAY and BLYTHE outline the difficulties in applying the dynamical systems techniques (developed for applications in physic) to biological data. Among these problems, there are the lack of long-term data, the presence of noise and transient behaviour.

Systems dynamics can be studied in the phase space, i.e., that euclidean space in which each axis is one of the variables involved in the motion. Consider, for example, a prey-predator system. We have two variables, that is, the number of preys and the number of predators. We can plot the number of preys against the number of predators in a given time step. This is a point in the phase space (in this case a plane). This point perfectly characterizes the system state at a given moment. At the next time we have another point. The sequence of points so constructed is called the trajectory. This and all the other possible trajectories (starting from different initial conditions) evolve towards a subset of phase space called the attractor. They are attracted by this topological subset and will remain on it. This attractor can be a fixed point (steady state), a limit cycle (periodic motion) or a fractal, strange attractor (chaotic motion, see Fig. 1). The characterization of the dynamics is only possible when the trajectory lies on the attractor. The
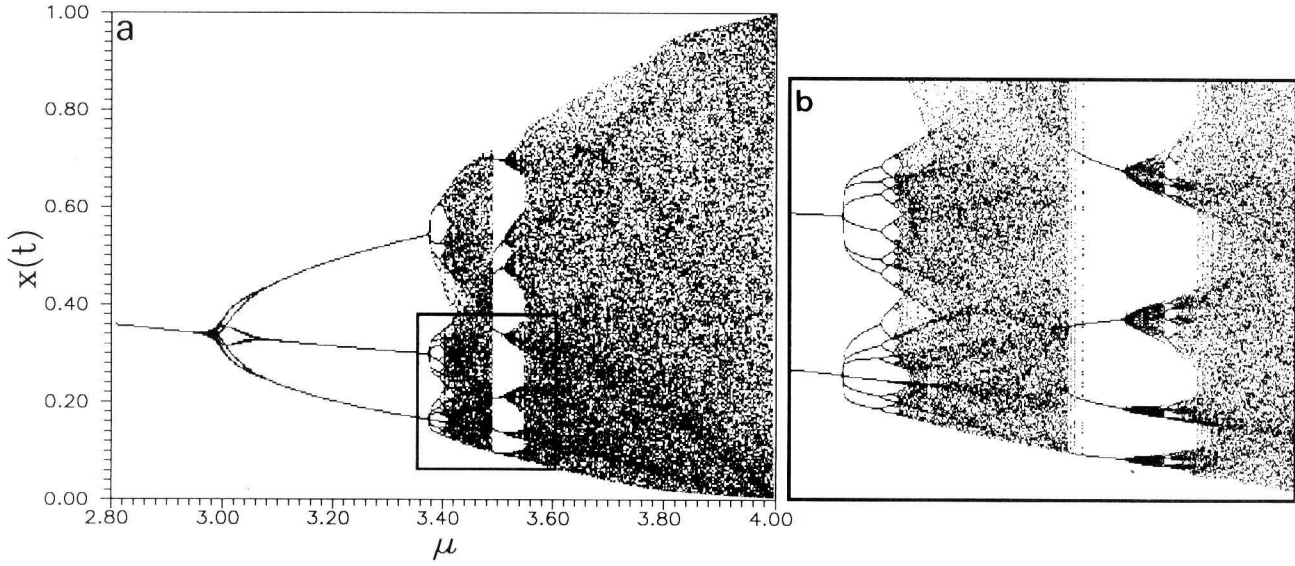
FIG. 2. — Bifurcation diagram for the Lotka-Volterra map (1). The asymptotic dynamics (values of X after an initial transient is discarded) are plotted against the bifurcation parameter μ. Right: magnification of a detail of the periodic window showing the self-similar (fractal) properties of the map.

transient behaviour must be excluded. If ecological systems are ussually evolving or displaying transients, the application of current physical tools on temporal series should be made with caution (BLYTHE and STOKES, 1988).

Planktonic time series can involve different reset successions, i.e., different environmental conditions. Thus, we may be considering transients. This can be the reason for the lack of convergence of correlation dimension as the embedding dimension increases. The aim of the present paper is to study how the change of the parameter values in nonlinear discrete maps can affect the numerical estimation of the system's dimension, and how this can be related with the problem of studying long-term planktonic data involving different stages of succession.

