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Study and modelling of a density dependent population using faltung (closed cycle type) equations

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Abstract *Faltung equations (closed cycle type) have a wide range of biological applications, nonetheless, they are poorly studied. We use a Volterra-Kostitzin model (which is a Faltung equation) to study the dynamics of a certain species, where the integral term represents a residual action. The complexity of resolution of this non-linear equation using classical numeric methods is here solved with the Adomian decomposition method. Our method provides the same graphic solution as others do, such as the numeric method Miladie. However, the decomposition method of Adomian has the advantage that neither time nor space are considered discontinuous and that it gives an analytical solution with a reliable approximation.*

1. Introduction

Faltung type equations, generally called convolution or closed cycle type (Tricomi, 1957), are a special kind of Volterra equation, incorporating convolution products. Integro-differential equations used by Volterra (1930) in the study of hereditary phenomena are applicable to biology in the study of fluctuations of the number of individuals of a species. This hereditary phenomenon is understood from a mathematics-physics point of view (electricity, electromagnetism, energy), not from a biological one. This means that the population at a time t not only depends on the initial conditions of the system, but on the past.

1.1 From Malthus to Volterra-Kostitzin models

Mathematical modelling of a single species began with Malthus, who in 1798, described exponential growth (equation (1)) (Malthus, 1798). Later, Verhulst (1838) introduced the logistic term to describe the reduction of growth rate at high population densities (equation (2)), K being the carrying capacity, where

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births equal deaths and thus, there is no net population change. dP/dt is positive for $P < K$, and dP/dt is negative for $P > K$. Rates of population growth and decline are influenced by r, the intrinsic growth rate.

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP, \tag{1}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP\left(\frac{1-P}{K}\right). \tag{2}$$

Later, Pearl (1925, 1927), and Pearl and Reed (1920) insisted that logistic growth should be considered as a population regulation law, applicable to all kind of populations. This self-regulation would allow a population to persist without extinction or explosion. However, it was poorly received due to Pearl's insistence that the equation should be considered as an universal law.

Subsequently, Régnier and Lambin (1934) conducted growth experiments on individual bacterial strains in a non-renewed medium. These experiments showed a kind of growth which fitted neither exponential nor logistic growth. This was because, after the growth and stabilization phases, the number of individuals decreased.

It was at this point when Régnier enquired about this phenomenon of Volterra. Volterra and his son-in-law, D'Ancona, explained that after the initial development stages, there was an intoxication of the meadow due to the excreted by-products of the bacteria (Régnier and Lambin, 1934; Israel and Millan-Gasca, 1993 p. 169). To model this latter decreasing stage, termed *residual action* or *toxic action*, Volterra introduced an integral term into the equation (2). He had applied the concepts of physics, where integro-differential equations were used to study elastic bodies that exhibit hereditary properties (Volterra, 1930) (equation (3)).

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \left(\varepsilon - hP(t) - \int_t^0 P(\tau)f(\tau)\mathrm{d}\tau\right)P(t), \tag{3}$$

where *hP(t)* models the Verhulst-Pearl effect and the integral term reflects the influence of the intoxication. Laboratory results were described in biological terms by Régnier and Lambin (1934) and in mathematical terms by Volterra (1934). The latter author studied the expression (3) qualitatively, and only offered an exact solution in a particular case, where the Verhulst-Pearl effect equals zero and f is a constant, so the resulting approximation did not offer a reliable approximation to the experimental data of Régnier and Lambin. In the same paper, Volterra also studied the co-existence of two species, superimposing the toxic effect of both species.

It was then Kostitzin, a close friend of Volterra, found a general solution to equation (3). He drew up an explicit calculus of the coefficients ε, h, and c,

where $f(t) = c$ (Kostitzin, 1935). The author pointed out that during the first stage of population growth, its dynamics differed little from Malthus growth (1). As culture progressed, however, the toxic action increased its effects (he termed this *residual action*), modifying the logistic dynamics.

