Study of a population model:

the Yoccoz-Birkeland model.

February 26, 2009

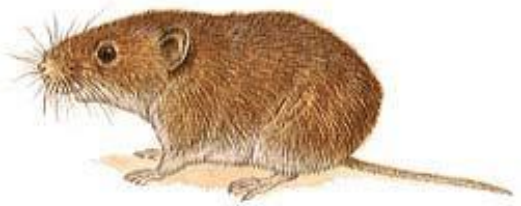

Figure: Bank vole (*Clethrionomys glareolus*)

Main reference:

Sylvain Arlot,
Étude d'un modèle de dynamique des populations,
http://www.di.ens.fr/∼arlot/

Summary:

1. Description of biological characteristics of the population of *Microtus epiroticus* (sibling vole) on Svalbard Isles in the Arctic Ocean.
2. Description of the mathematical model and available theorical results.
3. Simulations.

Where...?


ARCTIC
North pole
OCEAN
Severnaja Zemlja
Russia
Kara Sea
Franz Josef Land
Novaja Zemlja
80°
Longyearbyen
Barents Sea
Greenland (Den.)
Average Summer Ice Extent
SVALBARD (Norway)
Greenland Sea
Russia
Murmansk
Norway
Norwegian Sea
Iceland
Arctic Circle
Sweden
Finland

Biological description

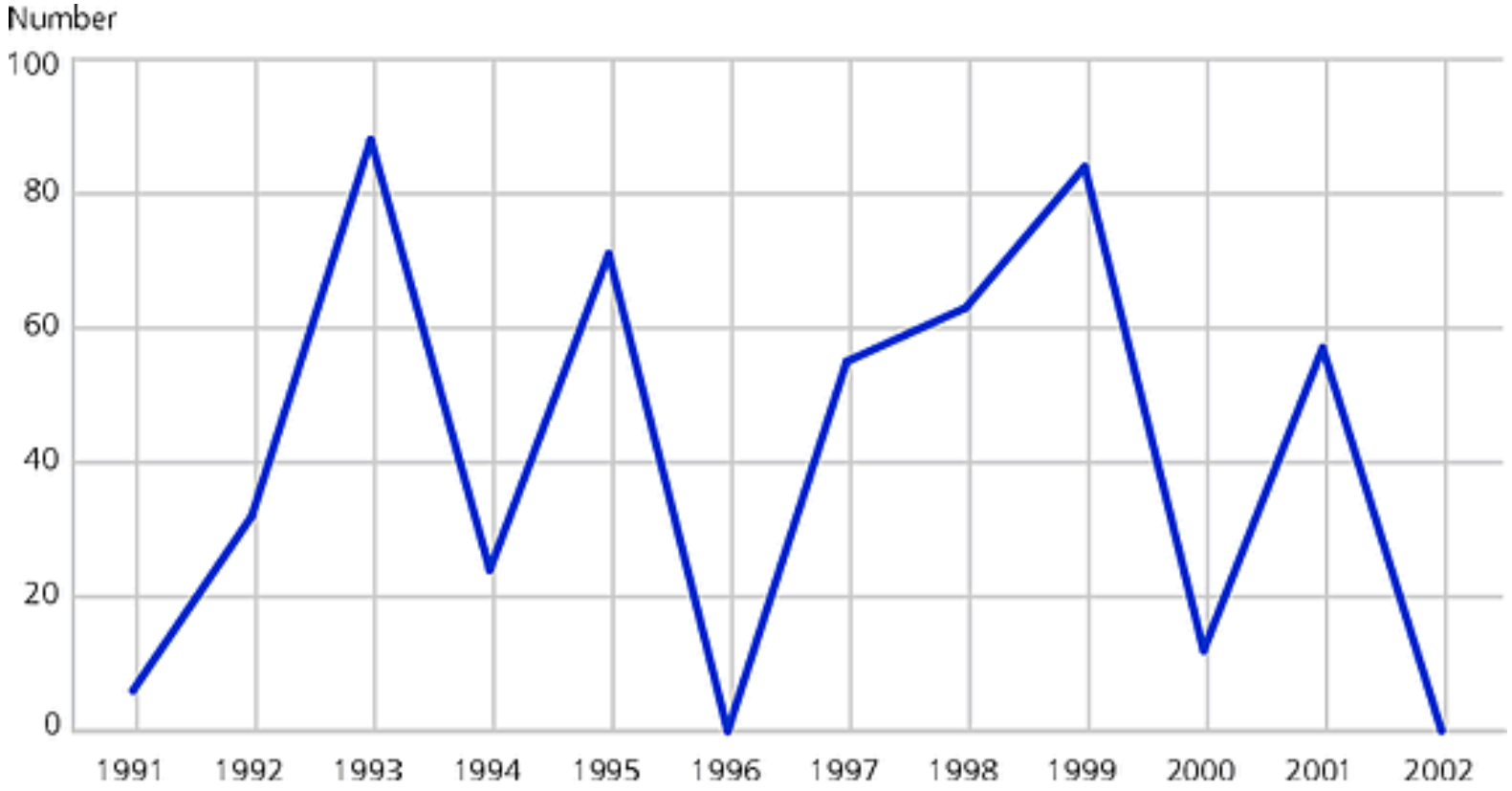

Figure: History

Biological description

- fertility depends on population density: few good reproduction spots whose quality decreases as the population increases;
- no significant predation, but high oscillations of population: $1 \div 100$ (not due to lack of food);
- seasonal factor: harsh and non stable weather conditions;
- high fertility and variable sexual maturation time.