TWO-DIMENSIONAL NONLINEAR MAPS

To begin with, consider the following two-dimensional map, which is applied to model a predator-prey interaction:

$$X_{n+1} = \mu X_n (1 - X_n - Y_n) \qquad (1a)$$
$$Y_{n+1} = \beta X_n Y_n \qquad (1b)$$

X_n, Y_n being respectively the prey and predator populations at a given iteration n. Here μ and β are the growth rates. This system has two steady states: $P_0 = \{0,0\}$ and $P_1 = \{1/\beta, 1 - (\beta + \mu)/\beta\mu\}$. We can study the stability properties of the non-trivial fixed point by defining the community matrix:

$$\Gamma = \begin{pmatrix} \dfrac{\delta F^{(1)}}{\delta x} & \dfrac{\delta F^{(1)}}{\delta y} \\[2ex] \dfrac{\delta F^{(2)}}{\delta x} & \dfrac{\delta F^{(2)}}{\delta y} \end{pmatrix}$$

For model (1) we have,

$$\Gamma = \begin{pmatrix} \mu(1 - 2x - y) & -\mu x \\[1ex] \beta y & \beta x \end{pmatrix}$$

In our study we will take $\mu = \beta$ for simplicity. For P_1, Γ will be:

$$\Gamma(P_1) = \begin{pmatrix} 0 & -1 \\[1ex] \mu - 2 & 1 \end{pmatrix}$$

which has an associated eigenvalue equation

$$\det(\Gamma(P_1)) = \det \begin{pmatrix} -\lambda & -1 \\[1ex] \mu - 2 & 1 - \lambda \end{pmatrix} = 0$$

The attractor will be stable provided that $|\lambda_\pm| < 1$ for both eigenvalues. This leads to the following stability domain:

$$S(P_1) = \{\mu \mid \mu \in (2, 3)\}.$$

By increasing the value of μ we obtain a bifurcation scenario with chaos beyond $\mu = 3.43$ (Fig. 2).

