Study of the Yoccoz-Birkeland population model

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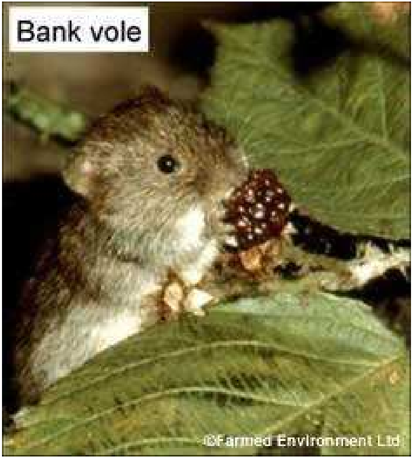
Plan

1. The model
   - Voles in the Arctic
   - Description of the model
   - Mathematical analysis
2. Simulation study
   - Principle
   - Exploring the parameter space
   - Study of an attractor: (0.15 ; 0.30 ; 8.25)

Clethrionomys glaerolus



Microtus epiroticus on Svalbard:

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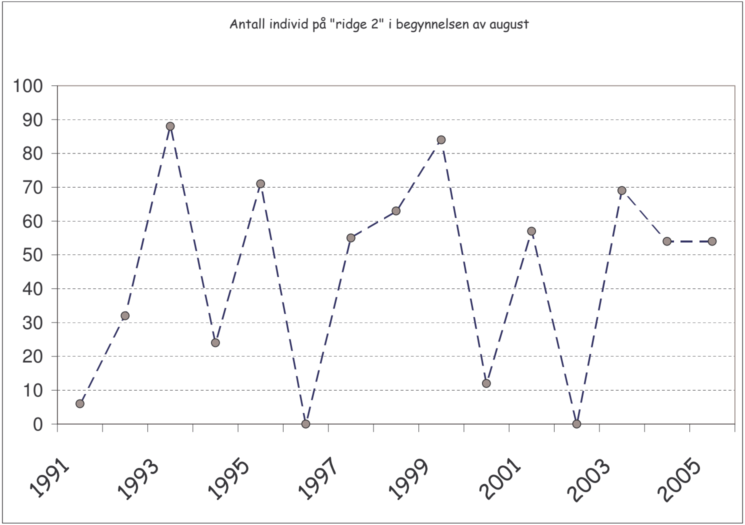
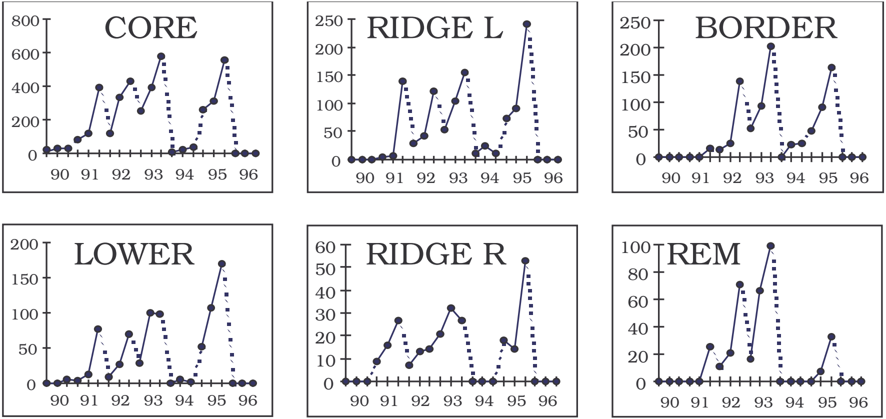
- arctic environment
- high fertility rate
- few breeding places (permafrost)
- no reproduction in winter (snow)

(N. Yoccoz, Ims & Steen 1993)

Between-year variation (N. Yoccoz *et al*)



Seasonal variation (N. Yoccoz *et al*)



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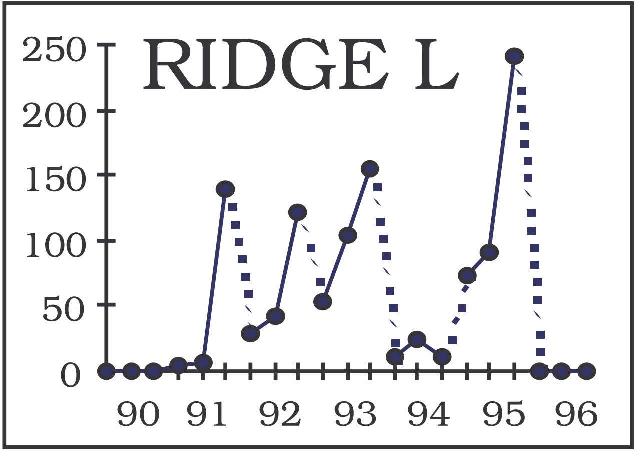

Possible mechanisms

High fertility rate, strongly density-dependent, and:

- available food quantity (N. Yoccoz *et al* 2001)
- predation by arctic fox (Turchin *et al* 2000; Frajford 2002)
- environmental variability (N. Yoccoz & Ims 1999)
- plasticity of the maturation age (Lambin & N. Yoccoz 2001)

Are such variations still possible if the maturation age and the environment are constant?

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The model (J.-C. Yoccoz & Birkeland 1998)

$$N(t) = \int_{A_0}^{A_1} S(a) m_\rho(t-a) N(t-a) m(N(t-a)) da$$

(female and mature population; A_0: maturation age)

Fertility: $$m(N) = \begin{cases} m_0 \text{ if } N \leq 1 \\ m_0 N^{-\gamma} \text{ otherwise} \end{cases}$$

Seasonal parameter: $$m_\rho(t) = \begin{cases} 0 \text{ if } 0 \leq t \leq \rho \text{ mod. } 1 \\ 1 \text{ if } \rho \leq t \leq 1 \end{cases}$$

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Parameters (N. Yoccoz, Ims, Steen 1993)

- fertility $m_0 \approx 54$.
- maturation age $A_0 \in [0.14\,;\,0.20]$, minimum $= 0.10$.
- maximal age $A_1 \approx 2$.
- winter length $\rho \in [0.35\,;\,0.45]$ (temperate climate) ou $\rho \approx 0.7$ (arctic climate).

- winter survival rate ≈ 0.1
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- density-dependence γ
- spring length ε .

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Mathematical analysis: dynamical system

- $\forall t_0 \in [0,1)$, Y_{t_0} is the set of continuous functions N: $[-A_1, 0] \mapsto [0, +\infty)$ such that

$$N(0) = \int_{A_0}^{A_1} S(a) m_\rho(t_0 - a) N(-a) m(N(-a)) da$$

- Phase space:

$$Y^\sharp = \{(t, N) \,/\, t \in \mathbb{R}/\mathbb{Z},\ N \in Y_t\}$$

- Semi-group $(T^s)_{s \geq 0}$: $T^s(t,N) = (t + s \bmod. 1,\ N_t^s)$

$$N_t^s(-a) = \begin{cases} N(s-a) \text{ if } 0 \leq s \leq a \leq A_1 \\ \int_{A_0}^{A_1} S(b) N(s-a-b) m(N(s-a-b)) m_\rho(t+s-a-b) db \text{ otherwise} \end{cases}$$

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- $N \mapsto Nm(N)$ is K_f Lipschitz
- $m_0 \geq m(N) \geq m_0/2$ if $N \leq 1$
- $m_0 N^{-\gamma} \geq m(N) \geq \min\{1/2, N^{-\gamma}\} m_0$
- $1 \geq m_\rho(t) \geq 0$ for every $t \in [0,1]$
- $m_\rho(t) = 1$ on some interval of length $1 - \rho - \varepsilon > 0$

- large domain of the parameter space:
  - $\gamma \geq 1$
  - $A_1 \geq \max\{2A_0, A_0 + 1\}$
  - $m_0 \int_{A_0+\rho+\varepsilon}^{A_0+1} S(a)da > 2$

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($N_{\min}$, $N_{\max}$ and L are explicit functions of m_0, A_0, A_1 and γ)

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- Theorem: Λ is an attractor for $(T^s)_{s \geq 0}$, which attracts any initial condition $(0, N)$ with $N \in Y_0$.
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Plan

Discretization of the dynamical system

- Each year is divided into $p = 100$ intervals
- Define $I_k = [(k-1)/p; k/p)$ for $k \geq -pA_1$, $k \in \mathbb{N}$
- n_k : number of births in I_k
- N_k : average number of mature females during I_k
- e_k : average of $m_{\rho,\varepsilon}$ over I_k
- s_k : fraction of surviving mature females among females born k time intervals before

$$n_i = \frac{m(N_i) \times N_i \times e_i}{p}$$

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Principle of the simulation experiments

- $A_1 = 2 \quad m_0 = 50 \quad \varepsilon = 0.1$
- $(A_0\,;\,\rho\,;\,\gamma)$ varying

- Stationary behaviour: $t \geq t_0 = 10000$ (for *one* arbitrary initial condition).