Kostitzin solution was applied to isolated culture dynamics, offering a good fit, although with small deviations, due to other factors such as food or space (Kostitzin, 1937a). This model was also applied to organism growth (Kostitzin, 1937b) and population extinction (Kostitzin 1937a) improving fitting to experimental data, since Volterra's theoretical analysis foresaw an extinction in an infinite time, while experimental data offered extinction in a finite time.

Kostitzin published the latter paper on residual action together with Volterra in 1938 (Kostitzin and Volterra, 1938). In this latter paper, they discussed the new experiment by Régnier and Lambin (1938) on bacteria population when there was no food limitation, and where the Verhulst-Pearl effect and the residual action were treated together (4).

1.2 Biological applications

Volterra-Kostitzin (V-K) dynamics can be applied to a broad range of populations that exhibit some kind of density-dependence (direct or inverse density dependence).

Direct density dependence is defined as a change in the influence of an environmental factor – a density dependent factor – that affects population growth as population density changes, tending to retard population growth, by increasing mortality or decreasing fecundity, as population density increases, or to enhance population growth, by decreasing mortality or increasing fecundity, as density decreases.

Inverse density dependence is defined as a change in the influence of an environmental factor – a density dependent factor – that affects population growth as population density changes, tending to enhance population growth, by decreasing mortality or increasing fecundity, as population density increases, or to retard population growth, by increasing mortality or decreasing fecundity, as density decreases. The Allee effect is an example of inverse density dependence, where as populations become very small, the per capita birth rate declines because of failure of sexual organisms to find mates, or death rates can also increase at small population sizes because of loss of any survival advantages of being in groups (Allee *et al.* 1949).

After the studies of density dependent self-regulation by Kostitzin, Volterra and Régnier, more studies appeared against their model than in its favor. It was in the 1990s that density-dependence was considered a self-regulation process in many populations. Andrewartha and Birch (1954) insisted that only climate controlled insect population abundance. Nicholson (1958) suggested that density dependence was necessary for regulation, but pointed out that no appropriate methods were available to test density dependence. Maelzer (1970) criticized the density dependence testing methods. First light appeared with

Bulmer (1975) who improved statistics to test for density dependence. Dempster (1983) reviewed the density dependence frequency in some insects, and he stated that it was very infrequent. However, after applying modern statistics, density dependence appeared to be very common, although in some cases it was camouflaged due to time lags (Turchin, 1990; Woiwod and Hanski, 1992) even in Dempster's original data (Hoyloak, 1993).

The (V-K) equation has other applications apart from population dynamics; it may also be applied to: (1) molecular processes such as the synthesis of the protein *fibroin* (main component of silk) in the worm *Bombyx mori*. In this case, the integral term reflects the inhibiting effect of the RNA-degrading enzyme on the RNA that codifies the protein (Fournier, 1974; Prudhomme, 1976); (2) embryo and individual development; and (3) bacterial growth modelling in human and veterinarian pharmacological problems, such as the growing dynamics of *Staphiloccocus aureus* modelled by Renard *et al.* (1993), who used both the logistic and the V-K approach, both being similar adjustments due to the low value of the integral term in the V-K model.

Furthermore, the growth characteristics described by the V-K when $c < 0$ has a wide application field in cell, tissue and micro-organism cultures, such as bacterium, fungi or yeast, where a death phase, or low growth phase, occurs after the exponential phase.

The most common application of the V-K model is for modelling the dynamics of a density variable (N) over time, which once trespassing a threshold, affects N positively (inverse density dependence) or negatively (direct density dependence). Nonetheless, the V-K model has been used to analyse the relationship between two variables. These are RNA-degrading enzyme over RNA concentration per gland (Pavé, 1997); in fish populations, egg-production over recruitment (Beveton and Holt, 1957, p.56, 278; Ricker, 1954), where high population forces a negative density-dependent relationship between both variables. Woiwod and Hanski (1992) used a regression method based on Ricker equation to detect density dependence.

