MONTE CARLO SIMULATION OF AN ECOSYSTEM : A MATCHING BETWEEN TWO LEVELS OF OBSERVATION

Antoni GIRÓ
J.A. PADRÓ
J. VALLS
J. WAGENSBERG

RR84/01

RESUM

Mitjançant el mètode de Monte-Carlo s'ha dissenyat un programa de Simulació per descriure l'evolució d'un ecosistema sotmés a uns lligams energètics. Els primers resultats d'aplicació a un cas senzill ens donen una bona aproximació per relacionar el comportament individual dels components i el comportament global de tot l'ecosistema, estant aquest últim, d'acord amb el seu model determinístic.

MONTE CARLO SIMULATION OF AN ECOSYSTEM: A MATCHING BETWEEN TWO LEVELS OF OBSERVATION

A. Giró
Departamento de Tecnología de Computadores
Universidad Politécnica de Barcelona
C/ Jorge Girona Salgado, 31
Barcelona-34.- SPAIN

J.A. Padró, J. Valls and J. Wagensberg †
Departamento de Termología. Facultad de Física.
Universidad de Barcelona
C/ Diagonal, 645.
Barcelona-28.- SPAIN

ABSTRACT.- A Monte Carlo computer simulation is designed in order to describe the evolution of an ecosystem under imposed environmental conditions of energy. Some preliminar results of a simple situation show a suggestive matching between the detailed random behaviours of individuals and a global deterministic model. This fact may provide a new insight into the understanding and control of biomass production processes.

1.- INTRODUCTION.- Consider the state of an ecosystem by the space-time distributions of the ecological occupation numbers, namely

$$n_j = n_j(\vec{r}\ , t) \qquad j = 1, 2, \ldots, m \qquad (1)$$

where n_j is the number of individuals of species j, $\vec{r}$ is the spatial location and t is time. Two main lines of reasoning may be adopted in order to derive such a description. The first procedure lyies on the statement of some mathematical models in the form of differential equations which integration should provide equation (1) or, at the stationary case, by postulating certain global variational principles. This is the case of the well known Lotka-Volterra equations, the logistic models of growth or certain biomass distribution functions (Lurié et al. 1983 a,b). A second procedure consists in the

† To whom correspondence should be addresed.

direct simulation of whatever happens to each individual "living" in the ecosystem concerning all the physically relevant effects, i.e. motion, nutrition, reproduction and life time. The aim of this work is to compare both approaches for a simple idealized situation. We procede in this way encouraged by the new insights obtained in Molecular Dynamics (Alder and Wainwright 1959, Rahman 1964, Verlet 1967) where the macroscopic world of the thermodinamical models of liquids is explored versus the microscopic world which is governed by the specific intermolecular potentials of particles.

As noted before, we shall represent the state of the ecosystem by a population of individuals classified in a number m of possible species. We do not take here the concept of species in the common genetic sense, but in a rather physical meaning: a species is a class of biomass value. More precisely, two individuals occupy the same species if they enter in the same -preassigned- biomass interval.

In Section 2 we show a Monte Carlo computer simulation designed in order to describe the ecosystem from the detailed point of view, that is, following the individual interactions for a simple idealized case. In Section 3 we develop a global deterministic model designed in order to describe the same phenomenon with an overall treatment. Finally, in Section 4, both results are reported and discussed.

2.-MONTE CARLO SIMULATION.- It has been shown in Physics that the microscopic simulation of matter is available using a low population of molecules ($N \sim 10^3$). The programm that we are proposing for the ecological case is able to simulate in principle a systems of about 100,000 individuals owing to ten species. In the preliminar version of the programm we consider the situation in which all individuals feed themselves from the same substrate, a set of nourrishing particles that we shall call "nutritons". Each species is characterized by its mean biomass and our working hypothesis is to accept some general properties associated to this magnitude. That is to say, we shall assume the following parameters to be specific of each class of biomass: the reproduction rate, the nourrishing rate, the maximum value of life time, the maximum consumption rate of nutrit_ons and the spatial area of influence (concerning motion or the available amount of nutrit_ons).