- $t = 0$ at the end of summer
- Bifurcation diagram: $(x, N(t))$.
- Projection on $\mathbb{R}^3$: $(N(t), N(t+1), N(t+2))$ (Whitney theorem, assuming a fractal dimension $D < 3/2$ for $\omega(N)$).

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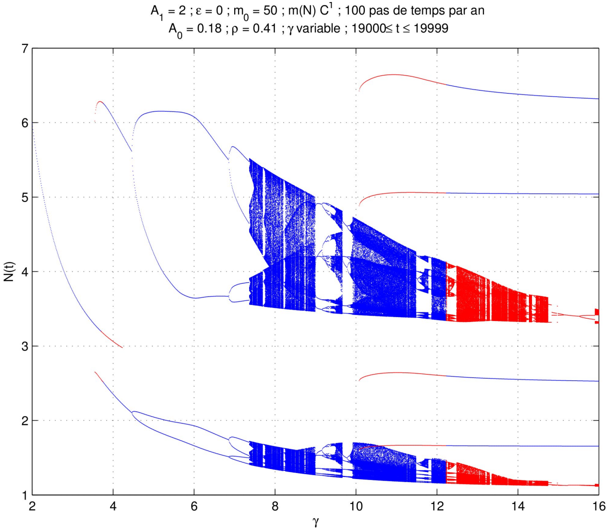
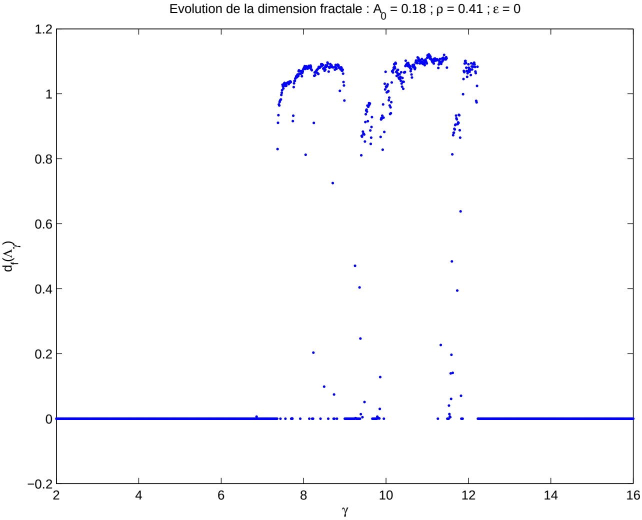
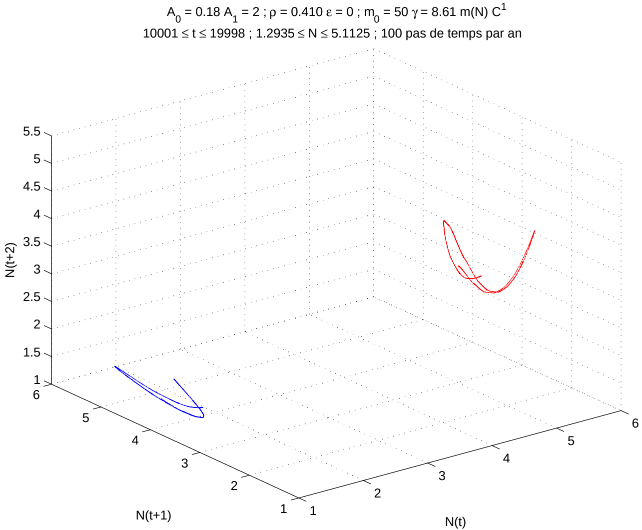


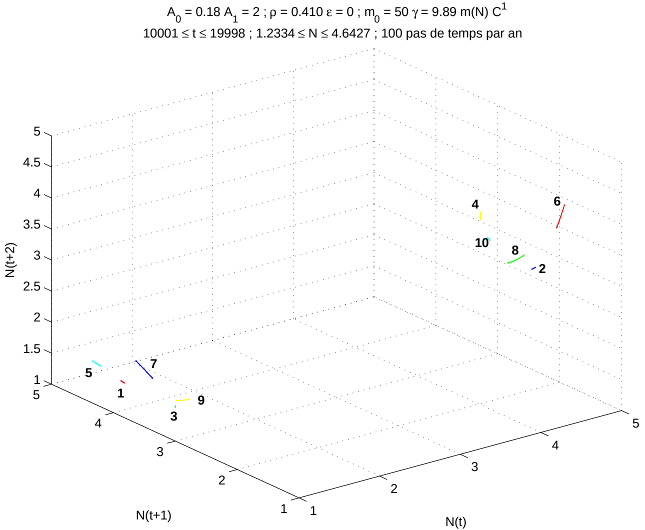
$(A_0 = 0.18\,;\ \rho = 0.41\,;\ \gamma \in [2;16])$: Fractal dimension



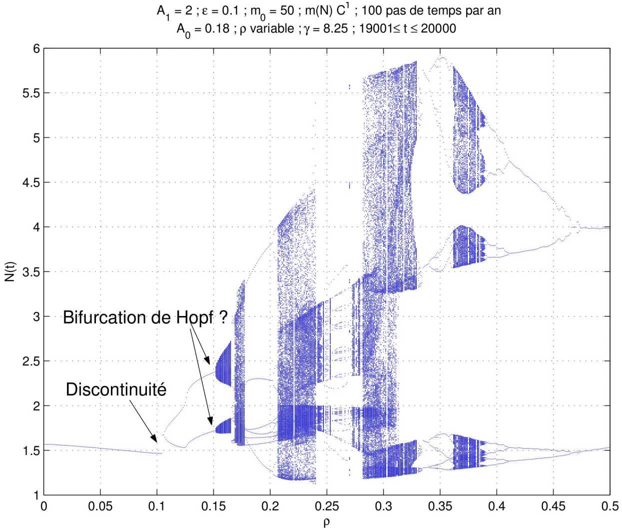
$(A_0 = 0.18\,;\ \rho = 0.41\,;\ \gamma = 8.61)$: $d_f \approx 1.06$



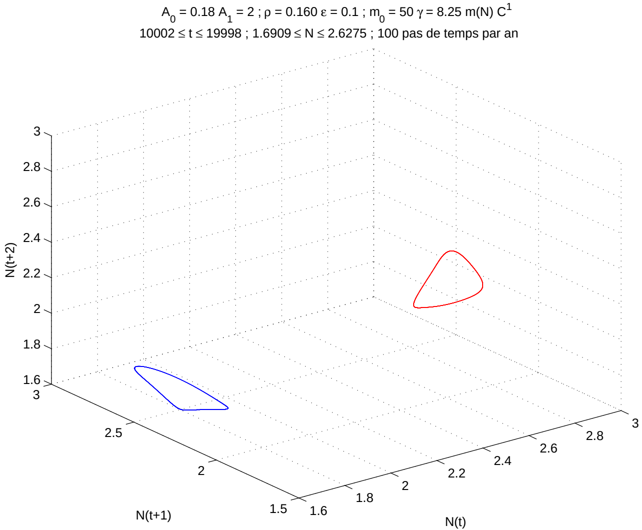
$(A_0 = 0.18\,;\ \rho = 0.41\,;\ \gamma = 9.89):\ d_f \approx 0.92$



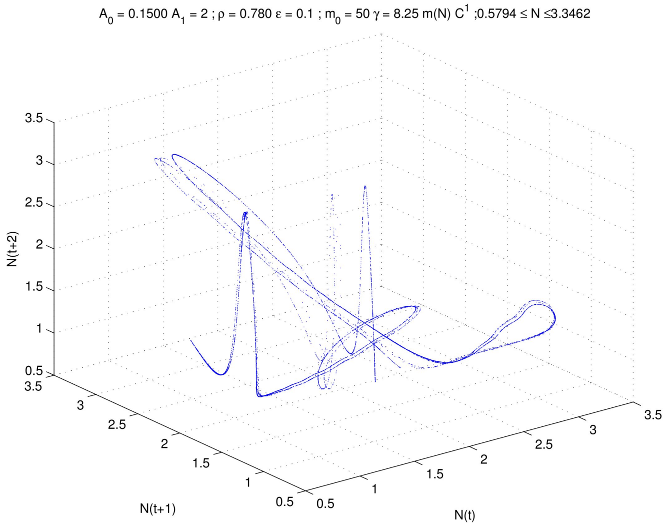
$(A_0 = 0.18\,;\ \rho \in [0\,;\,0.5]\,;\ \gamma = 8.25)$ [see video]



