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A new instability phenomenon in the Malthus–Verhulst model

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Abstract. The population dynamics model known as the Malthus–Verhulst model is shown to exhibit, for particular values of the rate parameters, a new regime characterised by a relaxation time which is exponentially small in inverse of the competition rate between individuals of the species. This result is obtained by means of a representation of the time evolution of the system in terms of a stochastic process which describes the Brownian motion of a particle under the action of a unidimensional periodic potential. The long-time behaviour of the first moment of the population is calculated by a suitable extrapolation of a perturbative expansion around the Wiener process result.

1. Introduction

The Malthus–Verhulst (MV) model was originally introduced as a model for population dynamics and it had many applications in this respect. More recently (Schlögl 1972, McNeil and Walls 1974, Chaturvedi *et al* 1976, Gardiner and Chaturvedi 1977, Van Kampen 1976, Goldhirsch and Procaccia 1981) the model was considered a prototype to describe an autocatalytical chemical reaction. Within this phenomenon an analogy with second-order phase transitions has been established. Another interpretation of the model as describing the photon population in a laser cavity was introduced by McNeil and Walls (1974). It may be pointed out that in the chemical interpretation of the model the rate parameters ν, γ are considered as depending on the size of the system: this means that the immigration ν and the competition γ are thought to be respectively directly and inversely proportional to the volume Ω. Such being the case, the evolution of the system in the limit $\Omega \to \infty$ may be described by a macroscopic decay equation for the concentration:

$$dc/dt = \nu/\Omega + (\lambda - \mu)c + \gamma\Omega c^2. \tag{1}$$

This equation shows an instability point for $\nu/\Omega = 0$ and $\mu = \lambda$. This instability remains in a context that admits the presence of fluctuations (De Pasquale *et al* 1980, 1981). Moreover, it is to be noticed that in terms of population dynamics, the immigration rate ν is not necessarily proportional to the system size Ω, and the case of a large size is not necessarily the only physically interesting one. From this point of view there is no longer a clear distinction between macroscopic behaviour and fluctuations, so that we may expect new instability phenomena, unexpected from the previous macroscopic analysis, to occur. This paper shows that this is the case of the MV model.

The instability phenomenon will be associated in the following with the qualitative modification in the time evolution of the system. From this point of view an instability phenomenon can be associated not only with the steady state but also with the transient behaviour of the system.

The method used to find the model instabilities is based on the possibility of introducing a stochastic variable x which allows us to describe the population moments and in terms of which it is easy to perform a qualitative analysis of the time evolution of the system (see § 2).

This x representation has been introduced by De Pasquale *et al* (1980, 1981): I just mention that the x representation is defined for $\nu \geqslant \lambda/2$, $\mu \geqslant \gamma$. The parameter region in which $0<\nu<\lambda/2$, $0<\mu<\gamma$ can exist physically, but cannot be described with this representation, and it is still unexplored. It may be studied by a representation in which an analytical extension to a complex space should be made (Gardiner and Chaturvedi 1977).

In the x representation the time evolution of the system is equivalent to the stochastic, overdamped, unidimensional motion of a particle under the action of an external potential and an additive Gaussian stochastic force. This external potential appears to be a periodic one with singularities at $x = \pm n\pi/2$. Accordingly the motion of the particle whose initial position is at $x = 0^+$ (this state corresponds to a vanishing population at $t = 0$) is confined between $x = 0$ and $x = \pi/2$ where two repulsive barriers appear. The first instability appears when $\nu = \lambda/2$ and is associated with a doubling of the potential period. The motion of the particle whose initial state is $x = 0$ is now confined to the range $-\pi/2 \leqslant x \leqslant \pi/2$.

The initial state appears to be stable if $\mu - \gamma < \lambda$ and unstable if $\mu - \gamma > \lambda$. This instability induces qualitative differences in the transient behaviour of the population during the decay from the initial state to the stationary one (De Pasquale *et al* 1980, 1981).

The second instability for $\nu = \lambda/2$ and $\mu = \gamma$ corresponds to the vanishing of the singularities of the potential, so that the motion of the particle is extended to the range $-\infty \leqslant x \leqslant +\infty$.

In the latter case the x process can be seen as the motion of a particle subjected to a Gaussian stochastic force and whose velocity is given by a deterministic force equal to the derivative of a periodic potential. It is expected that for long times the motion of this particle should be a diffusive motion controlled by the probability of overcoming the peak value as a consequence of the stochastic perturbation. In these conditions there follows a decay to the equilibrium state of the population, exponentially much slower than that which occurs when the x variable is confined on a finite range of the real axes.