Moreover, two basic ideas used in Physics for the microscopic simulations of matter (Hansen and McDonald 1976, Giró et al. 1980) are incorporated to our simulation, namely: a) the periodic boundary conditions and b) the cellular grid-like structure. The former avoids the boundary effects in the system. In fact, it enables to consider the simulated spatial area as a good representation of an indefinite large ecosystem. Space is supposed to be divided in squares cells. The central cell -the cell under consideration- is in contact with eight identical cells (true copies of the central cell) through completely transparent walls (Fig. 1). In other words, when one individual leaves the central cell then the corresponding image enters through the opposite wall. Walls are therefore shockless spatial limits.

The second idea, the cellular method, is one of the time honored tools in Molecular Dynamics (Giró et al. 1979), where the time-saving or efficiency of the calculus is very important for the viability of the simulation. The cellular method for our purposes in Ecology is a natural application, since we assume that the localization of an individual is completely determined by the occupation of a certain subcell, one of the identical squares in which the central cell is subdivided (Fig. 1). The cellular method is based on the so called interaction table, a matrix that states the correspondence between each subcell and the surrounding subcells that are available according to the spatial area of influence mentioned before.

To sum up, the simulation of the time evolution of the ecosystem works as follows. It starts with an initial configuration created by the random location of each individual in a subcell and by assigning -also at random- a biomass and an age to each individual from the available ranges of values. The programm follows then each individual taking all eventual "living" effects into account: motion, nourrishement, reproduction and death. All this effects are simulated accordingly to the specific properties of each class of biomass and using the creation of random numbers in order to take the final decision for motion of each individual. Priority for nutriton feeding of individuals is also decided at random. Once this process is completed for the whole population occupying the central cell a new configuration is created. And so on. Figure 2 shows the flow chart of this programm -the Barcelonagramm- a simulator of the time evolution of an idealized ecosystem in a plane surface.

As a preliminar simulation we shall consider the simplest case, that is to say, one single species growing under a constant inflow of nutritons. We shall call this, briefly, the SN case.

3.- DETERMINISTIC POPULATION EQUATIONS.- We begin by representing the dynamics of a community of N species by a set of deterministic differential equations

$$\dot{n}_i = f_i(n_1, \ldots, n_i, \ldots, n_m, c_1, \ldots c_j, \ldots) \qquad (2)$$

where the n_i's are species abundances and the c_j's are parameters of the system that depend on the environment and the biology of the component species. We look for a particular form of equation (2) in order to describe the simple idealized case (SN): one single species that grows with a population of nutritons that are supplied at constant rate into the system. A whole spectrum of models can be recognized in the literature which ranges from the descriptive, empirical type to the general form. Using Holling's (1966) terminology we look for a "tactical" model, that is, a model that is designed to answer a specific question rather than a "strategic" model that would be devoted to examine general ecological principles. Let us therefore state for the SN case the mass-balance equations for the number of individuals n and for the number of nutritons s in the form:

$$\dot{n} = (f(n,s) - g(n,s)) \cdot n + R_n \qquad (3)$$

$$\dot{s} = -v(n,s) \cdot n + R_s \qquad (4)$$

where f(n,s) and g(n,s) are the natality and mortality functions of the species, the R's are the sums of inflows and outflows and v(n,s) is the intensity of nutritons consumption. Equations (3,4) represent in fact one particular case of the general producers-consumers equations for an ecological community (Svirezhev and Logofet 1983). Some simple considerations from the global point of view yield an explicit model for the SN case.

We first assume R_n=0. This condition is equivalent, as it was in the computer simulation, to a dynamic equilibrium between inmigrants and emigrants individuals. On the other hand we take $R_s = k_4$, a constant external supply of nutritons. In addition we state $g(n,s) = k_1$, the constant natural rate of death of the species, and we take the species' functional response f(n,s) to the mean

nutriton population density to be a linear function of the number of available nutritons per head of the population, namely $f(n,s) = k_2(s/n)$. In the Monte Carlo simulation this assumption obviously represents that in each subcell i the number of individuals n_i have s_i/n_i available nutritons per unit time and this density is equal to s/n in the averaged distribution of the population considered here by the deterministic model. The domain of vality of this term is, of course, under a certain saturation value for the nutritons, that is to say, as long as (s/n) is a limitating factor of growth.