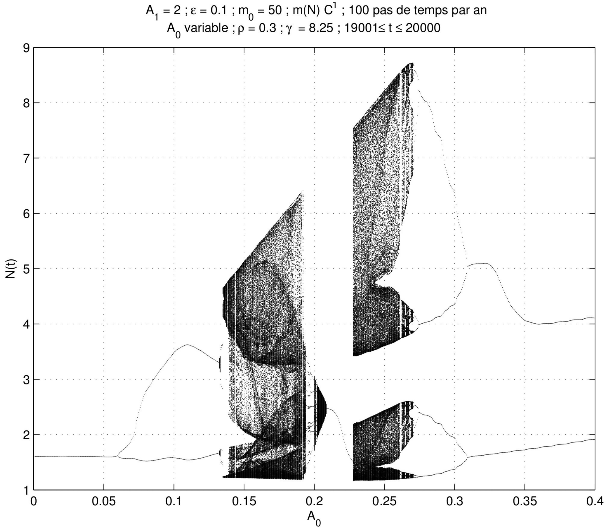
$(A_0 = 0.18\,;\ \rho = 0.16\,;\ \gamma = 8.25)$: $d_f \approx 0.99$



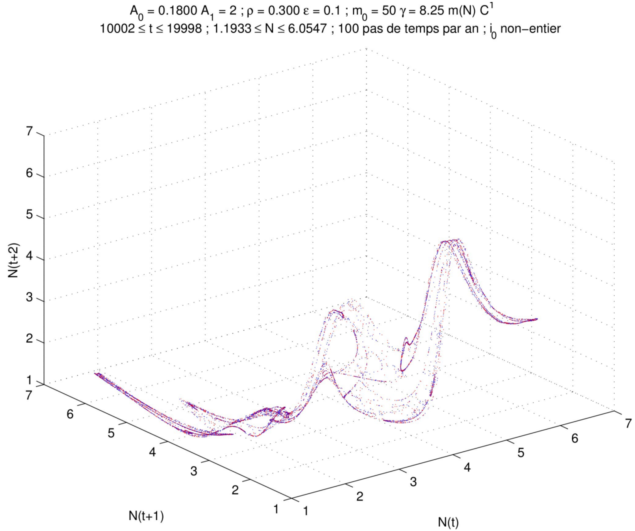
$(A_0 = 0.15\,;\ \rho = 0.78; \gamma = 8.25):\ d_f \approx 1.25$



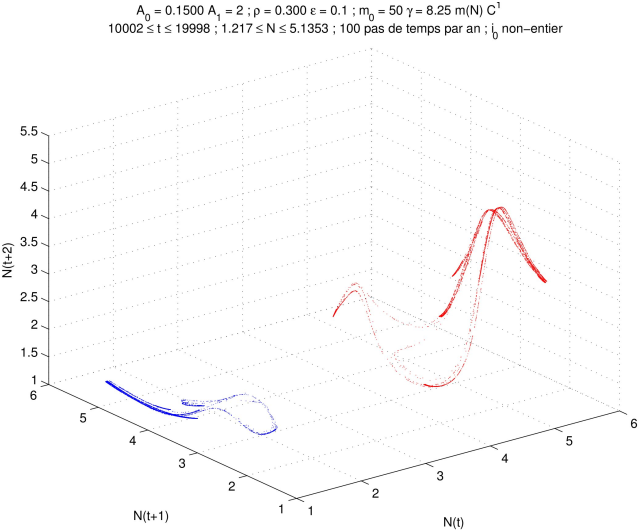
$(A_0 \in [0\,;\,0.4]\,;\, \rho = 0.30\,;\, \gamma = 8.25)$



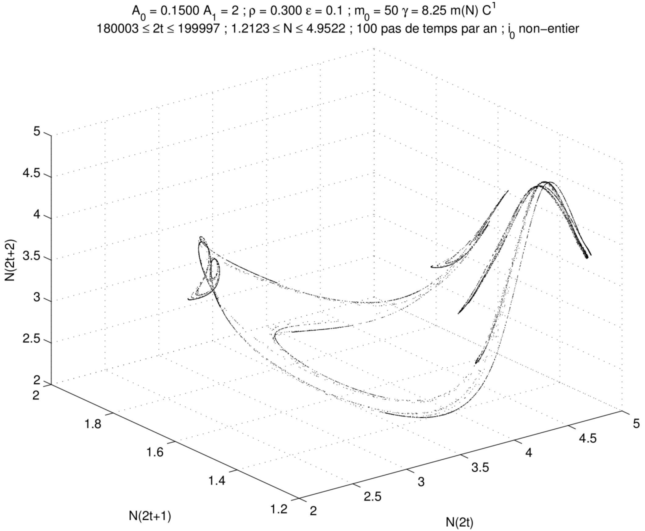
$(A_0 = 0.18\,;\ \rho = 0.30\,;\ \gamma = 8.25)$: $d_f \approx 1.19$



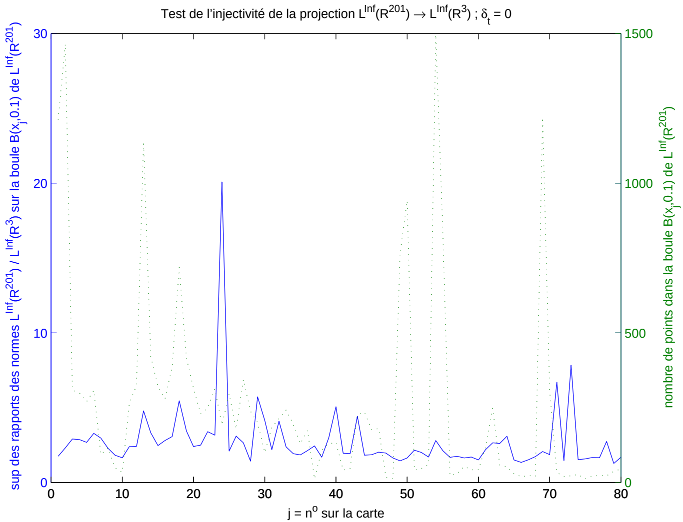
$(A_0 = 0.15\,;\ \rho = 0.30\,;\ \gamma = 8.25):\ d_f \approx 1.33$



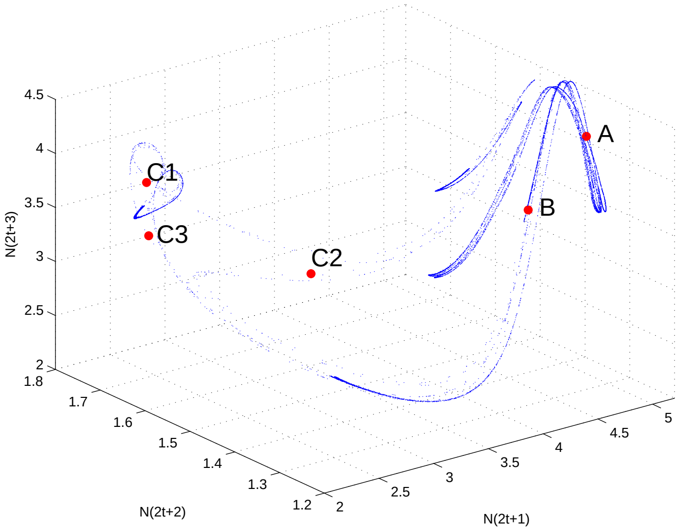
One connex component (physical measure)



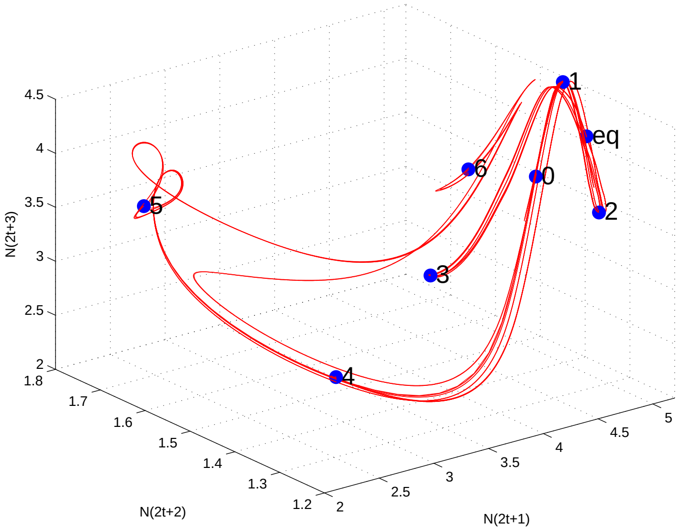
Injectivity of the projection $\mathbb{R}^{201} \mapsto \mathbb{R}^3$