In § 2 the x representation is introduced and its main properties are summarised. In § 3 the qualitative analysis of the behaviour of the stochastic x process is described; in § 4 an evaluation of the x moments is performed in the extreme case of large γ up to the $1/\gamma$ second order, so as to show that the process becomes a diffusive one; the related calculations are shown in the Appendix.

In § 5 the results for the evolution of the population are concluded and the extrapolation to small values of γ is obtained. In § 6 results are discussed.

2. The model

The model considered is

$$A \underset{\gamma}{\overset{\lambda}{\rightleftarrows}} 2A, \qquad A \underset{\nu}{\overset{\mu}{\rightleftarrows}} R, \tag{2}$$

where A is the component whose evolution is studied, R is an external reservoir able to emit and absorb A and λ, μ, ν, γ are the rate parameters. Its evolution is governed by the stochastic differential equation (De Pasquale *et al* 1980, 1981)

$$\mathrm{d}\alpha = a(\alpha)\,\mathrm{d}t + b(\alpha)\,\mathrm{d}w(t) \tag{3}$$

where the drift term is

$$a(\alpha) = \nu + (\lambda - \mu)\alpha - \gamma\alpha^2 \tag{3a}$$

and $b(\alpha)\,\mathrm{d}w(t)$, which is the term of stochastic noise, is a Wiener process:

$$b(\alpha)\,\mathrm{d}w(t) = [2(\lambda\alpha - \gamma\alpha^2)]^{1/2}\,\mathrm{d}w(t). \tag{3b}$$

In another paper (De Pasquale *et al* 1980) has been introduced the stochastic x process related to α by the relation

$$\alpha = (\lambda/\gamma)\sin^2 x \tag{4}$$

as it arises from an integral representation of the population moments generative function. Its evolution is governed by the equation

$$\mathrm{d}x = -(\mathrm{d}V(x)/\mathrm{d}x)\,\mathrm{d}\tau + (\gamma/\lambda)^{1/2}\,\mathrm{d}w(\tau) \qquad (\tau = \tfrac{1}{2}\lambda t) \tag{5}$$

where the noise term is only an additive term, and

$$V(x) = \frac{\gamma}{2\lambda}\left(-\frac{\nu}{\lambda}+\frac{1}{2}\right)\ln\sin^2 x - \frac{1}{2}\left[\frac{\mu}{\lambda} - \frac{\gamma}{\lambda}\left(\frac{\nu}{\lambda}+\frac{1}{2}\right)\right]\ln\cos^2 x + \tfrac{1}{2}\cos^2 x \tag{5a}$$

so that the stochastic process may be seen through the motion of a particle in the potential $V(x)$ under random pulses. The study of the potential $V(x)$ shows (De Pasquale *et al* 1980) the existence of instabilities depending on sudden changes of the potential form (when $\nu = \lambda/2$ and when $\mu = \gamma$). In particular, for $\nu = \lambda/2$, $\mu - \gamma = \lambda$ a critical point appears. Instabilities appearing in correspondence to the change of form of this potential when $\nu = \lambda/2$ have been discussed elsewhere (De Pasquale *et al* (1981)). But where both $\mu = \gamma$ and $\nu = \lambda/2$, there is another change of the potential shape that becomes suddenly periodic,

$$V(x) = \tfrac{1}{2}\cos^2 x. \tag{6}$$

As the x process is expressed as a particle moving in a force field with a period π, and since all the α moments are related to the x process moments, the study of the behaviour of the α process can be carried out through the study of a one-dimensional periodic potential.

3. The x process

It is known (Galleani *et al* 1978) that a Brownian particle in a one-dimensional periodic potential has a diffusive motion with a diffusion coefficient that is, in our case,

$$D=(\gamma/2\lambda)I_0^{-2}(\lambda/2\gamma) \tag{7}$$

where $I_0(\lambda/2\gamma)$ is the modified Bessel function.