On the other hand, v(n,s) obviously represents the amount of nutritons which one individual consumes in a unit time and we shall assume $v(n,s) = k_3$, a characteristic constant of the species voracity. Equations (3,4) read now:

$$\dot{n} = -k_1 n + k_2 s \qquad (5)$$

$$\dot{s} = -k_3 n + k_4 \qquad (6)$$

for n, s, k_1, k_2, k_3, k_4 being positive. The population adapts itself to the external constraints $n(\infty) = (k_4/k_3)$ following the typical transitory evolution of a damped oscillator subjected to an external constant force. Indeed, by eliminating s by substituting equation (6) into the derivative of equation (5) we may rewrite both equations in the form

$$\ddot{n} + k_1 \dot{n} + k\, n = k_0 \qquad (7)$$

where $k = k_2 k_3 > 0$ and $k_0 = k_2 k_4 > 0$. Equation (7) has a well known analytic solution depending on the condition $k_1^2 \gtrless 4k$:

a) If $4k > k_1^2$ the trend of the population shows damped oscillations when approaching to the stationary state

$$n(t) = A\, e^{-\gamma t} \cos(\omega t + \theta) + n(\infty) \qquad (8)$$

where $\gamma = k_1/2$, $\omega = (k - (k_1/2)^2)^{1/2}$ and where the constants A and θ depend on the initial conditions, i.e. quantity n(0) and quality $\dot{n}(0)$ of the initial population.

b) If $4k < k_1^2$ the population approaches aperiodically the same final stationary state value $n(\infty)$

$$n(t) = C\, e^{-\gamma_1 t} + C'\, e^{-\gamma_2 t} + n(\infty) \qquad (9)$$

where $\gamma_1 = (k_1/2) + ((k_1/2)^2 - k)^{1/2}$ and $\gamma_2 = (k_1/2) - ((k_1/2)^2 - k)^{1/2}$

and where C and C' depend on the initial conditions.
c) $4k = k_1^2$ corresponds to the critical behaviour between the overdamped case a) and the underdamped case b), namely

$$n(t) = (C + C't)\, e^{-\gamma t} + n(\infty) \qquad (10)$$

These solutions remember, if $n(0) < n(\infty)$, the logistic sigma-like curve to the final state $n(\infty)$; in particular, the overdamped situation shows the same qualitative behaviour predicted by the Lotka-Volterra equations for the parasite-hosts population cycles in whose a cross term of the type $(k \cdot n \cdot s)$ is included.

In the next Section we fit these solutions to the output data of the Monte Carlo simulation for some fixed initial and external conditions.

4.- RESULTS AND DISCUSSION.- The matching between the detailed and the overall treatments expounded in the preceding Sections is explored by the very computer programm. The data analysis element attached to the data bank of Monte Carlo simulation has available a Gradient-expansion least-squares fit for the analytical solutions of equation (7) (Bevington 1969). This method minimizes the goodness of fit criterion χ^2 defined as

$$\chi^2 = \sum_i |y_i|^{-1} (y_i - y(x_i))^2 \qquad (11)$$

where the y_i's are provided by the data bank of the simulation and $y(x_i)$ are the corresponding values predicted by the deterministic model.

The preliminary results for the SN case are indeed encouraging. First, the Barcelonagramm provides, as predicted by the mathematical model, an approach to the externally imposed stationary state, that may be an aperiodic damping (a tipical sigma-like curve) or that of damped oscillations, accordingly to the specific properties of the species under consideration. The latter appears if the nutrition efficiency in transforming nutritons into biomass is favourised versus the species'natural death rate. A consistency check is easily performed by observing the effect of the shifting of one behaviour to the other in both descriptions if one changes accordingly the internal laws in the computer simulation or the appropiate constants in the deterministic model.