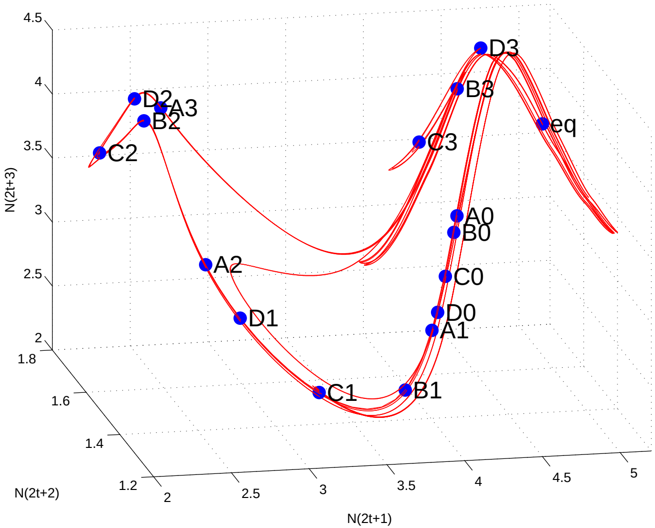
Dynamics (1): equilibrium, period-2, period-3



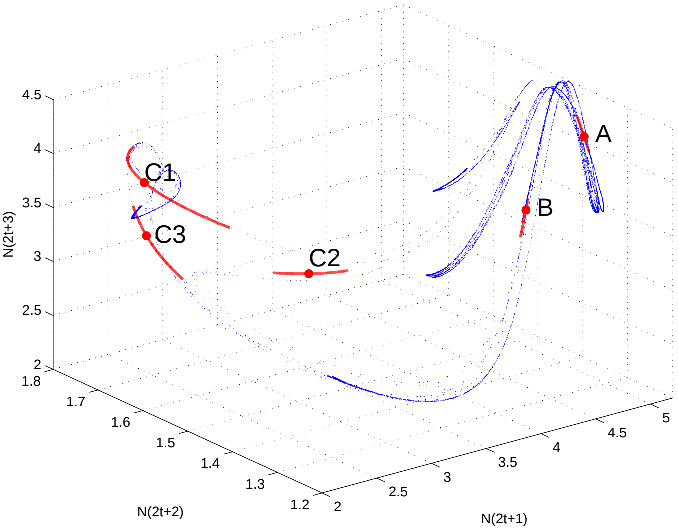
Dynamics (2)


4.5
4
3.5
3
2.5
2
N(2t+3)
1.8
1.7
1.6
1.5
1.4
1.3
1.2
N(2t+2)
2
2.5
3
3.5
4
4.5
5
N(2t+1)
0
1
2
3
4
5
6
eq

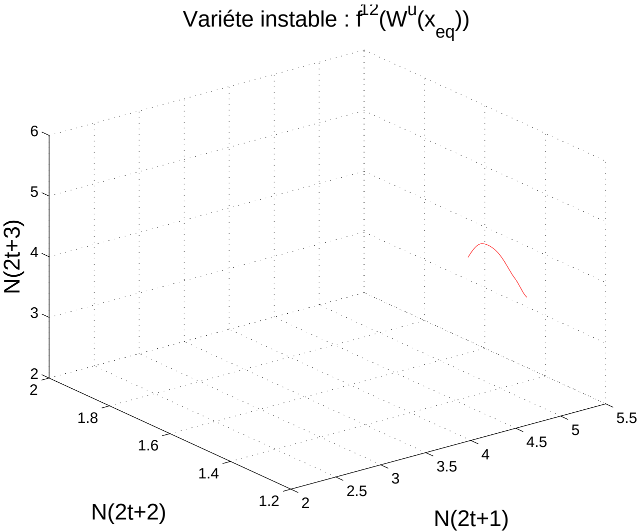
Dynamics (3) [+ see video]



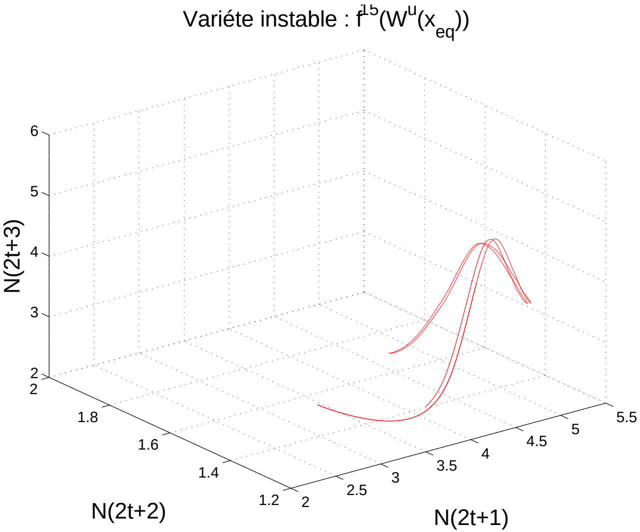
Remarkable points: local unstable manifolds



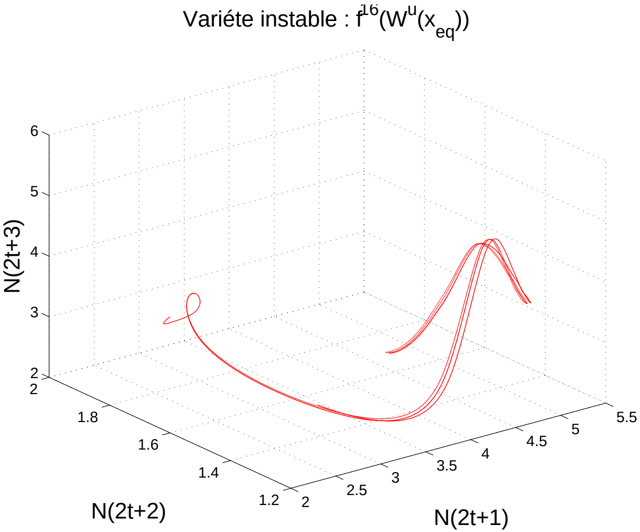
Equilibrium: expansion of the unstable manifold (1)



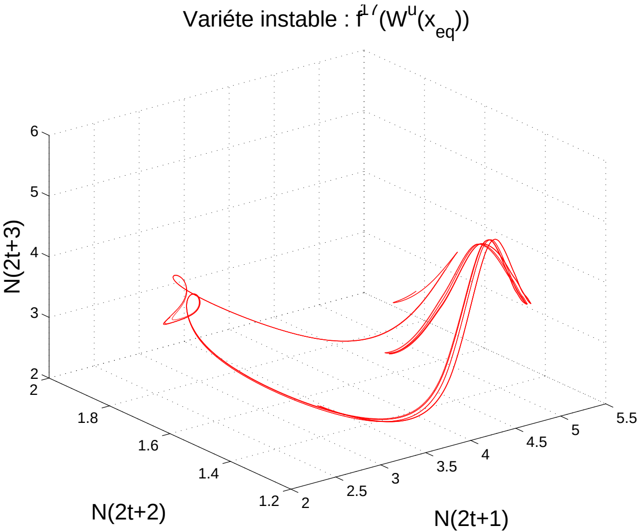
Equilibrium: expansion of the unstable manifold (2)



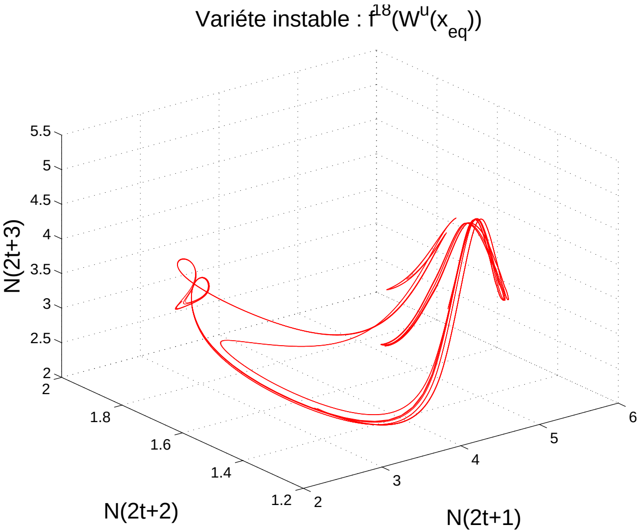
Equilibrium: expansion of the unstable manifold (3)