Find a simple deterministic model that includes all these aspects and produces complicated behavior for suitable values of its parameters.

Model description.

- t: time measured in years
- $N(t)$: active *female* population at time t;
- A_0: maturation age;
- A_1: maximal age;
- $S(\alpha)$: probability to survive up to α years;
- $m(N)$: annual individual reproduction rate for a population of N individuals;
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$$N(t-\alpha)m\big(N(t-\alpha)\big)\Delta\alpha m_\rho(t-\alpha)S(\alpha)$$

$$N(t) = \int_{A_0}^{A_1} N(t-\alpha)m\big(N(t-\alpha)\big)m_\rho(t-\alpha)S(\alpha)d\alpha$$

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- $A_1 = 2$
- $A_0 = 0.14$ (50 days)
- $m_0 = 50$
- $\rho = 0.7$ (winter lasts about 8-9 months)

Mathematical analysis: first remarks

$$N(t) = \int_{A_0}^{A_1} N(t-\alpha) m\big(N(t-\alpha)\big) m_\rho(t-\alpha) S(\alpha) d\alpha \qquad t \geq 0$$

- the value of N at time t depends on which was the situation in $[t - A_1, t - A_0]$
- if $N(s)$ is known for $s \in [-A_1, 0]$, then the equation allows direct computation of $N(t)$ for $t \in [0, A_0]$
- inductively, $N(t)$ can be computed for $t \in [(k-1)A_0, kA_0]$, $k \in \mathbb{N}$
- compatibility condition

$$N(0) = \int_{A_0}^{A_1} N(-\alpha) m\big(N(-\alpha)\big) m_\rho(-\alpha) S(\alpha) d\alpha$$

- non stationary (but 1-periodic in time) equation

Mathematical analysis: towards the dynamical system

Evaluation at integral multiples of the period:

$$\begin{aligned} N(k) &= \int_{A_0}^{A_1} N(k-\alpha) m\big(N(k-\alpha)\big) m_\rho(k-\alpha) S(\alpha) d\alpha \\ &= \int_{A_0}^{A_1} N(k-\alpha) m\big(N(k-\alpha)\big) m_\rho(-\alpha) S(\alpha) d\alpha \end{aligned}$$

In other words, the function $Y_k(s) = N(k+s)$, $s \in [-A_1, 0]$, satisfies the equation

- $Y(0) = \int_{A_0}^{A_1} Y(-\alpha) m\big(Y(-\alpha)\big) m_\rho(-\alpha) S(\alpha) d\alpha$
- is a reasonable picture of the situation at time k
- good choice as state variable.
- in which phase space?

Mathematical analysis: towards the dynamical system

Consider the set $\mathcal{Y}$ of continuous functions $Y : [-A_1, 0] \to \mathbb{R}$ such that

$$Y(0) = \int_{A_0}^{A_1} Y(-\alpha) m\big(Y(-\alpha)\big) m_\rho(-\alpha) S(\alpha) d\alpha$$

Then:

- take any initial condition $Y_0 \in \mathcal{Y}$
- find the unique solution N of the model equation such that $N(s) = Y_0(s)$ for $s \in [-A_1, 0]$
- the functions $Y_k(s) = N(k + s)$, $s \in [-A_1, 0]$, belong to $\mathcal{Y}$ for all $k \in \mathbb{N}$
- obtain the 1-period map $T : \mathcal{Y} \to \mathcal{Y}$, $T(Y_0) := Y_1$
- observe that $Y_k = T^k(Y_0)$
- $Ym(Y) = m_0 \min\{Y, Y^{1-\gamma}\}$ is L-Lipschitz continuous $\Longrightarrow$ T is Lipschitz continuous with constant $(A_1 - A_0)L$.

Mathematical analysis: global attractor?

Some assumptions:

- $\gamma \geq 1$
- $A_1 \geq \max\{2A_0, A_0 + 1\}$
- $m_0 c_0 := m_0 \int_{A_0+\rho}^{A_0+1} S(\alpha) d\alpha > 1$

The last condition is a worst case condition: a single female ($N = 1$) that becomes fertile at the beginning of winter (so that it can proliferate only at the age of $A + \rho$) will give birth in the following summer to *more than one* baby that will survive.

Indeed it is used to exclude extinction:

- for every initial condition $Y_0 \not\equiv 0$, if k is sufficiently large, then

$$\frac{c_0 m_0}{2} N_{max}^{1-\gamma} \leq T^k(Y_0)(s) \leq N_{max} \qquad \forall s \in [-A_1, 0]$$

where $N_{max} = m_0 \frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2$

Mathematical analysis: global attractor?

Moreover, the solutions $N(t)$ of our integral equation becomes Lipschitz continuous as soon as they leave the initial interval:

- $|N(t_1) - N(t_2)| \leq L|t_1 - t_2|$ if $t_1, t_2 \geq 0$ with $L := m_0 \left(3 - \frac{A_0}{A_1}\right)$

Define the set $\mathcal{K} \subset \mathcal{Y}$ of functions Y such that

- $\frac{c_0 m_0}{2} N_{max}^{1-\gamma} \leq Y(s) \leq N_{max}$ for $s \in [-A_1, 0]$
- Y is L-Lipschitz continuous

Then $\mathcal{K}$:

- is compact w.r.t. the uniform convergence
- is invariant $T(\mathcal{K}) \subset \mathcal{K}$
- is eventually absorbing: $T^k(Y) \in \mathcal{K}$ if k is large enough and $Y \not\equiv 0$

Mathematical analysis: global attractor!

