Modélisation mathématique en écologie : de l'individu à la population et à la communauté

Pierre Auger

IRD, UR Geodes et MOMISCO
Centre de recherche IRD de l'Ile de France, Bondy

E-mail: pierre.auger@bondy.ird.fr

Université de Rennes 1, 26 mars 2008

Outline of the presentation

⌘ Aggregation methods for ODEs : emergence

⌘ Predator-prey model in a patchy environment

⌘ Effects of density dependent migrations

⌘ Aggregation methods in time discrete models

Ecological levels of organization

- Individual level
- Population level
- Community level

Time scales and levels of organization

- Individual level : Day
- Population level : Year
- Community level : Evolutionary time scales

Aggregation of variables

- ⌘ More realistic models, i.e. structured population models : behaviour, age, species …

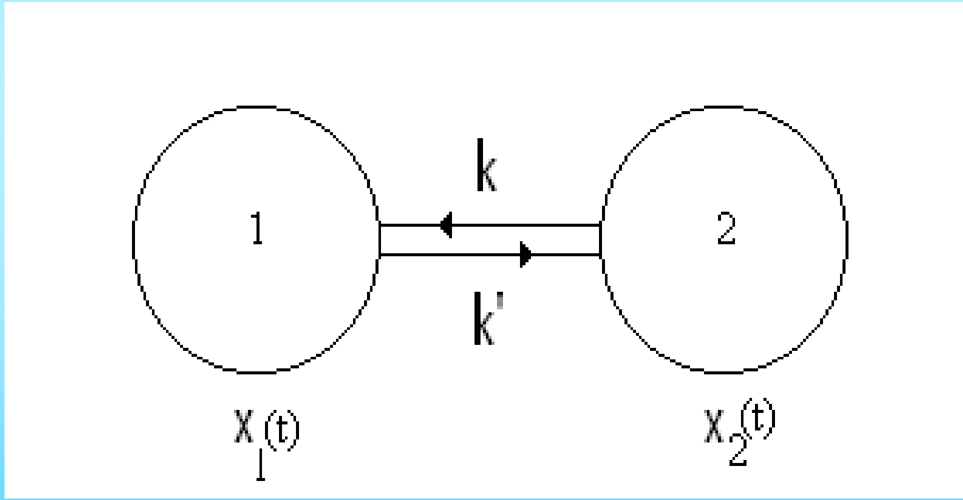
- ⌘ Take advantage of time scales to « aggregate » :

  Build an aggregated (reduced) model governing a few global variables at a slow time scale.

Predator-prey model in a two patch environment with fast migration

A patchy environment

- Two patches



Fast dispersal

$$\frac{dx_1}{d\tau} = kx_2 - k'x_1 + \varepsilon\left(r_1 x_1\left(1 - \frac{x_1}{K_1}\right) - a_1 x_1 p_1\right)$$

$$\frac{dx_2}{d\tau} = k'x_1 - kx_2 + \varepsilon\left(r_2 x_2\left(1 - \frac{x_2}{K_2}\right) - a_2 x_2 p_2\right)$$

$$\frac{dp_1}{d\tau} = mp_2 - m'p_1 + \varepsilon\left(b_1 x_1 p_1 - d_1 p_1\right)$$

$$\frac{dp_2}{d\tau} = m'p_1 - mp_2 + \varepsilon\left(b_2 x_2 p_2 - d_2 p_2\right)$$

R. Mchich, P. Auger and N. Raïssi, 2000. « The dynamics of a fish stock exploited on two fishing zones ». Acta Biotheoretica. Vol. 48, N. ¾, pp. 207-218.