Figure 3. for example. exhibites the best fit between both approaches (in the conditions detailed in the figure caption) with a $\chi^2 = 1.7$ for an evolution of t = 250 time intervals. Further consistency checks may be done by changing some Monte Carlo parameters and observing the effect of such variations concerning the constants characterizing the fitted analytical solution. This is shown in Table I. The first three columns correspond to parameters of the detailed treatment, namely, the initial amount of individuals n(0), the constant input flow of nutritons Φ and the maximum time that individuals can live τ . The other columns correspond to the four constants determining the best analytic fit (χ^2 is always < 2.0), that is: k_1, k_2, k_3 and $n(\infty) = k_4/k_3$. Table I-A proves that a change of the initial conditions keeps the solution invariable; only the constants A and θ of equation (8) are affected. Table I-B shows the same result if one varyies the external constraint Φ , except, logically, for $n(\infty)$. Finally, the change of the life time τ -an internal parameter of behaviour- provides, as shown in Table I-C, new solutions that vary accordingly.

The Monte Carlo simulation works therefore satisfactorily with a population of about 10,000 individuals for the SN case and provides the necessary connection in order to identify the constants appearing in deterministic models in terms of the detailed-random behaviours. This kind of simulation is then a tool to be considered for further generalizations. It is in these more complex systems where such a method would be actually of relevant application. The stability of ecosystems can be searched, for example, in many interacting species system for a wide range of energetic conditions, such as space-time depending sorrounding constraints. Some further new results will be reported soon, but let us do some comments on the method proposed in this note.

The Monte Carlo simulation takes the role of the experimental observations with perhaps the same handicap that in the case of the Molecular Dynamics, that is to say, a less credibility concerning what actually is happening in nature, but it has nevertheless the same interesting list of advantages. Simulations replace indeed adventageously the experiments in complex ecosystems for in the latter the control of the external constraints is almost impossible and the very observations are highly difficult to be recorded with a certain fiability. The double view is specially interesting to be applied in the neighbourhood of critical situations (eventual bifurcations

points predicted by the mathematical models) in order to test the sensibility of a many species ecosystem in front of internal or environmental fluctuations, a central problem regarding the concepts of biological adaptation versus internal or external noises.

Up to now we have,for instance, realized with the Barcelonagramm the critical nature of the values range of parameters which allows the stabilization of two species competing for a constant input of nutritons. Another relevant point concerns the biomass distribution of individuals (different species) at the stationary state predicted by some deterministic models (Lurié et al. 1983 a,b). The Monte Carlo simulation provides a tool in order to search the kind of individual interactions that are consistent with the natural observations or with the predictions of such models; the discussion of such interactions being relevant for the understanding and controlling of biomass production processes. In particular, such a technique may provide, we believe, the optimization of certain parameters for use in managing real natural or man-made ecosystems.

LITERATURE

Alder, B.J. and T.E. Wainwright. 1959. "Studies in Molecular Dynamics." J. Chem. Phys. 31, 459-466.

Bevington, P.R. 1969. "Data Reduction and Error Analysis for the Physical Sciences." p.235, New York: Mc. Graw Hill.

Giró, A., J.M. González and V. Torra. 1979. "A time-saving method in Molecular Dynamics." An. Fis. 75, 154-158.

Giró, A., J.M. González, J.A. Padró, V.Torra. 1980. "The structure of the liquid lead at 670 K through Molecular Dynamics." J. Chem. Phys.73, 2970-2972.

Hansen, J.P. and I.R.McDonald. 1976. "Theory of Simple Liquids." p.47. London: Academic Press.

Holling, C.S. 1966. "The Strategy of Building Models of Complex Ecological Systems" Systems Analysis in Ecology, 195-214. Ed. K.E.F. Watt. New York: Academic Press.

Lurié, D. and J. Wagensberg. 1983 a. "On Biomass Diversity in Ecology" Bull. Math. Biol. 45, 287-293.

———, J. Valls and J. Wagensberg. 1983 b. "Thermodynamic approach to Biomass Distribution in Ecological Systems" Bull. Math. Biol. 45, 869-872.