Now we will consider a version of model (1) that takes into account some kind of variability of the
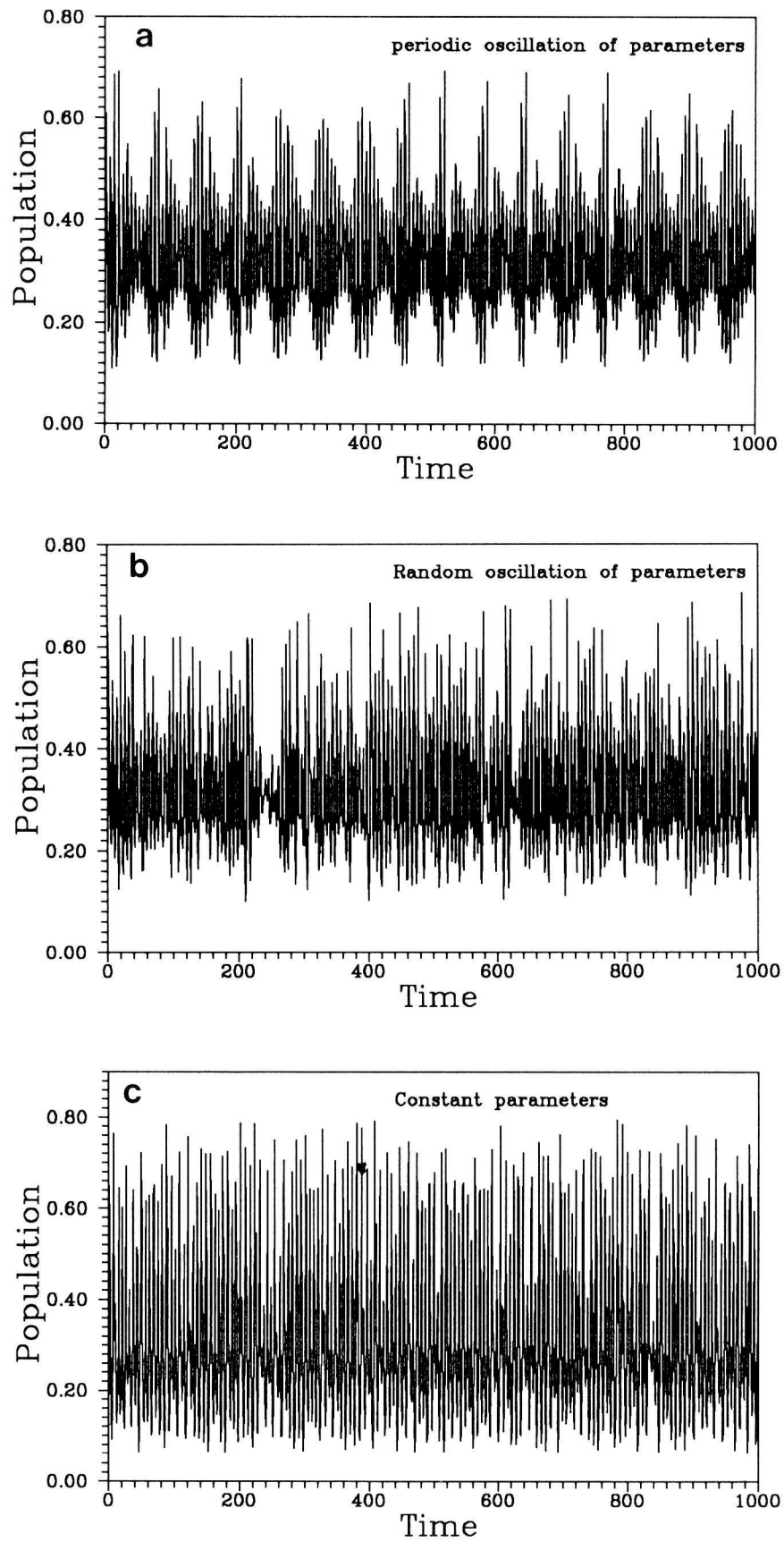
FIG. 3. — Prey temporal series obtained from model (2). In both (a) and (b) $\mu(t) \in (3,3.5)$, but in (a) the variation is periodic while in (b) is random. (c) shows the motion of the nonlinear map (1) with μ fixed and equal to 3.45.
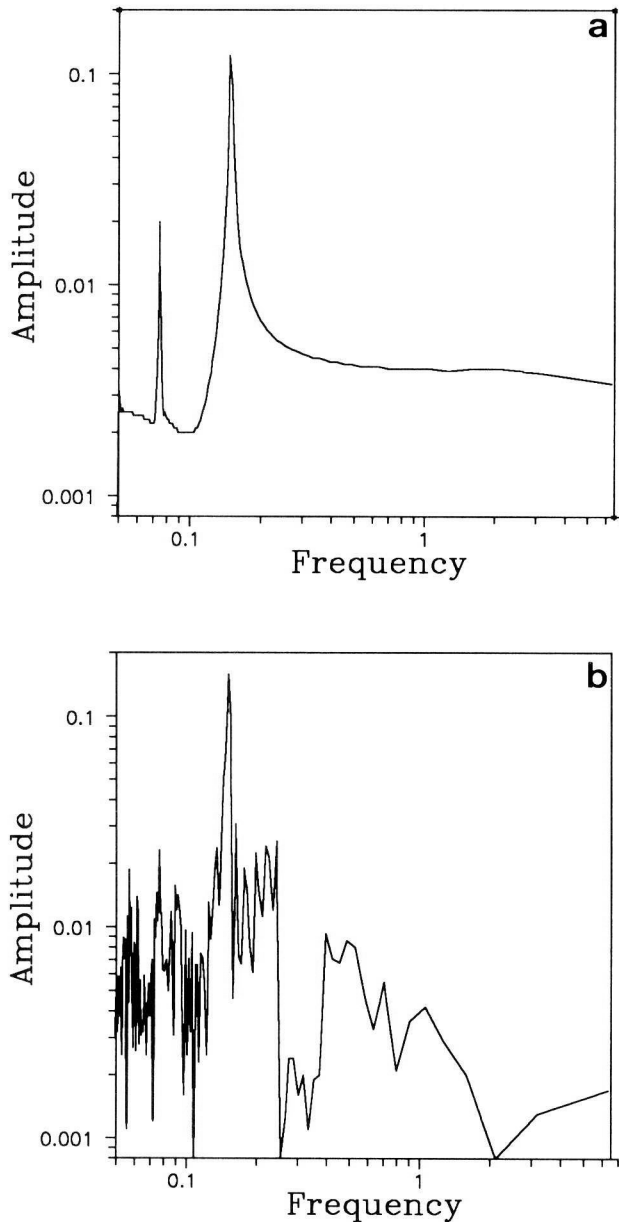
FIG. 4. — Fourier spectra obtained from the prey temporal series given by map (1). (a) $\mu = 3.1$ corresponding to a periodic motion. (b) $= 3.45$ corresponding to a chaotic attractor whose temporal series is shown in Fig. 3c.