The fast model

$$\frac{dx_1}{d\tau} = kx_2 - k' x_1$$

$$\frac{dx_2}{d\tau} = k' x_1 - kx_2$$

$$\frac{dp_1}{d\tau} = mp_2 - m' p_1$$

$$\frac{dp_2}{d\tau} = m' p_1 - mp_2$$

Total prey and predator densities are constant at fast time scale:

$$x = x_1 + x_2$$

$$p = p_1 + p_2$$

Fast and stable equilibrium

$$k(x - x_1) - k' x_1 = 0$$
$$m(p - p_1) - m' p_1 = 0$$

$$\Rightarrow$$

$$x_1^* = \frac{kx}{k + k'} = \nu_1 x$$
$$x_2^* = \frac{k' x}{k + k'} = \nu_2 x$$

$$p_1^* = \frac{mp}{m + m'} = \mu_1 p$$
$$p_2^* = \frac{m' p}{m + m'} = \mu_2 p$$

The aggregated model

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - axp$$

$$\frac{dp}{dt} = bxp - dp$$

with

$$r = r_1\nu_1 + r_2\nu_2$$

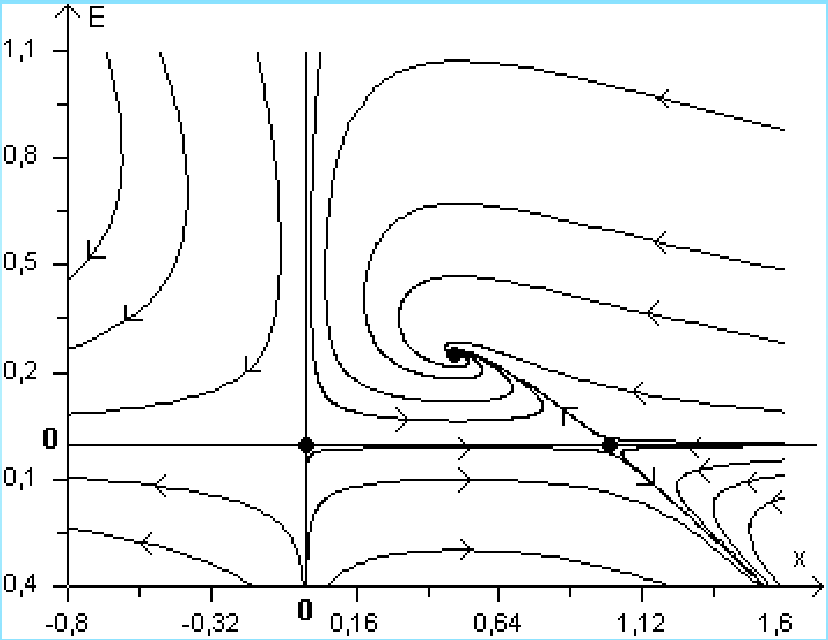
$$a = a_1\eta_1\nu_1 + a_2\eta_2\nu_2$$