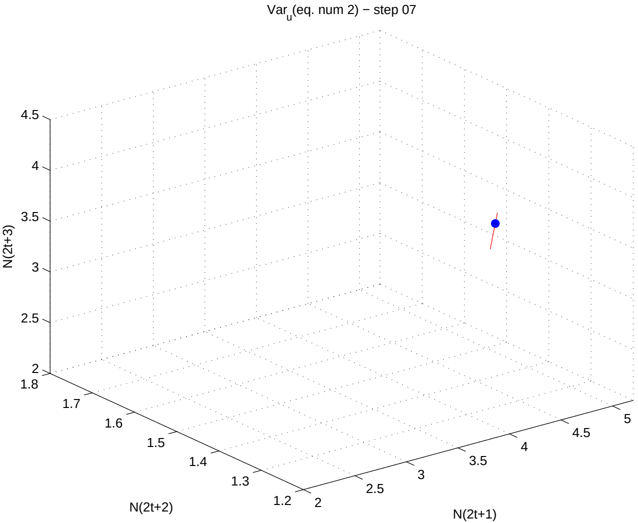
Equilibrium: expansion of the unstable manifold (4)



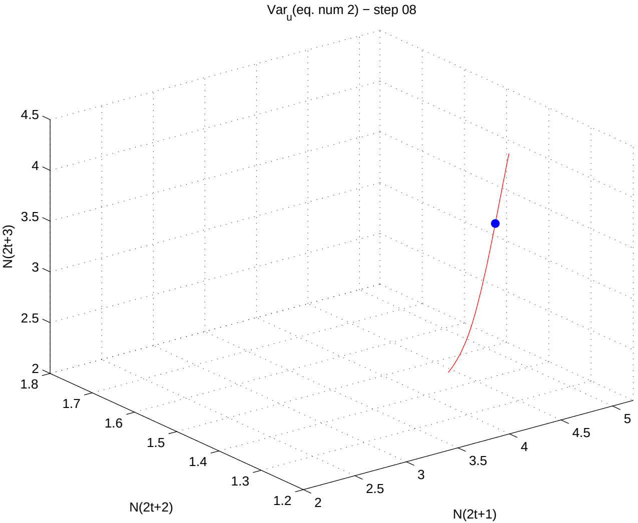
Equilibrium: global unstable manifold



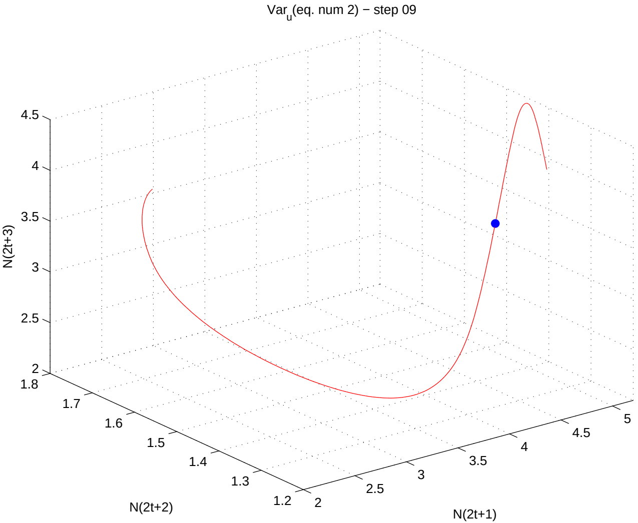
Period 2: expansion of the unstable manifold (1)



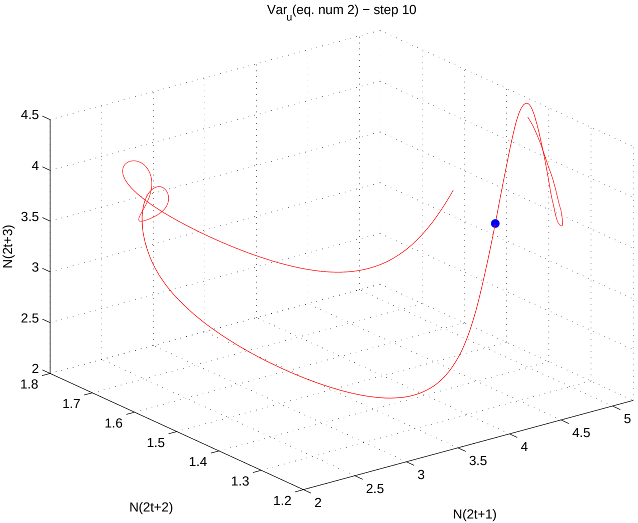
Period 2: expansion of the unstable manifold (2)



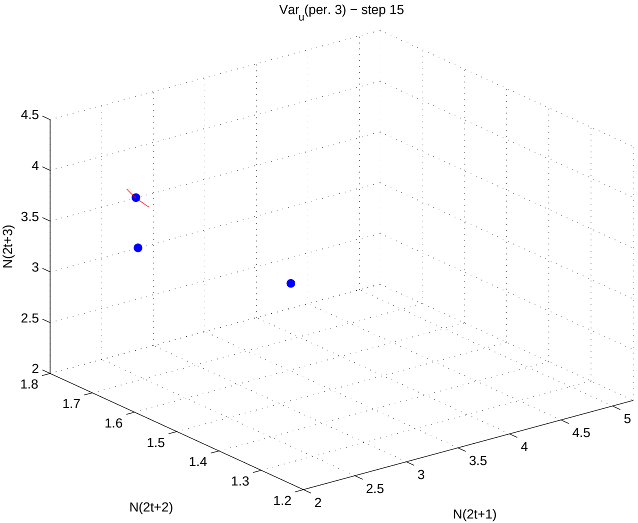
Period 2: expansion of the unstable manifold (3)



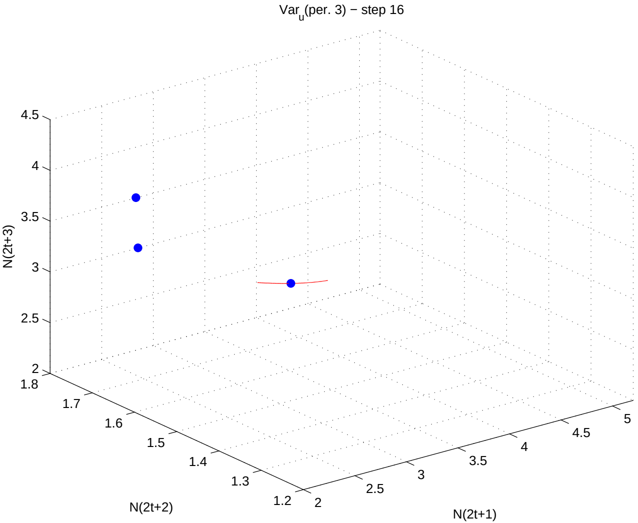
Period 2: expansion of the unstable manifold (4)



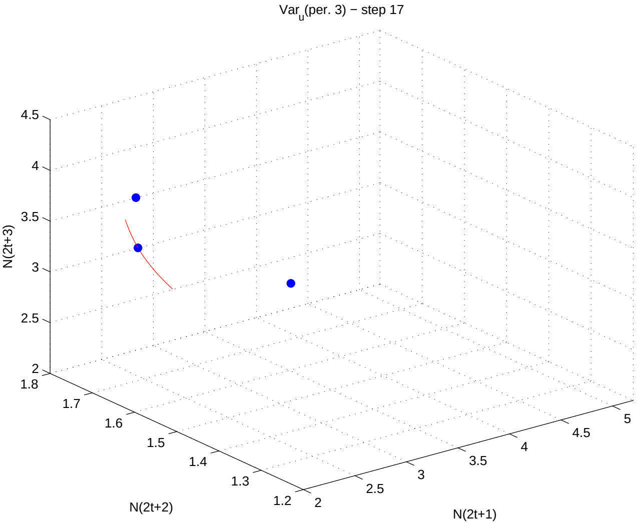
Period 3: expansion of the unstable manifold (1)



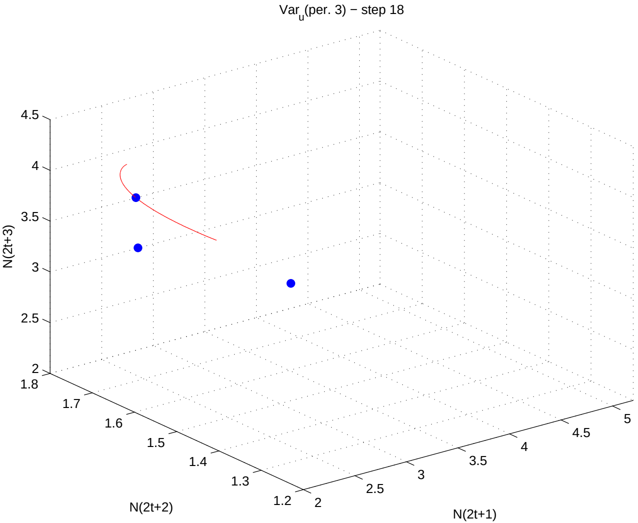
Period 3: expansion of the unstable manifold (2)