Let

$$\Lambda := \bigcap_{k \in \mathbb{N}} T^k(\mathcal{K})$$

then

- Λ is a compact subset of $\mathcal{Y}$
- $T(\Lambda) = \Lambda$
- for every neighborhood U of Λ and every initial datum $Y \in \mathcal{Y}$ we have that $T^k(Y) \in U$ for every k large enough
- Λ is a global attractor for the dynamical system $(T^k)_{k \in \mathbb{N}}$ on $\mathcal{Y}$.

Simulations: discretization of the model

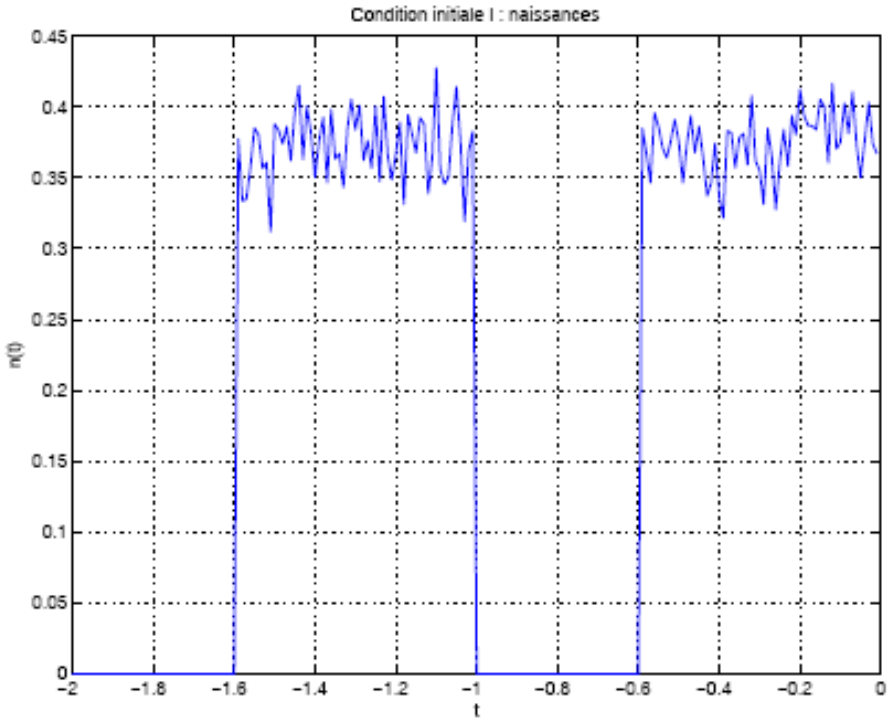
- divide each year into $p = 100$ intervals of length $h = 1/p$
- n_i: number of births in the interval $I_i := [(i-1)h, ih[$
- N_i: mean value of mature population in I_i
- e_i: mean value of the seasonal factor m_ρ in I_i
- s_i: fraction of surviving mature females that were born i time intervals before

then

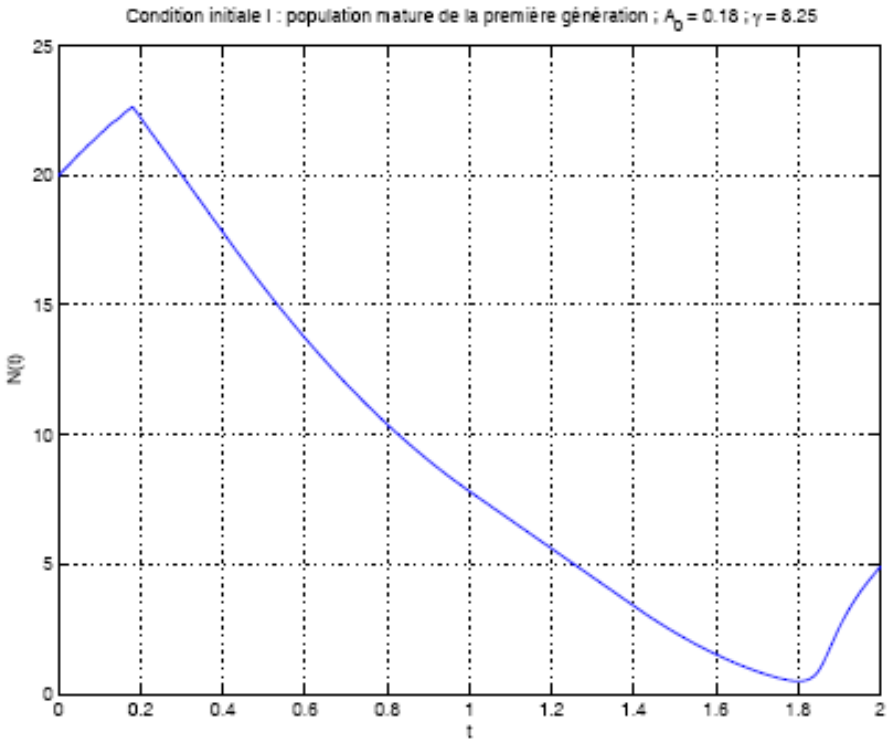
$$\begin{cases} n_i = N_i \times m(N_i) \times e_i \times h \\ N_i = \displaystyle\sum_{k=1}^{2p} s_k \times n_{i-k} \end{cases}$$

Given the initial condition $(n_i)_{1 \leq i \leq 2p}$, the system allows to compute n_i for all $i > 2p$.