Rahman, A. 1964. "Correlations in the Motion of Atoms in Liquid Argon. I. General Method." Phys. Rev. A. 136, 405-411.

Svirezhev, Yu.M. and D.O. Logofet. 1983. "Stability of Biological Communities" p. 116; Moscow: Mir Publishers.

Verlet, L. 1967. "Computer "Experiments" on Classical Fluids. I. Thermodynamical Properties of Lennard-Jones Molecules" Phys. Rev. 159, 98-107.

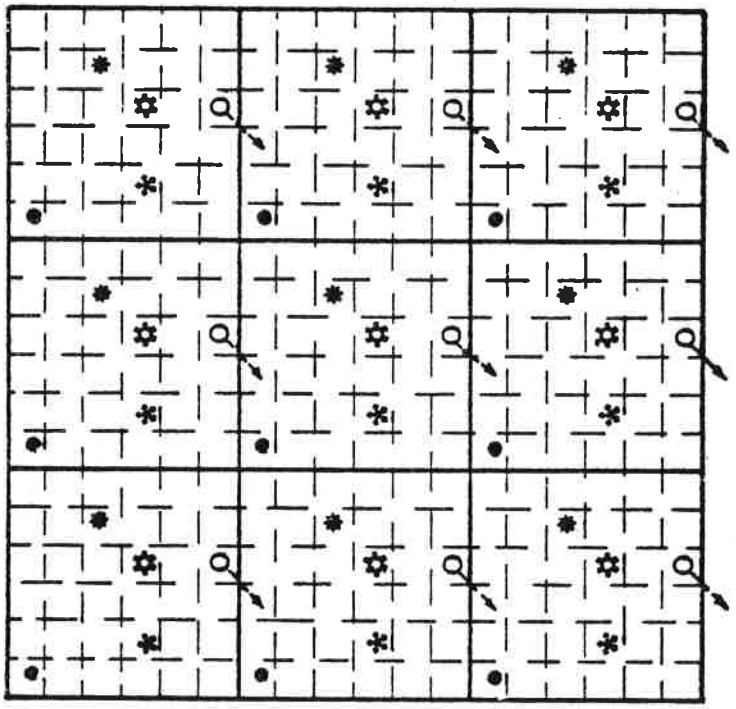

FIGURE 1

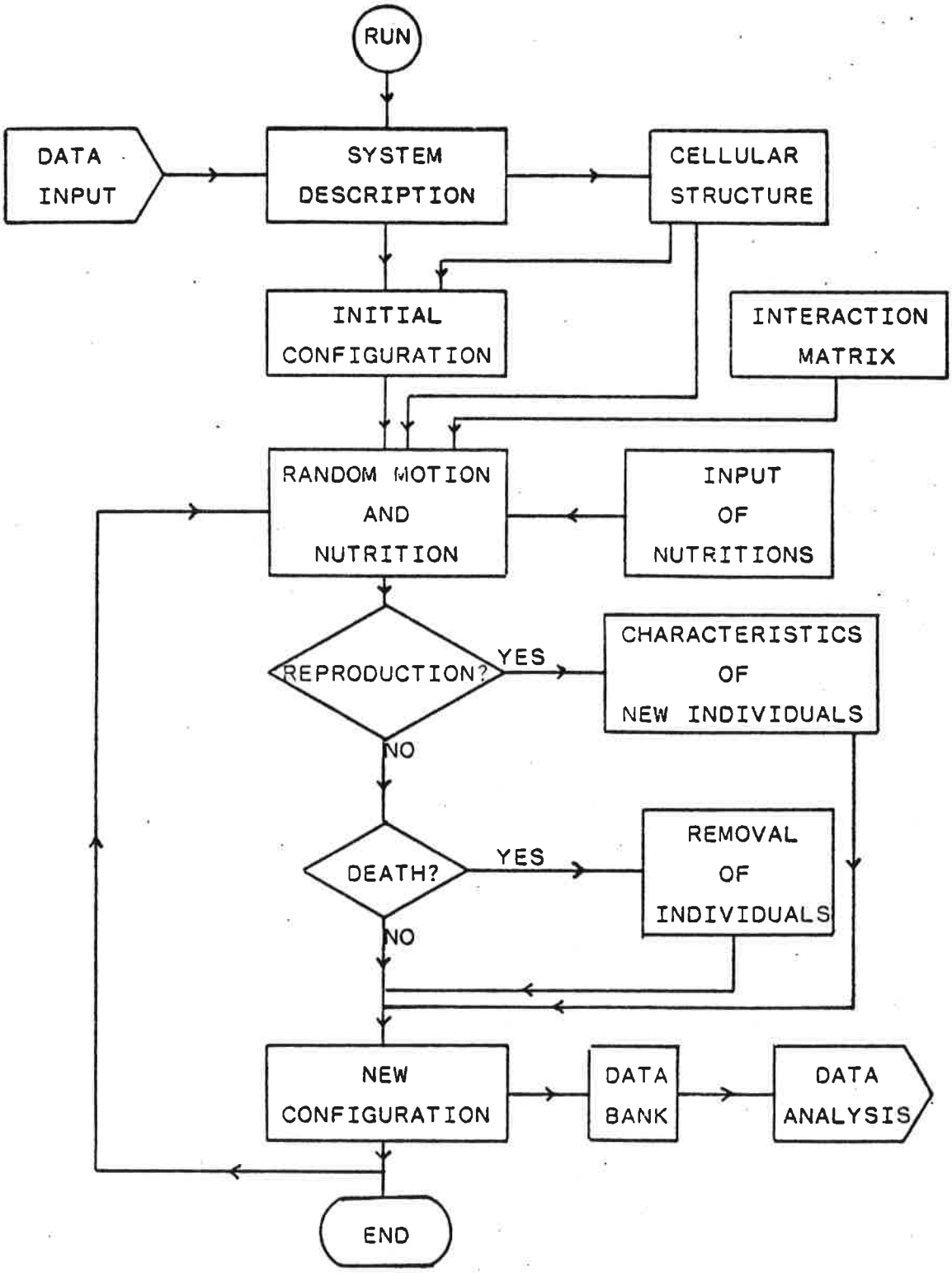
RUN
DATA INPUT
SYSTEM DESCRIPTION
CELLULAR STRUCTURE
INITIAL CONFIGURATION
INTERACTION MATRIX
RANDOM MOTION AND NUTRITION
INPUT OF NUTRITIONS
REPRODUCTION?
YES
CHARACTERISTICS OF NEW INDIVIDUALS
NO
DEATH?
YES
REMOVAL OF INDIVIDUALS
NO
NEW CONFIGURATION
DATA BANK
DATA ANALYSIS
END