However, I do not know the whole statistics of the process, because higher moments than the second one are known only asymptotically for long times, so that we cannot foretell if the sum of all the moments (§ 5) might, for long times, involve the knowledge of other eigenvalues besides the ground state one (Galleani *et al* 1978). The form of the diffusion coefficient (7) shows that there is an increasing diffusive motion while γ increases. Exactly what we could expect; in fact, if we examine the process equation

$$\mathrm{d}x=\sin x\cos x\,\mathrm{d}\tau+(\gamma/\lambda)^{1/2}\,\mathrm{d}w(\tau) \tag{8}$$

it may be noticed that the stochastic term is determined by the ratio λ/γ: as $\lambda/\gamma\to\infty$ the stochastic term is very much smaller than the drift one, so that the deterministic motion is prevalent and the particle is bound in its potential well for infinite times. This explains too why it is impossible to obtain the correct diffusive process by a perturbative expansion around $\gamma=0$: it would mean remaining in regions in which the deterministic motion is prevalent and the particle cannot overcome the potential barrier. From another point of view, this limit corresponds to the infinite volume limit in which we could consider the x process as describing a global system where diffusion is forbidden (Arnold 1979).

In the opposite limit (large values of γ), the stochastic term is much greater than the drift one, and the particle no longer sees the periodicity of the potential: its behaviour is the one we expect for a free particle subjected to random pulses, that is to say a Brownian motion with a Gaussian distribution.

4. Long-times x moments

Among the possibilities I have to show the whole statistics of the process, I single out the clearest method (even if it is not mathematically rigorous).

The considerations made before suggest scaling the time so that it is possible to study easily the equation in the perfectly known limit $\lambda/\gamma\to 0$ (Wiener process) and to construct a perturbative theory around this known limit by introducing a small periodic potential.

Let us define the time $\bar{t}=\gamma\tau/\lambda$ so that the equation for the x process becomes

$$\mathrm{d}x=\eta c(x)\,\mathrm{d}\bar{t}+\mathrm{d}w(\bar{t}) \qquad \text{where } c(x)=\tfrac{1}{2}\sin 2x,\ \eta=\lambda/\gamma. \tag{9}$$

For $\eta\to 0$ it is possible to construct a perturbative expansion in η, and to study the x moments up to any order in η. By Ito's method, it is possible to construct the x moments:

$$\mathrm{d}\langle x^n\rangle/\mathrm{d}\bar{t}=\eta n\langle x^{n-1}c(x)\rangle+\tfrac{1}{2}n(n-1)\langle x^{n-2}\rangle, \tag{10}$$

which perturbatively becomes

$$\mathrm{d}\langle x^n\rangle^{(0)}/\mathrm{d}\bar{t}=\tfrac{1}{2}n(n-1)\langle x^{n-2}\rangle^{(0)}, \tag{11}$$

$$\mathrm{d}\langle x^n\rangle^{(1)}/\mathrm{d}\bar{t} = \eta n\langle x^{n-1}c(x)\rangle^{(0)} + \tfrac{1}{2}n(n-1)\langle x^{n-2}\rangle^{(1)}. \tag{12}$$

At once it may be noticed that all the odd moments are zero at any order, because they involve only the odd moments of $\mathrm{d}w(\bar{t})$. For the even moments a close set of equations solvable by induction may be written up to any order K in η.

For $n = 2$, $n = 4$ for long times, the result is (up to order η^2)

$$\langle x^2\rangle \underset{\bar{t}\to\infty}{\simeq} \left(1-\frac{\eta^2}{8}\right)\bar{t}, \qquad \langle x^4\rangle \underset{\bar{t}\to\infty}{\simeq} 3\left(1-\frac{\eta^2}{8}\right)^2 t^2. \tag{13}$$

The second moment corresponds to Galleani's result for the diffusion coefficient (see equation (7)) up to the λ/γ second-order limit.

Up to any order generally the following relation is satisfied:

$$\langle x^{2n}\rangle(t) \underset{\bar{t}\to\infty}{\simeq} (2n-1)!!\langle x^2(t)\rangle^n \tag{14}$$

so that for long times the x moments are all Gaussian ones. In the Appendix it is shown, up to order η^2, that if this relation is true for $n = 1$, it is also true for $n = l+1$. An extrapolation at any order η^k gives the relation (14) so that the effect of the introduction of the periodic potential is to change the diffusion coefficient $D = D(\lambda/\gamma)$, but for long times this introduction leaves the process statistics unchanged.