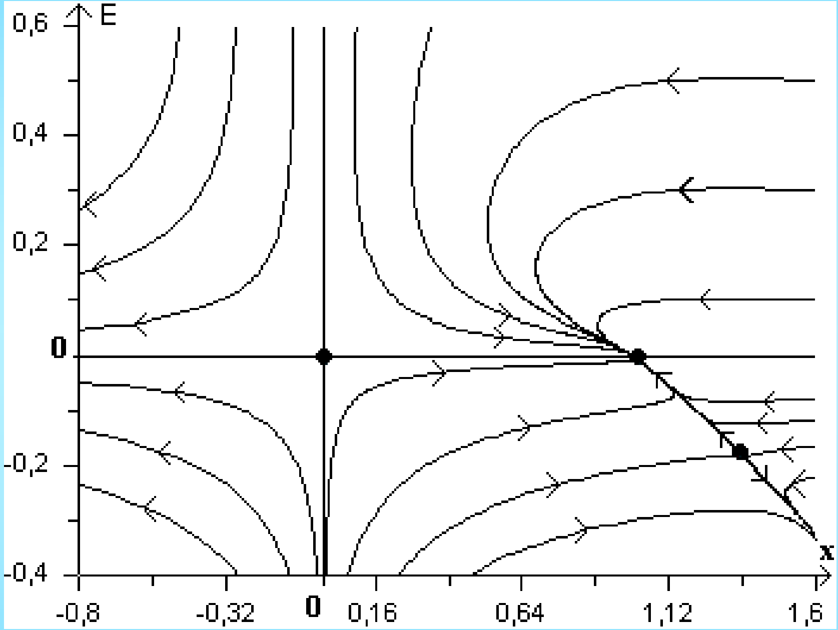
$$b = b_1\eta_1\nu_1 + b_2\eta_2\nu_2$$

$$d = d_1\eta_1 + d_2\eta_2$$

$$K = \frac{r}{\frac{r_1(\nu_1)^2}{K_1} + \frac{r_2(\nu_2)^2}{K_2}}$$

• **Condition for predator persistence**





$bK > d$

$bK < d$

Aggregated model similar to complete model

- Complete model

$$\frac{dx_1}{d\tau} = kx_2 - k' x_1 + \varepsilon\left(r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) - a_1 x_1 p_1 \right)$$

$$\frac{dx_2}{d\tau} = k' x_1 - kx_2 + \varepsilon\left(r_2 x_2 \left(1 - \frac{x_2}{K_2} \right) - a_2 x_2 p_2 \right)$$

$$\frac{dp_1}{d\tau} = mp_2 - m' p_1 + \varepsilon\left(b_1 x_1 p_1 - d_1 p_1 \right)$$

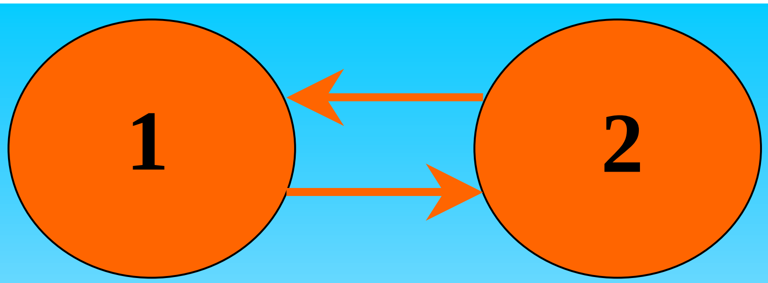
$$\frac{dp_2}{d\tau} = m' p_1 - mp_2 + \varepsilon\left(b_2 x_2 p_2 - d_2 p_2 \right)$$