In this paper, we model the dynamics of a certain species where the integral term of the integro-differential equation represents a *residual action*. The complexity of resolution of this non-linear equation, using classical numeric methods, is solved here with the new proposed decomposition method by Adomian. We also graphically compare the modelling results with Miladie method (Pave and Lebreton, 1973). We have taken up the V-K model again because, although it could be useful for several applications, the model has not been studied nor applied sufficiently.

2. The model

We express the V-K model by a simplified integro-differential equation, introduced by Kostitzin (1937b, p. 161):

$$\frac{dP(t)}{dt} = \varepsilon P^k - hP^{k+1}(t) - cP^k \int_t^0 P^m(\tau)d\tau, \quad \forall P, \tag{4}$$

where P is the number of individuals in the population, t is time, ε, h and c are constants and positive parameters. Kostitzin considered $c > 0$, so the integral term acted as a negative feed-back (direct density-dependence). However, it could also act as a positive feed-back when $c < 0$ (inverse density-dependence). Consider that when $h = 0$ and $c = 0$, then the equation (4) becomes equation (1). When $c = 0$, then equation (4) becomes equation (2), which is the logistic growth model of Verhulst.

In closed populations with an intoxication factor dependent on population density, their dynamics can generally be expressed as follows:

$$P'(t) = aP(t) - bP^2(t) - cP(t) \int_0^t k(t - \tau)\, P(\tau)\, d\tau \tag{5}$$

where $k(t-\tau)$ is a function that represents a residual action function, which is also decreasing and which can be considered without loosing generality as $k(t - \tau) = 1$.

Then, the equation (4) can be expressed as the following:

$$P'(t) = aP(t) - bP^2(t) - cP(t)\, Q(t), \tag{6}$$

where

$$Q(t) = \int_0^t P(\tau)\, d\tau \Rightarrow P(t) = Q'(t) \text{ and } P'(t) = Q''(t).$$

Then, the equation (6) would be

$$Q'' = aQ' - bQ'^2 - cQ'Q \tag{7}$$

with the initial conditions $Q(0) = 0$ and $Q'(0) = P(0) = P_0$.

This results in a non-linear second order differential equation, for which it is not possible to find the explicit solution, but only approximations can be made in parametric form as follows:

$$P = w(Q) = \frac{a}{b} + \frac{c}{b^2} - \frac{cQ}{b} - \left(\frac{a}{b} + \frac{c}{P^2} - P_0\right) e^{-bQ} \tag{8a}$$

$$t = \int_0^Q \frac{d\delta}{w(\delta)} \tag{8b}$$

Equation (8(a) and (b)) give the population P in time t, expressed as a function of the parameter q, where the population P cannot be negative. Furthermore, the solution of equation (7) can only be expressed in parametric form, and equation (8(b)) has no integrable integrate, which means that it cannot be solved numerically. As a result, this model has not been used more frequently. Thus, the use of the proposed numeric method (decomposition method) will allow this kind of equation to be dealt with and their solutions compared with those of other methods used previously, e.g. for qualitative analysis (Pavé, 1997) and numeric analysis (Pavé and Lebreton, 1973).

3. An introduction and presentation of the decomposition method of Adomian

In the early 1980s, Professor G. Adomian introduced a new, powerful and unique method that solved a wide range of functional equations (algebraic, differential, integral, integro-differential and partial differential Equations). It has been proven that this method is particularly effective in solving mathematical modelling of biomedical systems (Grimalt, 1995a, b). A complete introduction can be seen in Adomian (1990); convergence problems, in Abbaoui *et al.* 2001; applications to differential equations systems, in Grimalt and Pujol (1999), and Guelall *et al.* (1997); and applications to partial differential equations, in Guelall *et al.* (2000).