Simulations: initial conditions



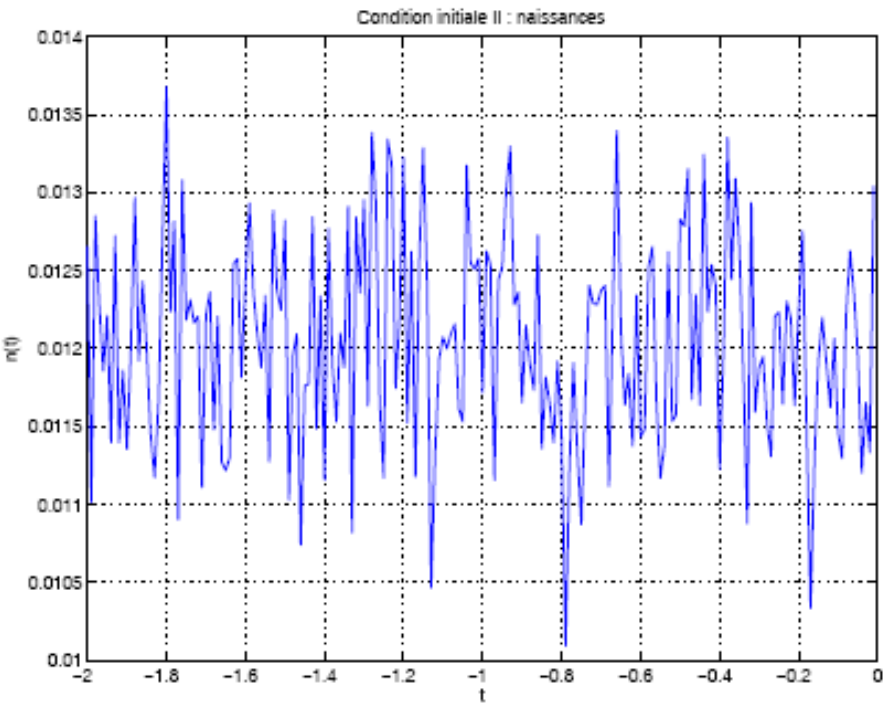
Naissances



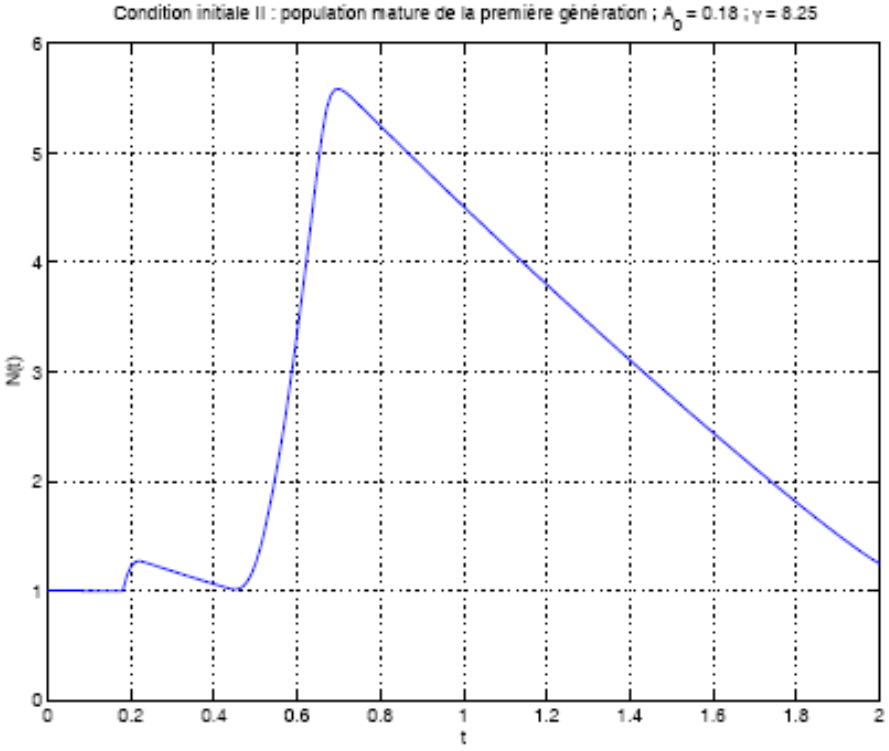
Première génération

Figure: initial condition 1

Simulations: initial conditions



Naissances



Première génération

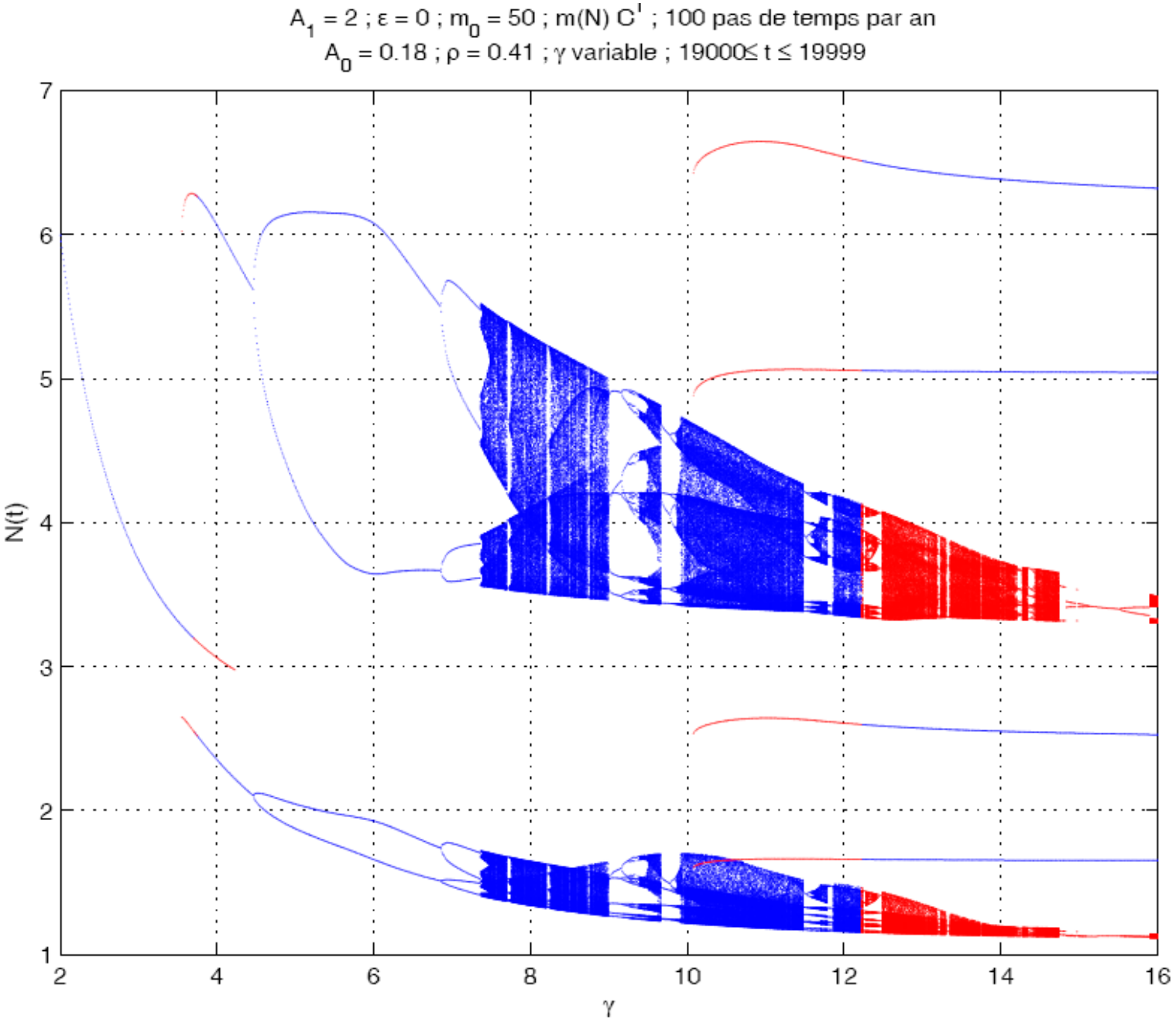
Figure: initial condition 2

Simulations: bifurcation diagrams

- fix $A_1 = 2$ and $m_0 = 50$
- play with A_0, ρ, γ
- calculate N_i up to $i = 20000$ and plot $(N_i)_{19001 \leq i \leq 20000}$ for different values of the parameters

For example, fix also $A_0 = 0.18$ and $\rho = 0.41$, while moving γ in $[2, 16]$