growth ratae (μ). It is as follows:

$$X_{n+1} = \mu(n)X_n(1 - X_n - Y_n) \qquad (2a)$$

$$Y_{n+1} = \mu(n)X_nY_n \qquad (2b)$$

We will study two different ways of varying the parameter value, that is:

(a) Variation of μ in a simple periodic function, i.e.,

$$\mu(n) = \mu_0 + 0.25\sin\left(\frac{n}{50}\right)$$

(b) Random variation of μ, i.e.,

$$\mu(n) = \mu_0 + \delta$$

where δ is a zero-centered gaussian variable of width 0.25. In both (a) and (b) we will take $\mu_0 = 3.25$. Thus, $\mu(n) \in (3,3.5)$. For comparison, we consider the simple case of μ fixed and equal to 3.45. Fig. 3 shows the temporal series obtained for the three situations for 1000 iterations. As can be observed, there is highly unstable behaviour with some degree of periodicity in case (a). But by looking at the temporal series we can obtain no much information about the underlying dynamics. In fact, both deterministic chaos and noise show a similar pattern in spite of the completly different causes. A noisy temporal series has random inputs and a very large number of variables are necessary in order to understand (if possible) the observed dynamics. The source of complexity is external. On the other hand, chaos is an apparently random behaviour shown by deterministic and simple systems. Often only a small number of degrees of freedom are necesary to characterize the motion. The complexity is, in such a situation, intrinsic to the system, due to the nonlinearity of interactions. In spite of the apparent randomness shown in Fig. 3c, there is an underlying order as can be seen in Fig. 1, where the attractor for model (1) has been plotted. So, we can use different tools from physical sciences in order to characterize and distinguish such complex temporal phenomena.

CHARACTERIZATION OF TEMPORAL SERIES

In this section we will define some of the tools that are used in the study of dynamical systems. In the following section we will make use of them to define the properties of our data. These measurements are:

Fourier spectra

The squared Fourier spectra is defined by the well-known transformation:

$$P(\omega) = \left| \frac{1}{n}\sum_{k=0}^{n-1} e^{-2\pi i \omega k} x(t_k) \right|^2$$

This analysis tells us the frequencies involved in the complex motion and their relative importance. Imagine a periodic motion, that is, a limit cycle attractor in phase space. In this case, the spectral analysis would show a thin peak corresponding to the frequency of

the motion, i.e., to the number of cycles per unit time. If we have more complex periodic behaviour involving different frequencies, the spectral analysis would show different peaks associated with such periodicities (see Fig. 4a). The more important a given frequency in driving the dynamics, the higher its peak.

On the other hand, noise involves an infinite number of different frequencies in a characteristic power law: the higher frequencies correspond to the smaller amplitudes. In the spectral analysis we can see a broad band. Although entirely deterministic, strange attractors can give rise to noisy spectra (see Fig. 4b). Consequently, spectral analysis by itself is unable to distinguish between chaos and noise.

Lyapunov exponents

Deterministic chaos is characterized by sensitive dependence on initial conditions. Originally very close trajectories separate exponentially. This unstable dynamical behaviour is, in fact, related with the topological stretching-and-folding processes that take place inside the strange attractor (SCHAFFER, 1984). Thus, although the motion is deterministic, long-term forecasting is not possible beyond a given temporal horizon. This is because the difference between a very good (but finite) knowledge about initial conditions and an infinite one.

Lyapunov exponents are a measure of this divergence of nearby trajectories. In this sense, there is one Lyapunov exponent for each dimension of the phase space. Thus, a dynamical system is called chaotic if there is at least one positive Lyapunov exponent. So, we need just to compute the largest one (λ_m) defined as follows:

$$\lambda_m = \frac{1}{r\tau} \left\{ \sum_{t=1}^{r} Ln\left(\Theta(t, \tau)\right) \right\}$$

r being the number of points sampled and

$$\Theta(t, \tau) = \frac{\| X(t + \tau) - X'(t + \tau) \|}{\| X(t) - X'(t) \|}$$

Here $X(t)$ and $X'(t)$ are two very close values of our variable (two different initial conditions) and $\| \|$ denotes, as usual, euclidean distance. We apply here the Wolf algorithm (WOLF et al., 1985) in order to estimate λ_m.