5. The α process long-times behaviour

Let me now show that the last relation is sufficient for the knowledge of the long-times behaviour of the α moments. In fact from (6), we have

$$\langle\alpha^m(t)\rangle = (\lambda/\gamma)^m\langle\sin^{2m} x\rangle \tag{15}$$

so that by a series expansion, we have

$$\langle\alpha^m(t)\rangle = N_0^{(m)} + \left(\frac{1}{2}\right)^{2m-1}\frac{\lambda}{\gamma}\sum_{r=1}^{m}(-1)^{2m-r}\frac{2m!}{(m+r)!(m-r)!}N_r(\bar{t}) \tag{16}$$

where

$$N_0^{(m)} = (\tfrac{1}{2})^{2m}(\lambda/\gamma)^m 2m!/m!^2 \tag{16a}$$

and

$$N_r(\bar{t}) = \sum_{n=0}^{\infty}\frac{(2ri)^n}{n!}\langle x^{2n}\rangle. \tag{16b}$$

But, as has been shown before (equation (14)),

$$\langle x^{2n}\rangle \simeq x_0(n, \eta) + (2n-1)!!D\bar{t}^n + \text{terms which decay for long times}$$

so that, by trivial calculations,

$$N_r(\bar{t}) = N_0\left(r, \frac{\lambda}{\gamma}\right) + \exp(-2r^2D\bar{t}) \underset{\bar{t}\to\infty}{\simeq} N_0\left(r, \frac{\lambda}{\gamma}\right) + \mathrm{e}^{-2D\bar{t}} \tag{17}$$

where D is the diffusion coefficient calculated by Galleani (equation (7)) and $N_0(\lambda/\gamma)$ can be calculated directly from the steady generative function (De Pasquale *et al* 1980)

$$G_s(z)=\frac{\int_0^{\pi/2} dx \exp[-(\lambda/\gamma)\cos^2 x]\exp[(\lambda/\gamma)(z-1)\sin^2 x]}{\int_0^{\pi/2} dx \exp[-(\lambda/\gamma)\cos^2 x]}.$$

There results for $r=1$

$$N_0\left(\frac{\lambda}{\gamma}\right)\simeq\frac{d\log I_0(\lambda/2\gamma)}{d(\lambda/\gamma)}\frac{1}{I_0(\lambda/2\gamma)}\qquad\begin{cases}\underset{\lambda/\gamma\to 0}{\simeq} O(\lambda/\gamma)\\ \\ \underset{\lambda/\gamma\to\infty}{\simeq}\frac{1}{2}-O(\gamma/\lambda)\end{cases}\tag{18}$$

where $I_0(\lambda/2\gamma)$ is the modified Bessel function.

Let us study for a moment the relation (17): by remembering (7), we see that the decay process to the steady state is governed by λ/γ. We know that the Bessel function $I_0(\lambda/2\gamma)\simeq_{\lambda/\gamma\to 0}1+\frac{1}{4}(\lambda/2\gamma)^2$ and diverges as $(\pi\lambda/\gamma)^{-1/2}\exp(\lambda/2\gamma)$ (Abramowitz and Stegun 1970) for $\lambda/\gamma\to\infty$, so that for long times we can expect a very slow decay to the steady state in the limit of large volumes. This behaviour can be compared with the case of the ordinary regime in which $V(x)$ is a simple well in the range $(0-\pi/2)$ (when $\nu>\lambda/2$, $\mu>\gamma$). In this case a perturbative expansion around $\gamma=0$ gives

$$\langle N\rangle \underset{t\to\infty}{\simeq}\frac{\nu-2\mu}{\lambda-\mu}(1-e^{-(\lambda-\mu)t})+\frac{\lambda-\mu}{\gamma}+O(\gamma^2)\tag{19}$$

so that we have a passage from a decay $e^{-(\lambda-\mu)t}$, which for $\mu\to\gamma$ is $e^{-\lambda t}$, to a decay $\exp[-\frac{1}{2}\pi\lambda t\exp(-\lambda/\gamma)]$ which is a much slower one.

6. Conclusion

We have studied the MV model in the particular case in which $\nu=\lambda/2$, $\mu=\gamma$ and we have seen that its process can be analysed through the process of a particle in a one-dimensional periodic potential; we have seen that such a process is a Gaussian one for long times so that we have calculated the long-time population moments and have shown that the point $\nu=\lambda/2$, $\mu=\gamma$ is an instability point in which we have a passage from a behaviour $e^{-\lambda t}$ to a behaviour $\exp[-\frac{1}{2}\pi\lambda t\exp(-\lambda/\gamma)]$.