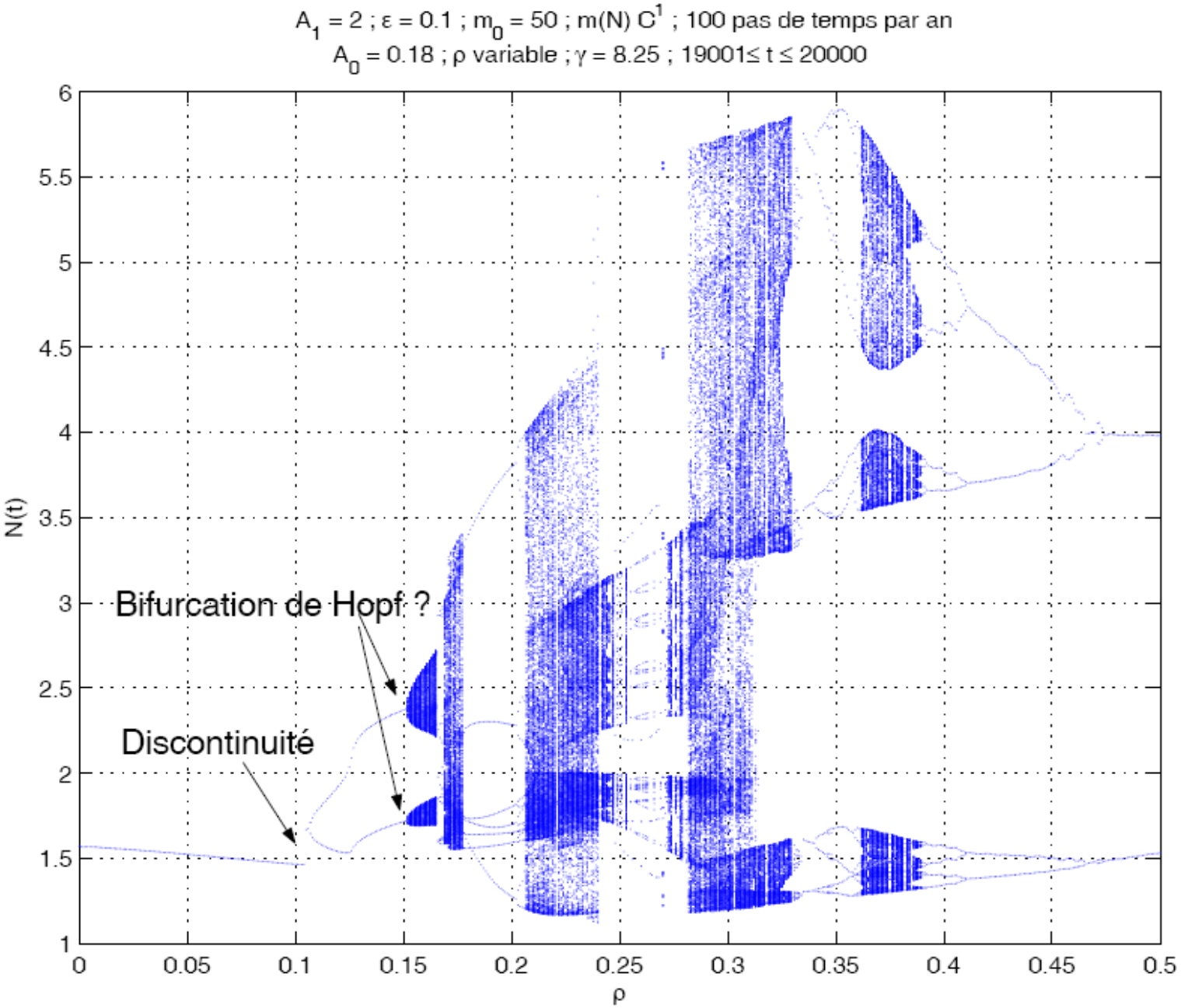
Simulations: bifurcation diagrams



Simulations: bifurcation diagrams

...or fix $A_0 = 0.18$ and $\gamma = 8.25$ and move ρ in $[0, 0.5]$...

Simulations: bifurcation diagrams



Simulations: visualization of an attractor

The discretized phase space is a point in $\mathbb{R}^{201}$

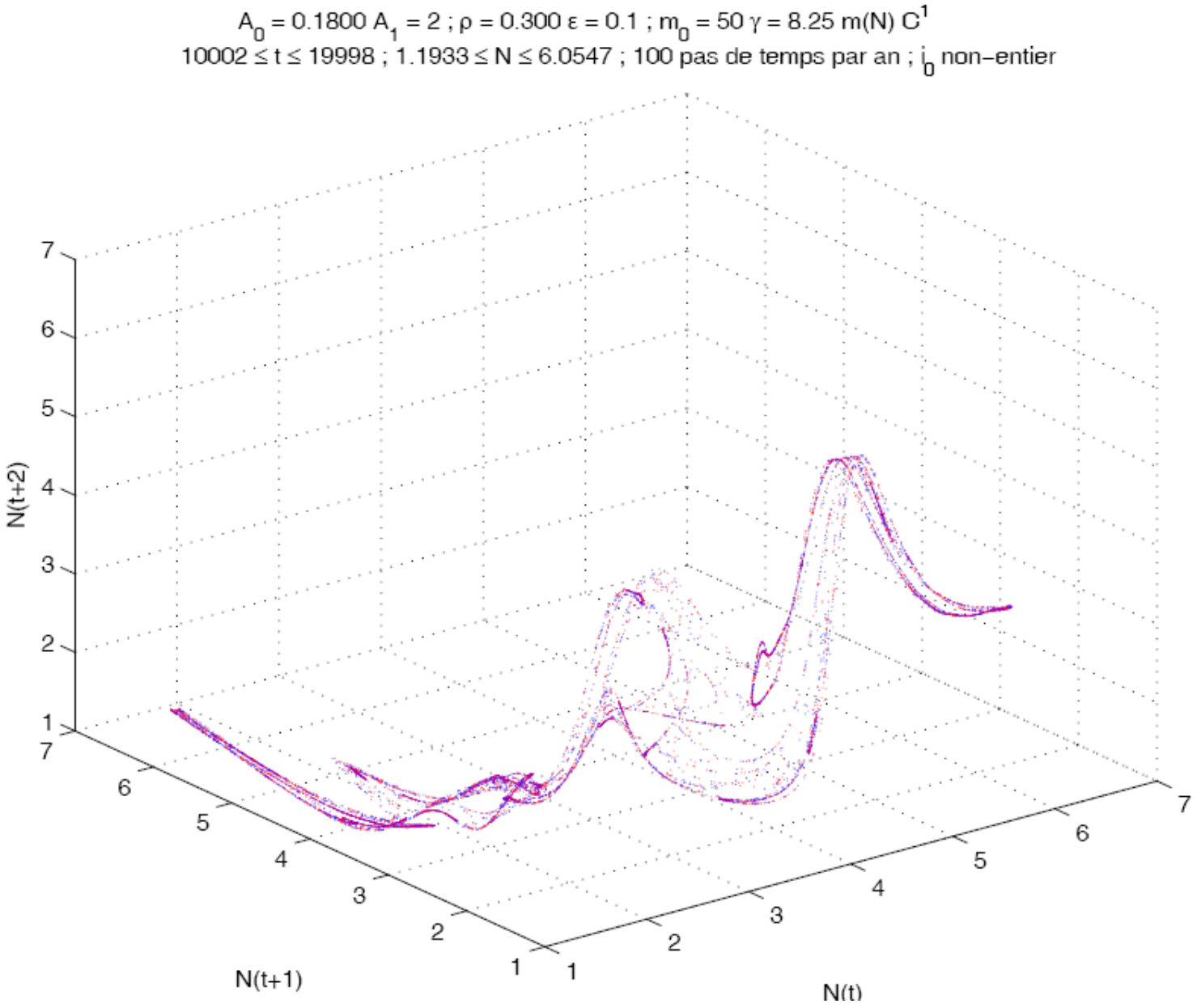
$$Y_k^{(201)} = (N_i)_{100k \leq i \leq 100k+200} \in \mathbb{R}^{201}$$