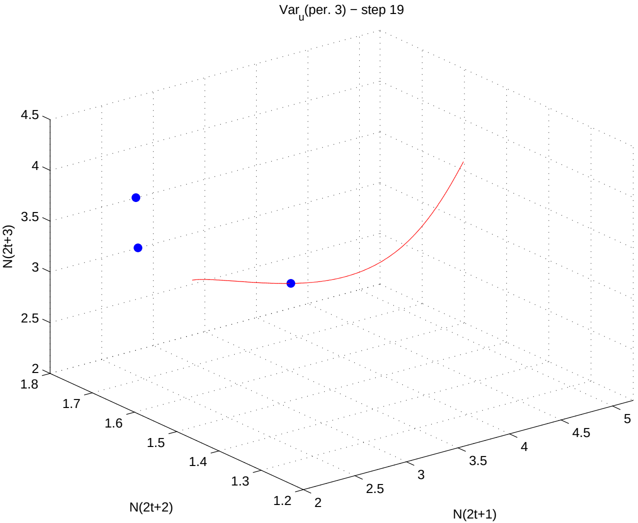
Period 3: expansion of the unstable manifold (3)



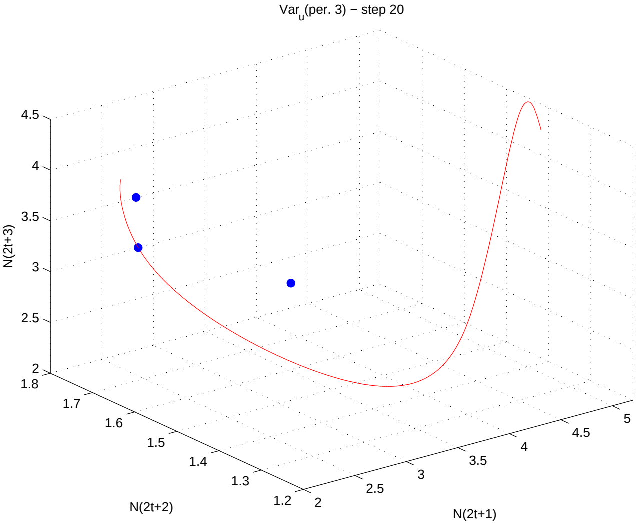
Period 3: expansion of the unstable manifold (4)



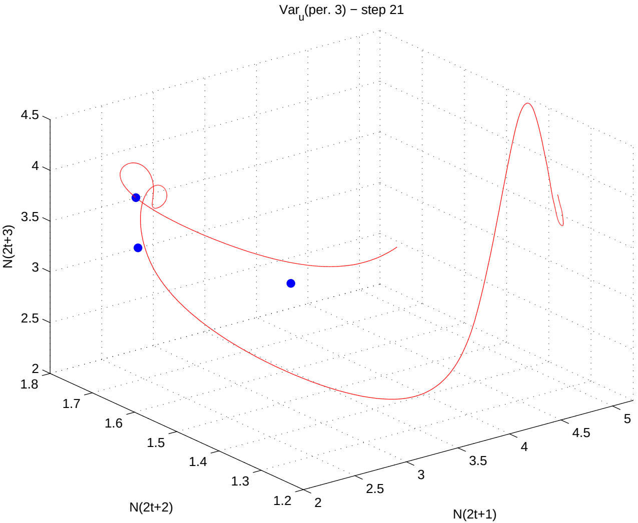
Period 3: expansion of the unstable manifold (5)



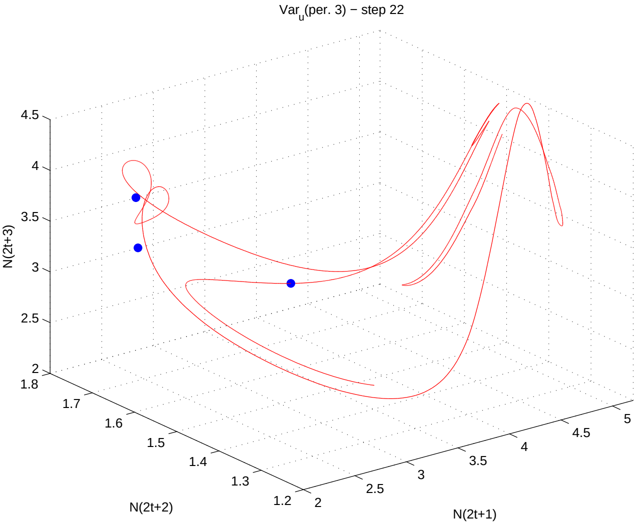
Period 3: expansion of the unstable manifold (6)



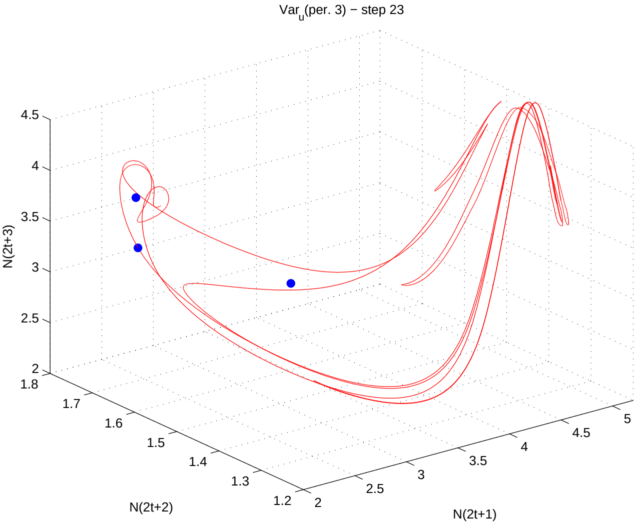
Period 3: expansion of the unstable manifold (7)



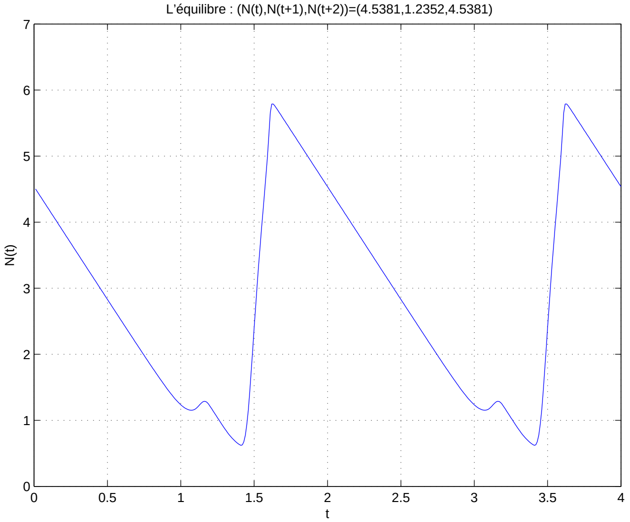
Period 3: expansion of the unstable manifold (8)



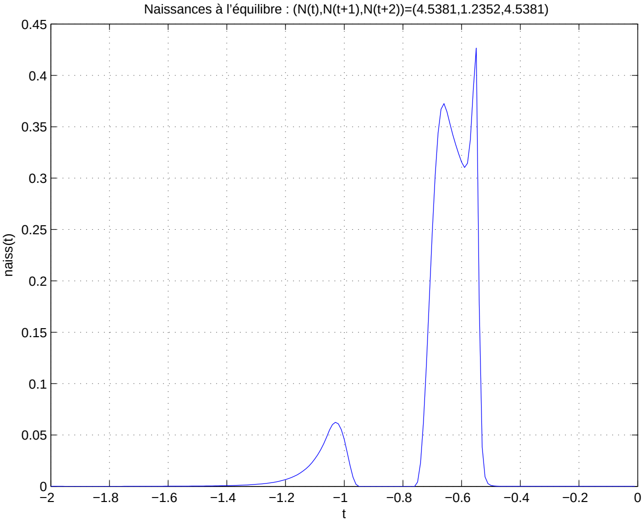
Period 3: global unstable manifold



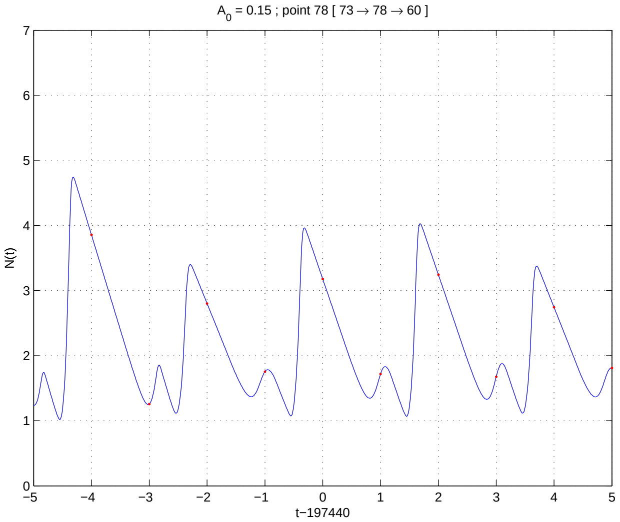
Dynamics in continuous time: equilibrium