In brief, Adomian's method involves finding a solution in the form of a series, when it exists, and decomposing a non-linear operator within a series (series substitution) where each term can be calculated recurrently using polynomials called Adomian polynomials. Under certain convergence conditions, the sum of the series is exact, and generally, the series is truncated. The error can also be calculated by giving an approximation.

Consider the non-linear functional equation

$$u - N(u) = f, \tag{9}$$

where N is a non-linear operator and f is a known function. N and f defined in a certain space (Hilbert or Banach).

The problem involves finding a solution to equation (9) in the form of a series, that is

$$u = \sum_{n=0}^{\infty} u_n, \tag{10}$$

and decomposing the non-linear term

$$N(u) = \sum_{i=0}^{\infty} A_i, \tag{11}$$

where A_i are the Adomian polynomials, which depend exclusively on $u_0, u_1 \ldots u_n$ which can be obtained from the formula

$$A_n = \frac{1}{n!} \frac{\mathrm{d}^n}{\mathrm{d}\lambda^n} \left[N\left(\sum_{i=0}^{\infty} \lambda^i u_i \right) \right]_{\lambda=0} \tag{12}$$

Replacing equations (10) and (12) in equation (9)

$$\sum_{n=0}^{\infty} u_n - \sum_{n=0}^{\infty} A_n = f, \tag{13}$$

the terms of the series solve $\sum_{n=0}^{\infty} u_n$ can be obtained by means of identification in equation (13).

$$\left.\begin{aligned} u_0 &= f \\ u_1 &= A_0 \\ &\vdots \\ u_{n+1} &= A_n \end{aligned}\right\} \quad \text{Adomian scheme for } n = 0, 1, \ldots \tag{14}$$

By using this method, the solution series of equation (9) are determined.

3.1 Resolution of the V-K model by the Adomian decomposition method

We shall now solve the V-K model using the Adomian decomposition method. Given the integro- differential equation n(10), we assume the initial conditions $Q(0) = 0$ and $Q'(0) = P_0$.

The Canonical equation is

$$Lu + Ru + Nu = f, \tag{15}$$

where L is a differential operator, R is a lineal operator, N is a non-linear operator and f is a known function.

Applying the decomposition method, the solution takes the form

$$u(t) = \sum_{k=0}^{n-1} \frac{(t-t_0)^k}{k!} u^k(t_0) + L^{-1}f(t) - L^{-1}R\left(\sum_{n=0}^{\infty} u_n(t)\right) - L^{-1}\left(\sum_{n=0}^{\infty} A_n\right), \quad A_n = \frac{1}{n!}\frac{\mathrm{d}}{\mathrm{d}\lambda^n}\left(N\left(\sum_{n=0}^{\infty} u_n\lambda^n\right)\right)_{\lambda=0}, \tag{16}$$

where $LQ = \mathrm{d}^2Q/\mathrm{d}t^2$, $NQ = b\left(\mathrm{d}Q/\mathrm{d}t\right)^2 + cQ\,\mathrm{d}Q/\mathrm{d}t$, $RQ = -a\,\mathrm{d}Q/\mathrm{d}t$, $n = 2$, $t_0 = 0$ and $f = 0$.

Identifying terms in equation (16) we have the Adomian schema

$$\begin{aligned} u_0 &= \sum_{k=1}^{n-1} \frac{(t-t_0)^k}{k!} u^k(t_0) + L^{-1}f \\ u_1 &= -L^{-1}u_0 - L^{-1}A_0 \\ u_2 &= -L^{-1}u_1 - L^{-1}A_1 \\ u_3 &= -L^{-1}u_2 - L^{-1}A_2 \\ &\vdots \\ u_{n+1} &= -L^{-1}Ru_n - L^{-1}A_n \end{aligned} \tag{17}$$