Instead, project $\pi : \mathbb{R}^{201} \to \mathbb{R}^3$ by taking only $Y_k^{(3)} = (N_{100k}, N_{100(k+1)}, N_{100(k+2)}) \in \mathbb{R}^3$.

It is like considering only the values $\big(N(t), N(t+1), N(t+2)\big)$ in the continuous time model for $t \in \mathbb{N}$ and, actually, $10002 \leq t \leq 19998$.

Example: $A_0 = 0.18$, $\rho = 0.30$, $\gamma = 8.25$

Simulations: visualization of an attractor



Simulations: injectivity of $\pi : Y_k^{(201)} \mapsto Y_k^{(3)}$

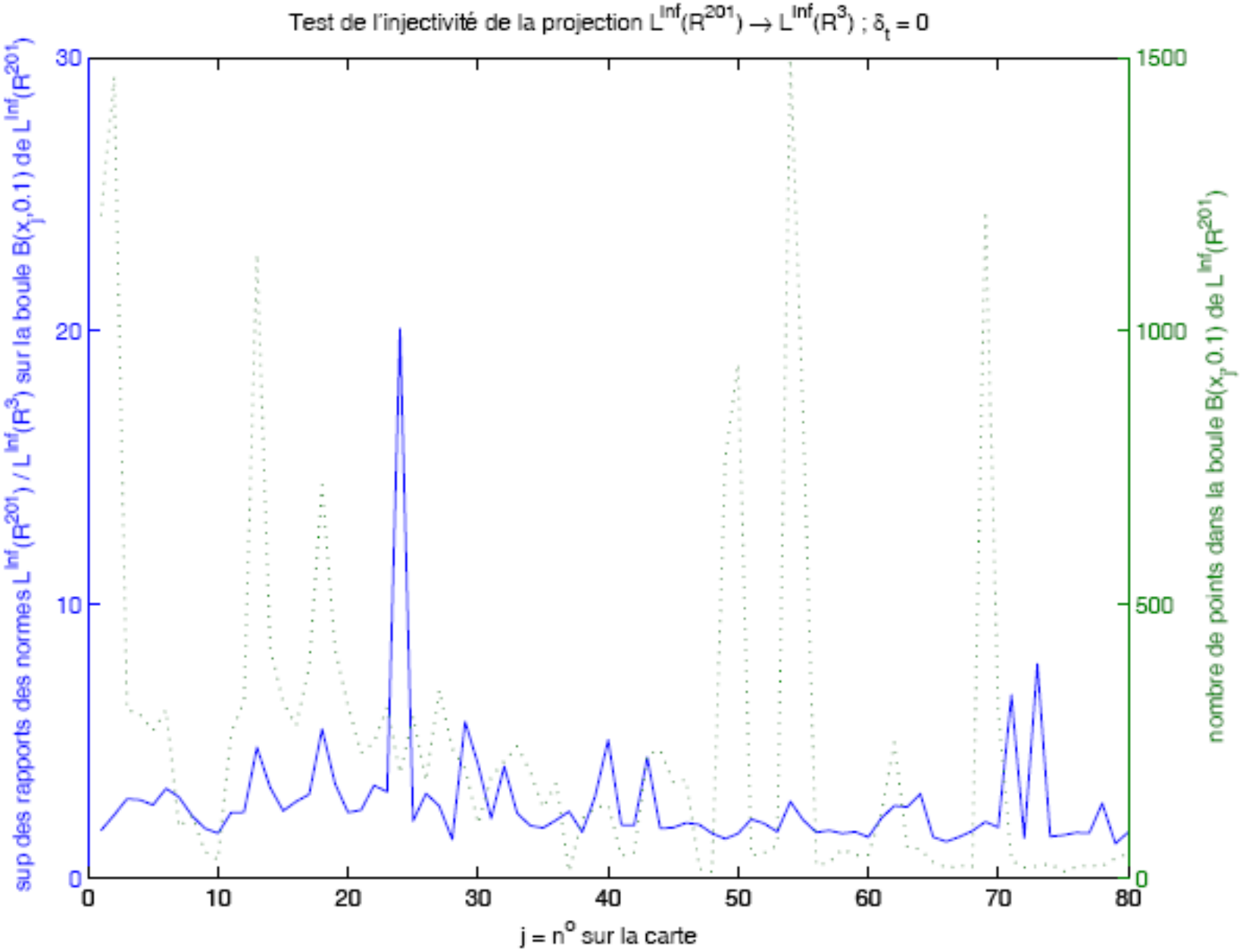
Are distant points on the attractor in $\mathbb{R}^{201}$ mapped to sufficiently distant points in $\mathbb{R}^3$?