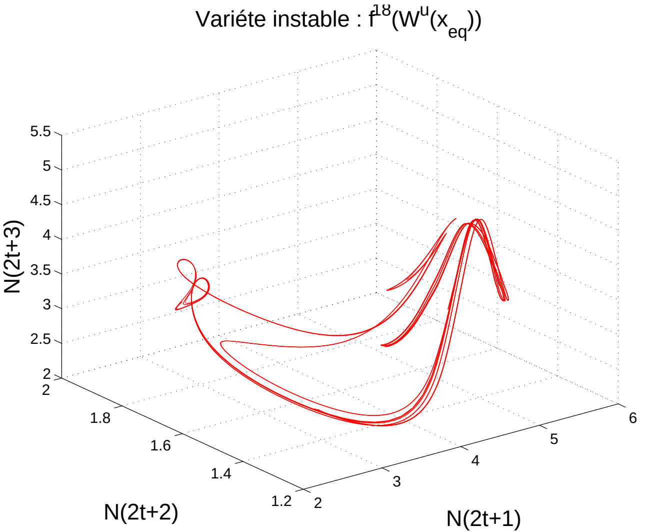
Dynamics in continuous time: birth at equilibrium



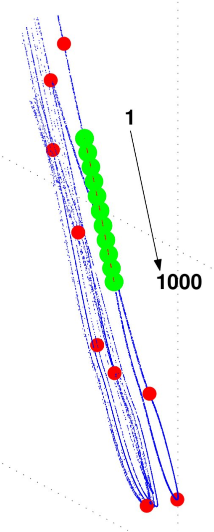
Dynamics in continuous time: period-3 orbit (triangle)



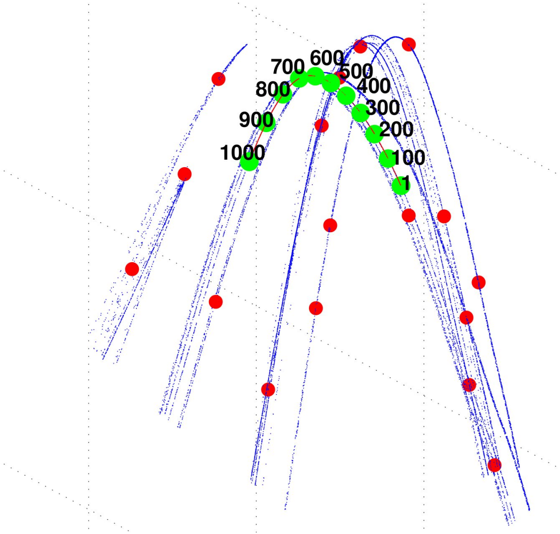
Attractor: there is a "fold"



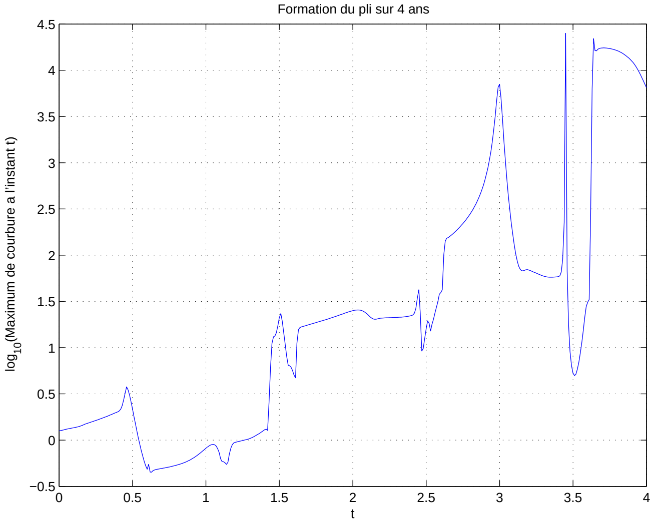
Folding (1): before the fold



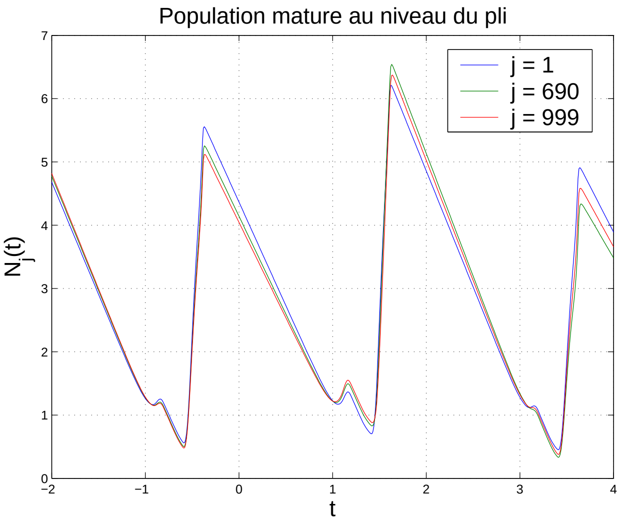
Folding (2)



Folding (3): curvature



Fold: dynamics in continuous time



Global dynamics: summary

- shrinking
- stretching
- folding (stable in the parameter space, see video)
- "branching" (from equilibrium/period-2 to period-3)

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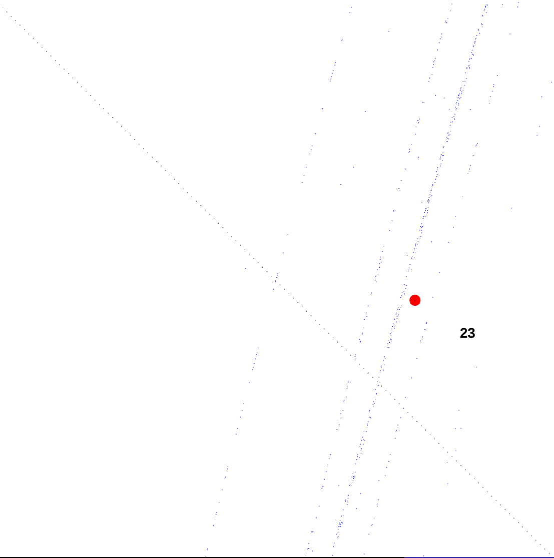
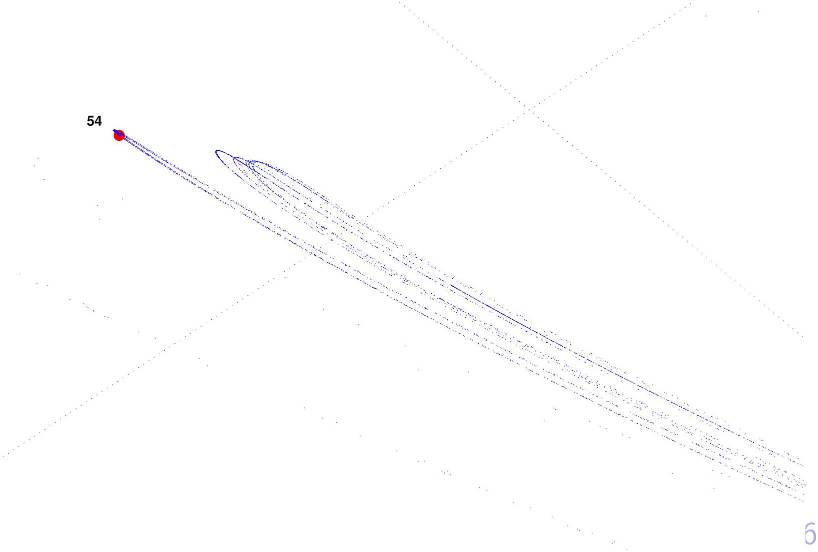
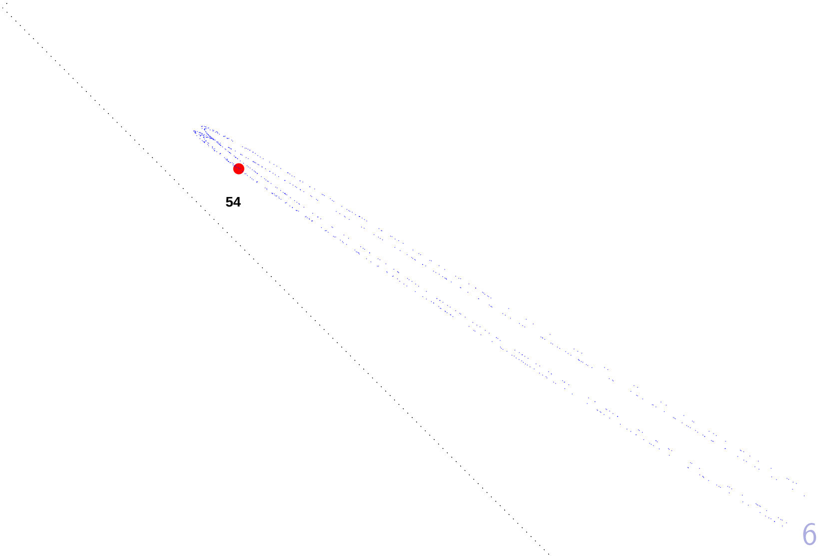
Local geometry: zoom on a “filament”