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Appendix

The set of equations for the even moments of the x process is

$$d\langle x^{2n}\rangle^{(K)}/d\bar{t}=\eta n\langle x^{2n-1}\sin 2x\rangle^{(K-1)}+n(2n-1)\langle x^{2n-2}\rangle^{(K)},\tag{A1}$$

$$\frac{d\langle x^{2n-1}\sin 2mx\rangle^{(K)}}{d\bar{t}}=\eta\frac{2n-1}{4}[\langle x^{2n-2}\cos 2(m-1)x\rangle^{(K-1)}-\langle x^{2n-2}\cos(m+1)x\rangle^{(K-1)}]$$
$$+\tfrac{1}{2}m\eta\langle x^{2n-1}\sin 2(m+1)x\rangle^{(K-1)}-\langle x^{2n-1}\sin 2(m-1)x\rangle^{(K-1)}$$
$$+(2n-1)(n-1)\langle x^{2n-3}\sin 2mx\rangle^{(K)}$$
$$+2m(2n-1)\langle x^{2n-2}\cos 2mx\rangle^{(K)}-\tfrac{1}{2}(2m)^2\langle x^{2n-1}\sin 2mx\rangle^{(K)}, \qquad \text{(A2)}$$

$$\frac{d\langle x^{2n-2}\cos 2mx\rangle^{(K)}}{d\bar{t}}=\frac{n-1}{2}\eta[\langle x^{2n-3}\sin 2(m+1)x\rangle^{(K-1)}-\langle x^{2n-3}\sin 2(m-1)x\rangle^{(K-1)}]$$
$$-\tfrac{1}{2}m\eta[\langle x^{2n-2}\cos 2(m-1)x\rangle^{(K-1)}-\langle x^{2n-2}\cos 2(m+1)x\rangle^{(K-1)}]$$
$$+(n-1)(2n-3)\langle x^{2n-4}\cos 2mx\rangle^{(K)}-2m(2n-2)\langle x^{2n-3}\sin 2mx\rangle^{(K)}$$
$$-\tfrac{1}{2}(2m)^2\langle x^{2n-2}\cos 2mx\rangle^{(K)} \qquad K, m, n=0, 1, 2, \ldots. \qquad \text{(A3)}$$

This is a closed system up to any order and it can be solved by induction. In fact, for long times this set of equations can be written, up to order η^2,

$$\frac{d\langle x^{2n}\rangle}{d\bar{t}}\underset{\bar{t}\to\infty}{\simeq}\eta n\langle x^{2n-1}\sin 2x\rangle^{(1)}+n(2n-1)[\langle x^{2n-2}\rangle^{(0)}+\langle x^{2n-2}\rangle^{(2)}], \qquad \text{(A4)}$$

$$\frac{d\langle x^{2n-1}\sin 2x\rangle^{(1)}}{d\bar{t}}\underset{\bar{t}\to\infty}{\simeq}\frac{2n-1}{4}\eta\langle x^{2n-2}\rangle^{(0)}+2(2n-1)\langle x^{2n-2}\cos 2x\rangle^{(1)}-2\langle x^{2n-1}\sin 2x\rangle^{(1)}, \qquad \text{(A5)}$$

$$\frac{d\langle x^{2n-2}\cos 2x\rangle^{(1)}}{d\bar{t}}\underset{\bar{t}\to\infty}{\simeq}-\frac{\eta}{2}\langle x^{2n-2}\rangle^{(0)}-2\langle x^{2n-2}\cos 2x\rangle^{(1)}, \qquad \text{(A6)}$$

where it has been observed that η-order terms decay rapidly; for long-times terms as $\langle x^k\cos 2(m+1)x\rangle$, $\langle x^k\sin 2(m+1)x\rangle$ equally decay and terms as $\langle x^{2n-k-1}\sin 2mx\rangle$, $\langle x^{2n-k-1}\cos 2mx\rangle$ are negligible because small compared with $\langle x^{2n-k}\sin 2mx\rangle$, $\langle x^{2n-k}\cos 2mx\rangle$ respectively. By supposing that relation (14) is true for $n=l$, the solution of this set of equations (A4)–(A6) gives, by using (13), for $n=l+1$:

$$\langle x^{2l}\cos 2x\rangle^{(1)}\underset{\bar{t}\to\infty}{\simeq}-\frac{\eta}{4}(2l-1)!!\bar{t}^l,$$

$$\langle x^{2l+1}\sin 2x\rangle^{(1)}\underset{\bar{t}\to\infty}{\simeq}(2l+1)!!\left(\frac{\eta}{8}-\frac{\eta}{4}\right)\bar{t}^l,$$

so that by trivial calculations

$$\langle x^{2(l+1)}\rangle\underset{\bar{t}\to\infty}{\simeq}(2l+1)!!(1-\tfrac{1}{8}\eta^2)^{l+1}\bar{t}^{(l+1)} \qquad \text{(A7)}$$

where we have put $(1-\frac{1}{8}\eta^2)^l\simeq 1-l\eta^2/8$. This can be done for any order, so that it is established that for long times the x process is Gaussian.

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