- suitably choose a set of times h (in our case they are 80) and a radius r ($= 0.1$)
- for each time h evaluate the supremum of the quotients

$$\frac{\| Y_k^{(201)} - Y_h^{(201)} \|_{\mathbb{R}^{201}}}{\| Y_k^{(3)} - Y_h^{(3)} \|_{\mathbb{R}^3}}$$

  on all the points $Y_k^{(201)}$ that falls into the ball B centered at $Y_h^{(201)}$ with radius r (with respect to some p-norm in $\mathbb{R}^{201}$).
- plot

Simulations: injectivity of $\pi : Y_k^{(201)} \longmapsto Y_k^{(3)}$



Simulations: fractal dimension of the attractor

If K is a compact set of a metric space, the fractal dimension of K is the number

$$D(K) = \limsup_{r \to 0^+} \frac{\log N_r(K)}{-\log r}$$

where $N_r(K)$ is the minimum number of balls of radius r that is needed to cover K.

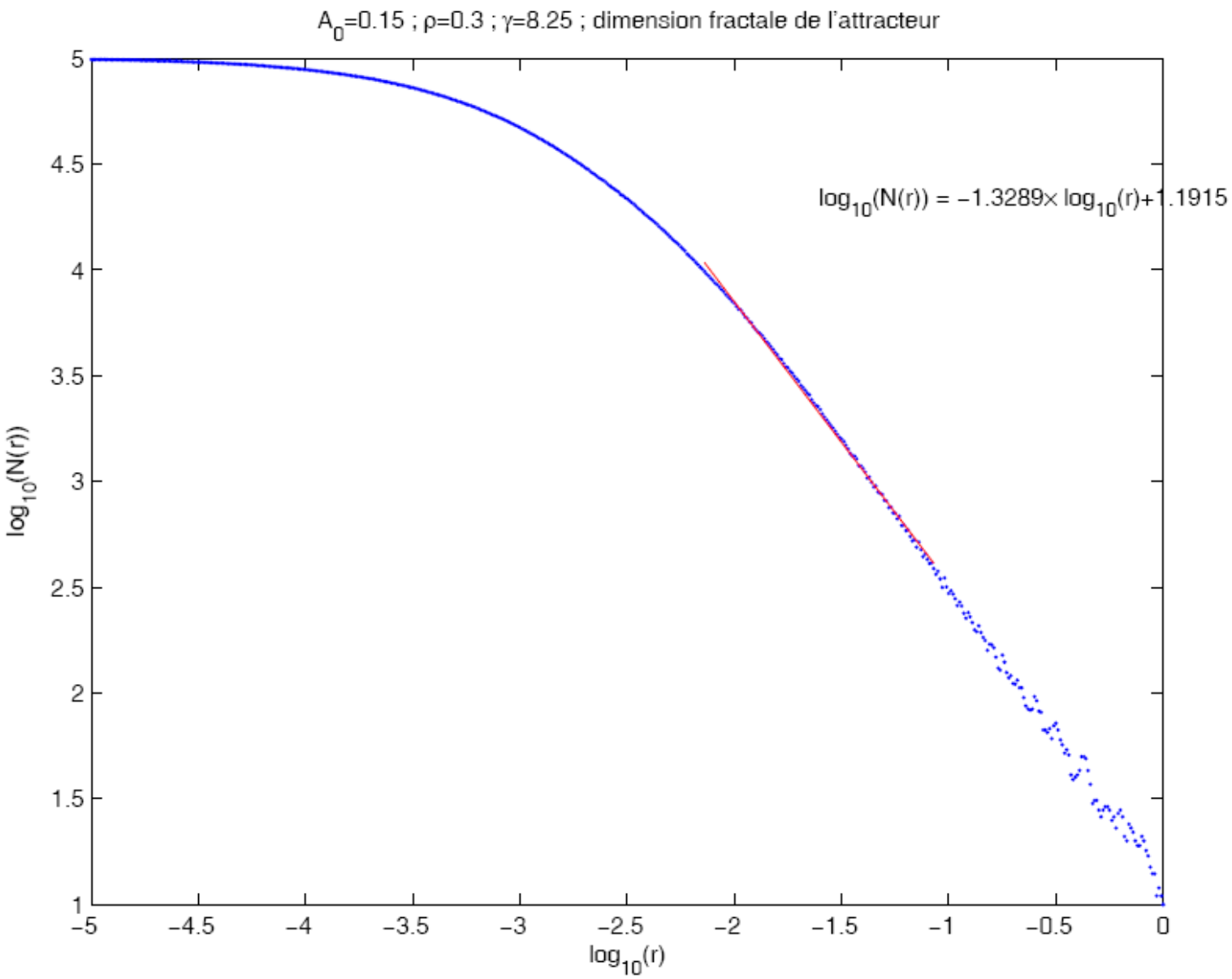
Here the cubes

$$C_{ijk} = [ir, (i+1)r] \times [jr, (j+1)r] \times [kr, (k+1)r]$$

are considered and $N_r(K)$ is the number of cubes containing at least a point of the attractor.

The slope of the graph of $\log r$ versus $\log N_r(K)$ gives the fractal dimension.

Simulations: fractal dimension of the attractor



Simulations: fractal dimension of the attractor

$$D(K) \simeq 4/3 < 1.5$$

It suggests an *a posteriori* justification of the visualization of the attractor in $\mathbb{R}^3$ by invoking the extension of Whitney's theorem to compact sets of fractal dimension d:

they can be visualized in $\mathbb{R}^n$ with $n > 2d$

And what about the fluctuations of the population of *Microtus epiroticus* in Svalbard Isles?

Simulations: solution behavior on attractor