FIGURE 2

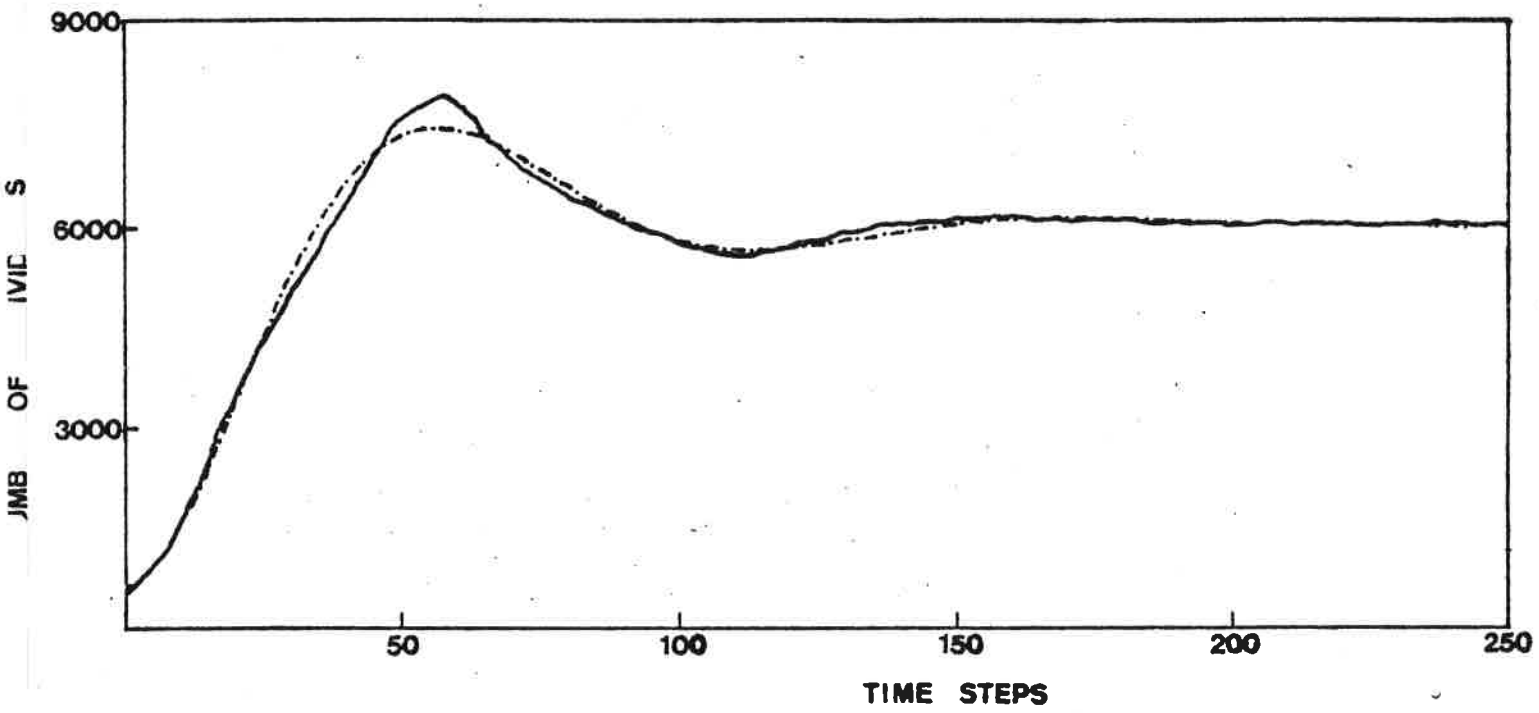

FIGURE 3

	MONTE CARLO SIMULATION			DETERMINISTIC MODEL			
	n(0)	Φ	τ	k_1	k_2	k_3	n(∞)
A	500	1000	50	.0540	.0068	.503	1988
	1000	1000	50	.0530	.0074	.502	1993
	2000	1000	50	.0540	.0070	.500	2001
	3000	1000	50	.0538	.0069	.496	2015
	4000	1000	50	.0608	.0071	.495	2021
B	500	1000	50	.0540	.0068	.503	1988
	500	1500	50	.0484	.0065	.504	2977
	500	2000	50	.0498	.0067	.503	3975
	500	2500	50	.0490	.0070	.502	4985
	500	3000	50	.0462	.0070	.503	5969
C	500	1000	30	.1066	.0130	.860	1163
	500	1000	40	.0672	.0087	.640	1562
	500	1000	50	.0540	.0068	.503	1988
	500	1000	60	.0428	.0059	.415	2412
	500	1000	80	.0316	.0043	.307	3258

TABLE I

FIGURE CAPTIONS

Figure 1.- Periodic boundary conditions used in the computer simulation; the dashed lines represent the subcellular structure.

Figure 2.- Flow-Chart of the Monte Carlo Simulation for an Ecosystem.

Figure 3.- Time evolution of individuals for the SN case. The continuous line represents the computer simulation with the following parameters: $n(0) = 500$, $\tau = 50$, $\Phi = 3000$. The dashed line is the best deterministic solution fitted with $\chi^2 = 1.7$, $k_1 = .0462$, $k_2 = .0070$, $k_3 = .503$ and $n(\infty) = 5969$.

Table I.- Consistency check between the Monte Carlo simulation and the deterministic model.