Knowing that $LP = \mathrm{d}^2P/\mathrm{d}t^2$, we obtain the following schema

$$\begin{aligned} u_0 &= \sum_{k=o}^{1} \frac{(t-0)^k}{k!} u^k(0) + \int_0^t \int_0^t 0\,\mathrm{d}\tau \\ u_1 &= -\int_0^t \int_0^t Ru_0\,\mathrm{d}\tau - \int_0^t \int_0^t A_0\,d\tau \\ u_2 &= -\int_0^t \int_0^t Ru_1\,d\tau - \int_0^t \int_0^t A_1\,\mathrm{d}\tau \\ &\vdots \\ u_{n+1} &= -\int_0^t \int_0^t Ru_n\,\mathrm{d}\tau - \int_0^t \int_0^t A_n\,\mathrm{d}\tau \end{aligned}$$

We use this iterative method to calculate the terms of the series.

We obtain the following terms u_i of the Adomian polynomials using an iterative process ($q = p_0$).

$$u(0) = tq$$

$$u(1) = \frac{1}{2}aqt^2 - \frac{1}{2}bq^2t^2 - \frac{1}{6}ct^3q^2$$

$$u(2) = -\frac{1}{2}bq^2at^3 + \frac{1}{3}b^2q^3t^3 + \frac{5}{24}bq^3ct^4 - \frac{1}{6}acq^2t^4 + \frac{1}{30}c^2q^3t^5 + \frac{1}{6}a^2qt^3$$

$$u(3) = -\frac{1}{4}t^4b^3q^4 - \frac{7}{24}bt^4a^2q^2 - \frac{17}{2520}c^3q^4t^7 + \frac{17}{360}ac^2q^3t^6 + \frac{1}{24}a^3qt^4$$
$$- \frac{11}{120}cq^2a^2t^5 - \frac{9}{40}cq^4t^5b^2 + \frac{1}{2}t^4aq^3b^2 - \frac{49}{720}bc^2q^4t^6 + \frac{37}{120}bq^3ct^5a$$

$$\vdots$$

4. Graphic representation of V-K dynamics

4.1 Basic graphs

Using the decomposition method, we only had to calculate up to seven terms of the series to obtain suitable graphics. Figures 1-4 show the variation of a given population (P) over time under different constant values, which reflect different particular cases. Figure 1 shows exponential growth (note that b and c equal 0). Figure 2 shows logistic growth and Figures 3 and 4 show V-K dynamics.