Correlation dimension

In our two dimensional map we know exactly how many variables are involved. But this is not usually the case in field studies. We could have only one temporal serie, for example the record of a phytoplankton species. Neither the attractor shape nor the minimum number of variables that must be introduced into the description of the system would be known. Fortunately, this problem can be solved. Whitney's embedding theorem (TAKENS, 1981) states that we can obtain a topological equivalent image of the attractor by working with $X(t)$ (our measured temporal series) and the set of variables obtained from it, by shifting its values by a fixed lag τ. So, we can reconstruct the attractor for different embedding dimensions defined by the new set of lagged variables:

$$\{X(t), X(t + \tau), ..., X(t + (n - 1)\tau)\}$$

Strange attractors have self-similar properties, i.e., they are fractal subsets. Their fractal dimension, according to GRASSBERGER and PROCACCIA (1983) can be estimated by the correlation dimension (d):

$$d = \lim_{r \to 0} \frac{Ln(C(r))}{Ln(r)} \tag{3}$$

where $C(r)$ is the correlation sum:

$$C(r) = \lim_{N \to \infty} \frac{1}{N(N - 1)} \sum_{i \neq j} H(r - \| X_i - X_j \|) \tag{4}$$

$\| X_i - X_j \|$ is the euclidean distance between a given pair of points on the attractor. $H(z)$ is the well-known Heaviside function, i.e., $H(z) = 1$ for $z > 0$ and $H(z) = 0$ otherwise.

Roughly speaking, expression (4) can be written in the following way:

$$C(r) = \lim_{N \to \infty} \frac{1}{N(N - 1)} \{ \text{ Number of pairs (i, j)}$$

$$\text{such that } \| X_i - X_j \| < r \}$$

Thus, the dimensionality d of the attractor, according to expression (3) is given by the slope of the $Ln(C(r))$ vs $Ln(r)$ in a certain range of values of r. We can construct the correlation sum and estimation the dimensionality (d) of the attractor by considering successively higher values of the dimensionality n of phase space. If d reaches a saturation limit beyond some relatively small n, i.e., d becomes asymptotic at a certain value of n, this saturation value (d_s) will be an estimation of the attractor dimension. On the other hand, the value of n beyond which saturation is observed will provide the number of variables (degrees of freedom) involved in the dynamics. Since deterministic chaos has a low dimensionality while random noise has no saturation limit, this technique provides us with a tool to distinguish them.
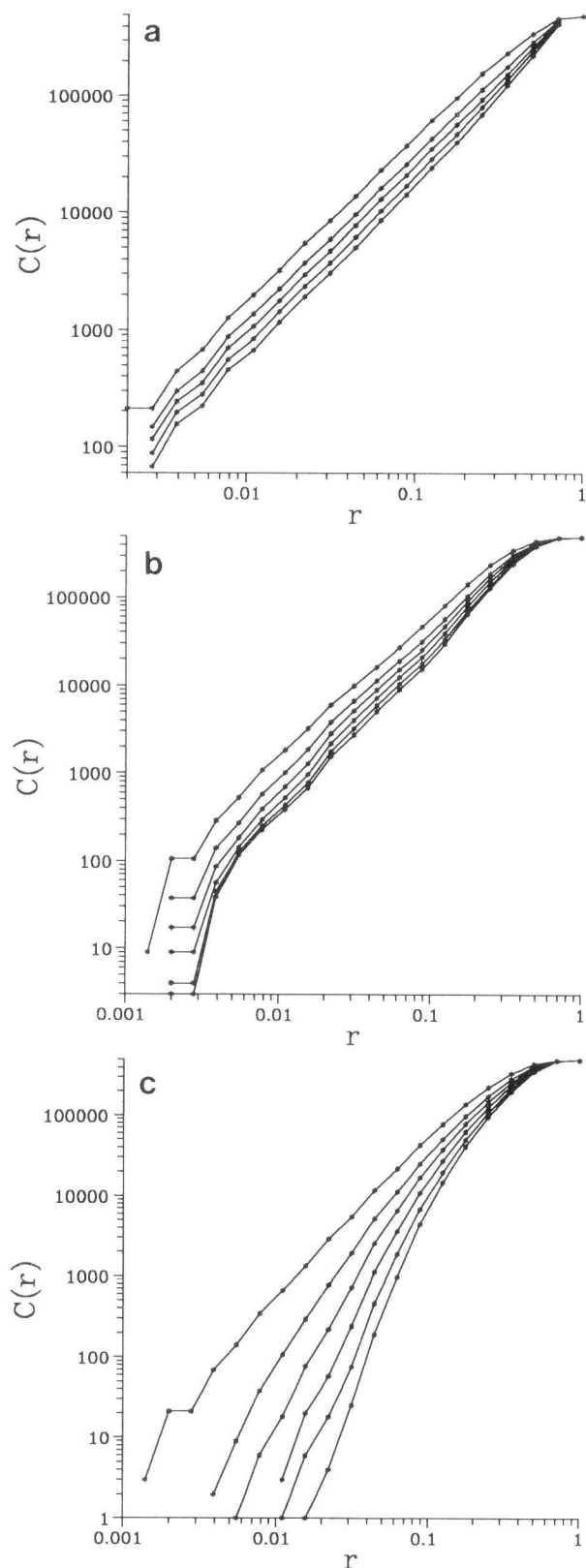
FIG. 5. — Correlation sum vs r in a log-log plot. The slope of the curves give us the correlation dimension d for the embedding dimension n. For (a), corresponding to μ fixed and equal to 3.45, d reaches a saturation limit as can be observed from the same slope of curves for n = 2,3,4,5 and 6. On the other hand, for (c), that is, the random variation of μ, there is a lack of convergence while (b) —corresponding to the periodic variation of μ— shows an intermediate situation.