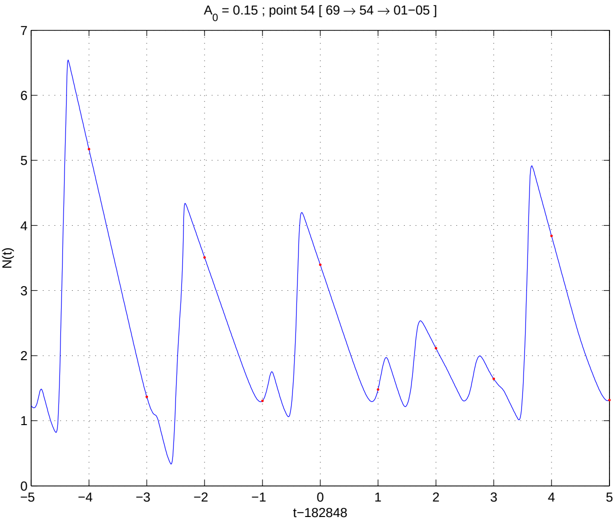
Local geometry: zoom on a peak



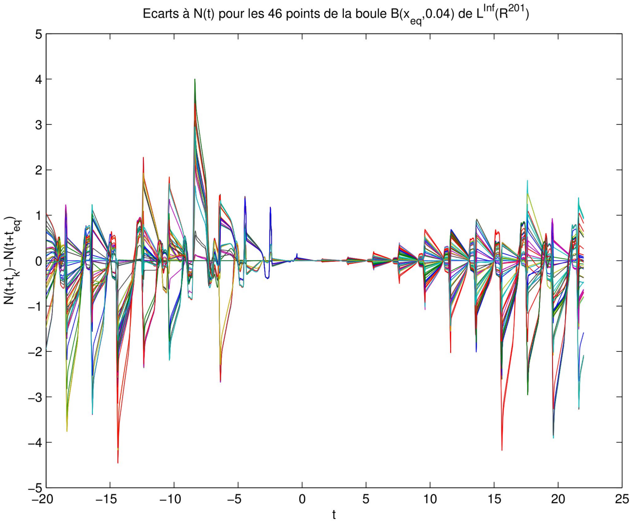
Local geometry: zoom on a peak



Dynamics in continuous time: in a “peak”



Sensitivity to initial conditions around the equilibrium



Conclusions: conjectures

For some of the parameter values:

- periodic orbits, doubling period bifurcations, sub-harmonic cascade.
- Hopf bifurcations.
- Chaotic dynamics, Henon-type attractors.

For the attractor $(0.15\,;\,0.30\,;\,8.25)$:

- Strange attractor. Persistent chaotic dynamics.
- Fractal dimension in $(1\,,\,3/2)$.
- Quasi-hyperbolicity.
- Spectral decomposition.

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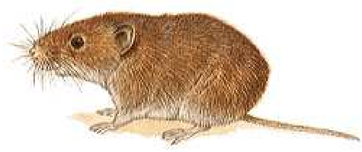
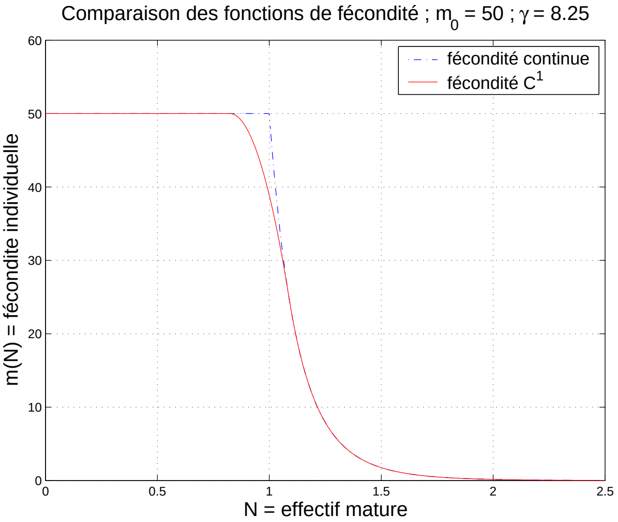
Biological conclusions

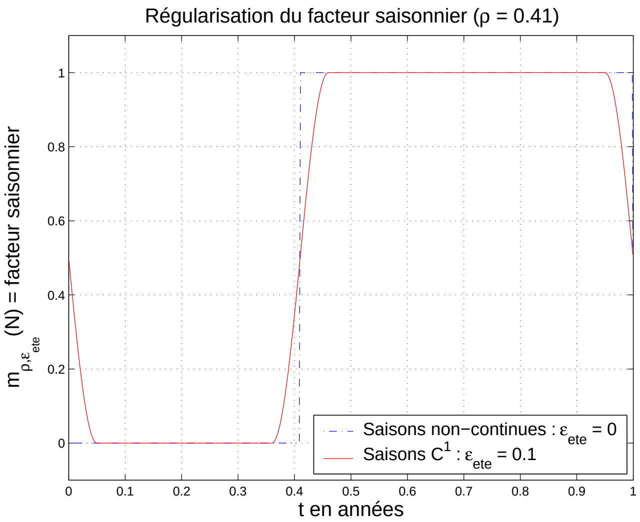
- Simple model, unrealistic.
- Sufficient to induce chaotic dynamics, not well understood mathematically.
- Qualitatively looks like real data.



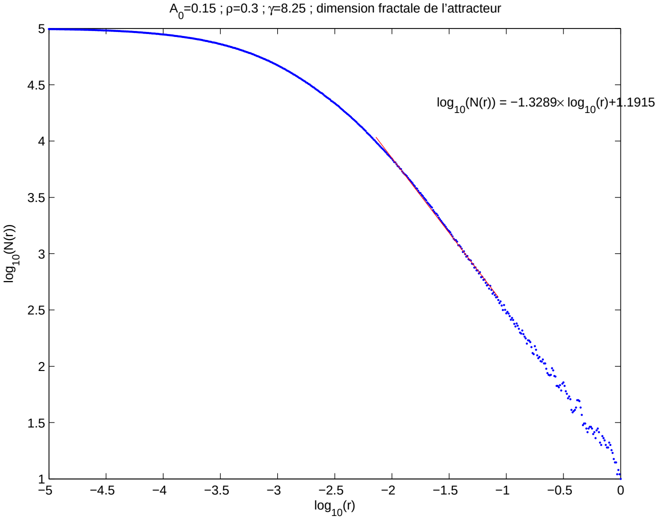
Smoothing of the fertility rate



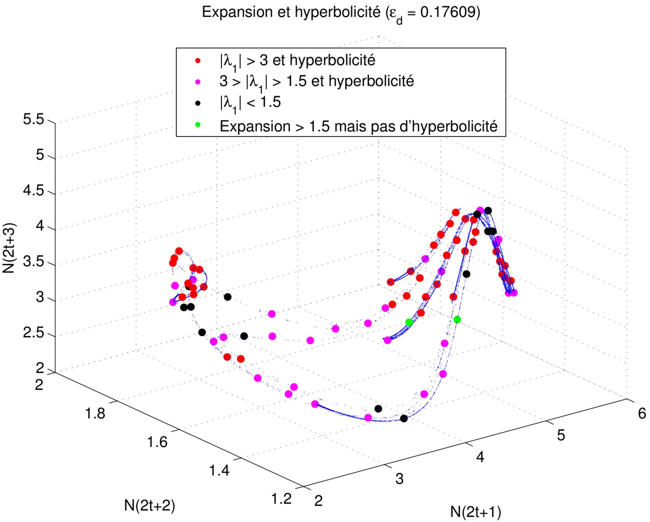
Smoothing of the seasonal factor



Estimation of the fractal dimension



Dynamics on the attractor: expansion areas



Fold: unstable direction