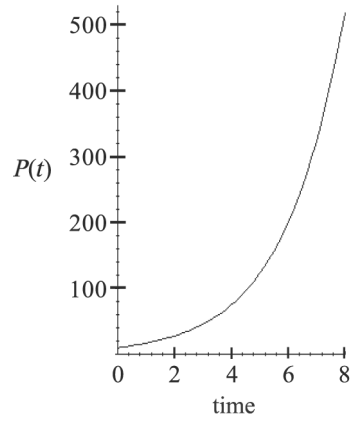


Figure 1.
Exponential population evolution under constant values

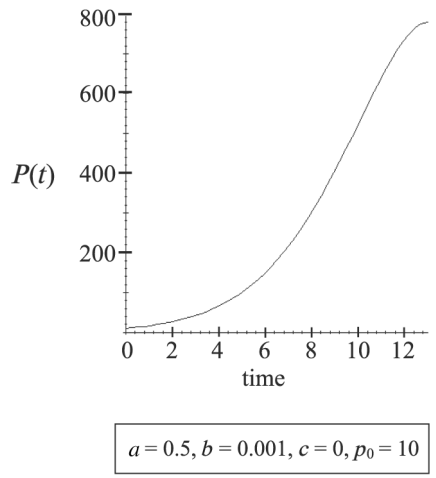


Figure 2.
Logistic population evolution under constant values

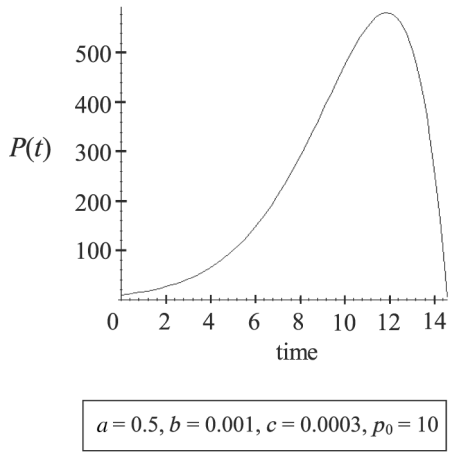


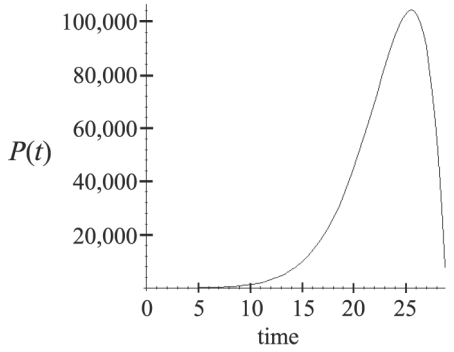
Figure 3.
V-K population evolution under constant values

Graphs 1-4 have been obtained from the polynomials calculated by Adomian decomposition.

The most important breakthrough of the decomposition method is that by using only a few terms of the series and easy and programmable no-operations, we may obtain an explicit solution of a non-linear second order differential equation, in contrast to the previously applied Miladie method (Pavé and Lebreton, 1973) that gives a parametric solution.

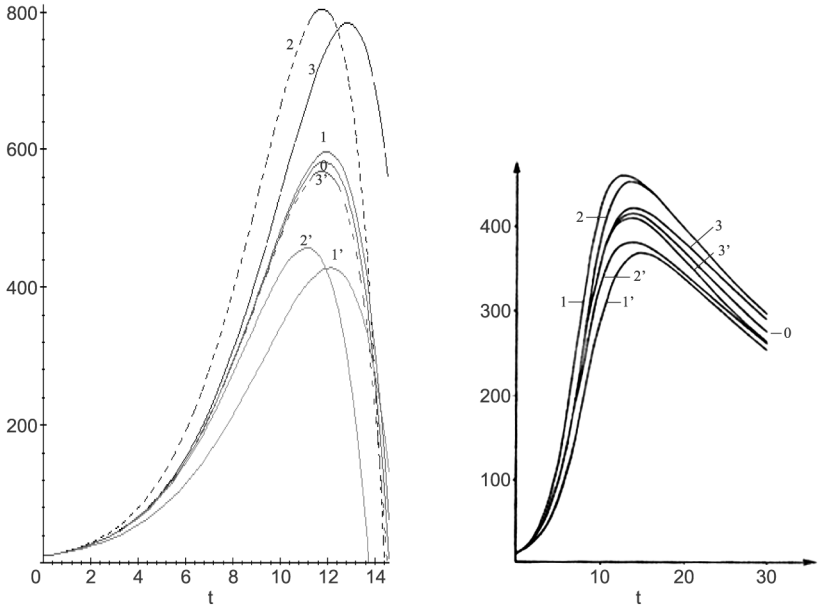
4.2 Graphic comparison of the Adomian results with the Miladie method

The Miladie resolution method was applied by Pavé and Lebreton (1973). In these graphs we make a graphic comparison between the Miladie results and the Adomian's, for different values of a, b, c and p_0 (Figure 5).