RESULTS AND DISCUSSION

We have computed the Largest Lyapunov exponent from the three time series shown in Fig. 3. For the simple Lotka-Volterra map with $\mu = 3.45$, $\lambda_m \approx 0.15$. This result (a positive Lyapunov exponent) indicates that the motion is chaotic. For the time series generated with a periodic variation of μ, we have estimated $\lambda_m \approx 0.08$. Given our level of accuracy, we can not distinguish this result from a value of zero indicating a periodic motion. Thus, the periodicity in the change of growth rate drags the qualitative behaviour of the dynamics towards a periodic regime. On the other hand, for the last situation, i.e., that of a random variation of μ, we have $\lambda_m \approx 0.27$. In this case, however, the convergence of the Lyapunov exponent is not as good as for the two mentioned above cases. The presence of noise makes its computation more difficult. One solution is to increase the data size, but this is in general impossible for biological time series. Thus, in order to decide whether the corresponding motion is an example of low-dimensional, deterministic chaos, we need to take into account extra information, that corresponding to the dimensionality of the underlying dynamics.

In Fig. 5 $Ln(C(r))$ vs $Ln(r)$ has been plotted for a given range of embedding dimensions. The slope of this representation gives us the estimated correlation dimension. For $\mu = 3.45$, i.e., a simple 2D chaotic map, d reaches a saturation limit for $n = 2$, as can be seen in Fig. 5a. All the curves are parallell, that is, they all have the same slope. In this case, an additional increase of n beyond $n = 2$ does not change the value of d, because of the low dimensionality of our system. This is an example of low-dimensional chaos. $d_s \approx 1.55$ and we only need 2 degrees of freedom in order to characterize this motion. On the other hand, when μ changes with time we have a different situation. In Fig. 5c (random variation), the slope of the plot has a higher value at increasing embedding dimension. In other words, the correlation dimension fails to converge, which is characteristic of noise. In Fig. 5b (μ changes in a periodic way) we can see an intermediate situation. However, the result depends on the frequency of the periodicity in the change of parameter. Thus, when the growth rate moves around a given value (especially in a random way), the system becomes of higher dimensionality because we are considering transient behaviour.

We believe that the last result is very important for understanding planktonic successions. If we are stydying a temporal series involving different stages of ecological history, i.e., with different interaction

and growth rates, we can detect an extra dimensionality in spite of the low-dimensionality of the underlying system. This may be the case for the plankton record data from the North Sea, studied by GODFRAY and BLYTHE (1990).

On the other hand, we are aware that the results given in the present paper are based in a simple discrete map, without any kind of spatial degrees of freedom, although space must be taken into account in order to understand the stability properties of chaotic dynamics (SOLÉ and VALLS, 1992). As planktonic successions involve a complex pattern over space (the well-known patchiness), we hope to report the generalization of these results by using a spatial counterpart of model (2) very soon.

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