$a = 0.5$, $b = 0$, $c = 0.00003$, $p_0 = 10$

Figure 4.
V-K population evolution under constant values



0: reference curve; $a = 0.5$; $b = 0.001$; $c = 0.00003$; $p_0 = 10$; 1: $a = 0.55$;

2: $b = 0.0009$; 3: $c = 0.000033$; 1': $a = 0.45$; 2': $b = 0.0011$; 3': $c = 0.000027$

Figure 5.
Evolution of p over time t. Left, graphs from Adomian method; right, graph obtained from Miladie method

5. Discussion

The re-adjustment by a V-K model of experimental data previously considered logistic, could improve the fitting, provide more information on growth phases and reveal the presence of any constraint, which may not have been considered by the logistic model. Thus, a reasonable application of the V-K model could offer new data about the dynamics of many biological variables, since many of them share a compatible dynamics with the proposed method.

We have reviewed the V-K model because of two reasons. Firstly, the mathematical difficulty involved in its solution, and, secondly, the broad field of applications, from population dynamics at any scale to the relationship between the two biological variables (see introduction).

From a mathematical point of view, we introduce the decomposition method, which allows the solution of the model to be obtained through a series with not more than five or seven terms. This means that the V-K dynamics may be represented graphically. Furthermore, our method provides the same graphic solution as others do, such as the numeric Miladie method (Pave and Lebreton, 1973). However, our decomposition method (Adomian) has the advantage that neither time nor space are considered discontinuously, providing an analytical solution with a reliable approximation.

References

Abbaoui, K., Pujol, M.J., Cherrault, Y., Himoun, H. and Grimalt, P. (2001), "A new formulation of Adomian method: convergence result", *Kybernetes*, Vol. 30 Nos 9/10, pp. 1183-91.

Adomian, G. (1990), "A review of the decomposition method and some results for non-linear equations", *Math. Comput. Modeling*, Vol. 13, pp. 17-43.

Allee, W.C., Emerson, A.E., Park, O., Park, T. and Schmidt, K.P. (1949), "Principles of animal ecology", in W.B. Saunders publishers, Philadelphia, USA.

Andrewartha, H.G. and Birch, L.C. (1954), "The distribution and abundance of animals", University of Chicago Press, Chicago, IL, USA.

Beverton, J.H. and Holt, S.J. (1957), "On the dynamics of exploited fish populations", Chapman and Hall, London, UK.

Bulmer, M.G. (1975), "The statistical analysis of density dependence", *Biometrics*, Vol. 31, pp. 901-11.

Fournier, A. (1974), "Contribution à l'étude de l'adaptation fonctionelle quantitative des tRNA à la biosynthèse protéique", PhD thesis, Lyon.

Grimalt, P. (1995a), "Modelos Determinísticos en el campo de la Medicina y Biología", *Arbor (CSIC)*, Vol. 591, pp. 133-50.

Grimalt, P. (1995b), "El Método de Descomposición y sus aplicaciones a Problemas Biomédicos", *Revista Academia Canaria de Ciencias*, Vol. 7, pp. 41-152.

Grimalt, P. and Pujol, M.J. (1999), "The decomposition method applied to chemistry kinetics", *Int. J. Informacion Tecnologica*, Vol. 10, pp. 129-32.

Guelall, S., Grimalt, P. and Cherrault, Y. (1997), "Numerical study of Lorenz's equation by the Adomian method", *Computer Math. Applied*, Vol. 23, pp. 25-9.

Guellal, S., Pujol, M.J., Grimalt, P. and Cherrault, Y. (2000), "The decomposition method applied to hydrology", *Kybernetes*, Vol. 29, pp. 499-504.

Hoyloak, M. (1993), "The frequency of detection of density dependence by means of regression", *Oecologia*, Vol. 10, pp. 347-72.

Israel, G. and Millan-Gasca, A. (1993), La correspondencia entre Vladimir A. Kostitzin y Vito Volterra (1933-1962) y los inicios de la biomatemática, *Llull*, Vol. 16, pp. 159-224.

Kostitzin, V. (1935), "Sur l'intoxication d'un milieu par les produits cataboliques d'une population", *Comptes Rendus de l'Académie des Sciences de Paris*, Vol. 201, pp. 516-18.

Kostitzin, V. (1937a), "Sur une généralisation des équations biologiques dans le cas d'une population intoxiquée par les produits de son activité chimique", *Comptes Rendus de l'Académie des Sciences de Paris*, Vol. 204, pp. 1683-5.

Kostitzin, V. (1937b), "Biologie mathématique", Armand Colin, Paris, France.

Kostitzin, V. and Volterra, V. (1938), "Remarques sur l'action toxique du milieu à propos de la note de M. Régnier et Mlle. Lambin", *Comptes Rendus de l'Académie des Sciences de Paris*, Vol. 207, pp. 1146-8.

Maelzer, D.A. (1970), "The regression of $log(Nn+1)$ on $log(Nn)$ as a test of density-dependence: an exercise with computer constructed density-independent populations", *Ecology*, Vol. 51, pp. 810-22.

Malthus, T. (1798), *Essay on Populations*, St. Paul's Church-Yard, London.

Nicholson, A.J. (1958), "Dynamics of insect populations", *Annual Review of Entomology*, Vol. 3, pp. 107-36.

Pavé, A. (1997), "Modelisation en Biologie et en Ecologie", Aleas, Paris.

Pavé, A. and Lebreton, J.D. (1973), "Miladie: un minilanguage pour le traitement numérique d'equations differentielles et de recurrence", *Revue Française d'Automatique, Informatique et Recherche Opérationnelle (RAIRO)*, Vol. 2, pp. 73-9.

Pearl, R. (1925), "The biology of population growth, A.A", Knopf, New York.

Pearl, R. (1927), "The growth of populations", *Quarterly Review of Biology*, Vol. 2, pp. 532-48.

Pearl, R. and Reed, L. (1920), "On the rate of growth of population of the United States since 1790 and its mathematical representation", *Proceedings of the National Academy of Sciences*, Vol. 6 No. 6, pp. 275-88.

Prudhomme, J.C. (1976), "Contribution à l'étude de la biosynthèse de la soie dans la glande sérigène de Bombyx mori", PhD dissertation, Lyon, France.

Régnier, J. and Lambin, S. (1934), "Etude d'un cas d'antagonisme microbien (Bacillus Coli-Staphyloccoccus aureus)", *Comptes Rendus de l'Académie des Sciences de Paris*, Vol. 199, pp. 1682-3.

Régnier, J. and Lambin, S. (1938), "Etude sur le croît microbien en fonction de la quantité de substance nutritive des milieux de culture", *Comptes Rendus de l'Académie des Sciences de Paris*, Vol. 207, p. 1263.

Renard, L., Sanders, P. and Laurentie, M. (1993), "M. Modélisation de l'effet bactéricide de la spiramycine. Choix d'un modèle pharmacodynamique", *Veterinarian Research*, Vol. 24, pp. 33-45.

Ricker, W.E. (1954), "Stock and recruitment", *J. Fish. Res. Bd. Canada*, Vol. 11, pp. 559-623.

Tricomi, F.G. (1957), "Integral equations", Interscience Publisher, New York.

Turchin, P. (1990), "Rarity of density dependence or population regulation with lags?", *Nature*, Vol. 344, pp. 660-3.

Verhulst, P.F. (1838), "Recherches mathématiques sur la loi d'accrossement de la population", *Mémoires de l'Académie Royal Bruxelles*, Vol. 18, pp. 1-38.

Volterra, V. (1930), "Theory of functionals and of integral and integro-differential equations", Blackie and Son Limited, London, Glasgow, UK.

Volterra, V. (1934), "Remarques sur la note de M. Régnier et Mlle. Lambin", *Comptes Rendus de l'Académie des Sciences de Paris*, Vol. 199, pp. 1684-6.

Woiwod, I.P. and Hanski, I. (1992), "Patterns of density dependence in moths and aphids", *Journal of Animal Ecology*, Vol. 61, pp. 619-29.