- Aggregated model

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K} \right) - axp$$

$$\frac{dp}{dt} = bxp - dp$$

When the « fast derivation » method fails



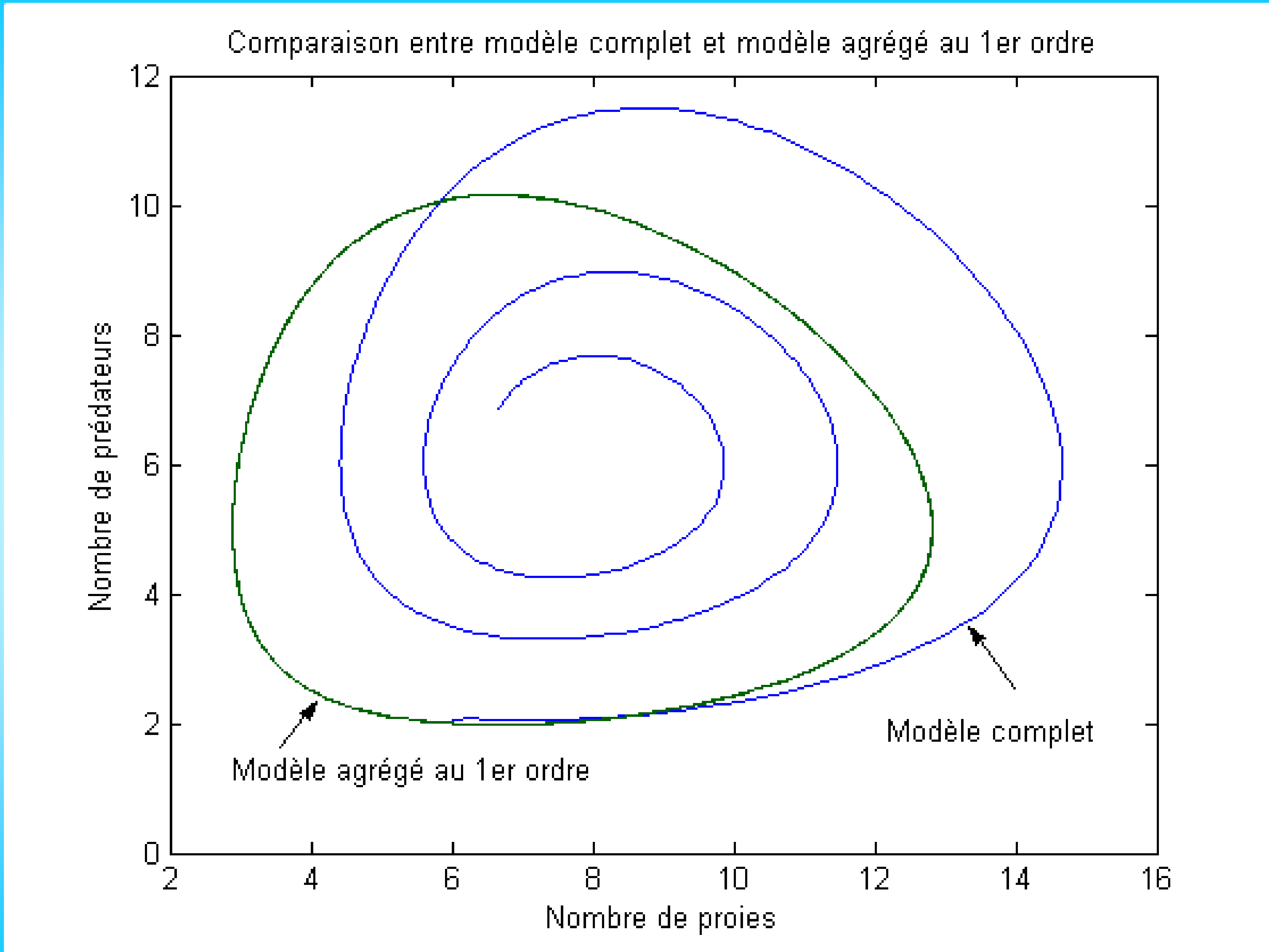
$$\begin{cases} \dfrac{dN_1}{d\tau} = m_{12}N_2 - m_{21}N_1 + \varepsilon N_1\left(r_1 - a_1 P\right) \\ \dfrac{dN_2}{d\tau} = m_{21}N_1 - m_{12}N_2 + \varepsilon r_2 N_2 \\ \dfrac{dP}{d\tau} = \varepsilon P\left(e b_1 N_1 - \mu\right) \end{cases}$$

Reduction of the model

$$N_1^* = \frac{m_{12} N}{m_{12} + m_{21}} \qquad N_2^* = \frac{m_{21} N}{m_{12} + m_{21}}$$

$$\begin{cases} \dfrac{dN}{dt} = rN - aNP \\ \dfrac{dP}{dt} = eaNP - \mu P \end{cases}$$

$$r = r_1 \frac{N_1^*}{N} + r_2 \frac{N_2^*}{N} \qquad a = a_1 \frac{N_1^*}{N}$$


Comparaison entre modèle complet et modèle agrégé au 1er ordre
Nombre de prédateurs
Nombre de proies
Modèle complet
Modèle agrégé au 1er ordre
0
2
4
6
8
10
12
14
16

Théorème de Fénichel (1971)

$$\begin{cases} \dfrac{dx}{d\tau} = f(x;y;\varepsilon) \\ \dfrac{dy}{d\tau} = \varepsilon g(x;y;\varepsilon) \\ \dfrac{d\varepsilon}{d\tau} = 0 \end{cases}$$

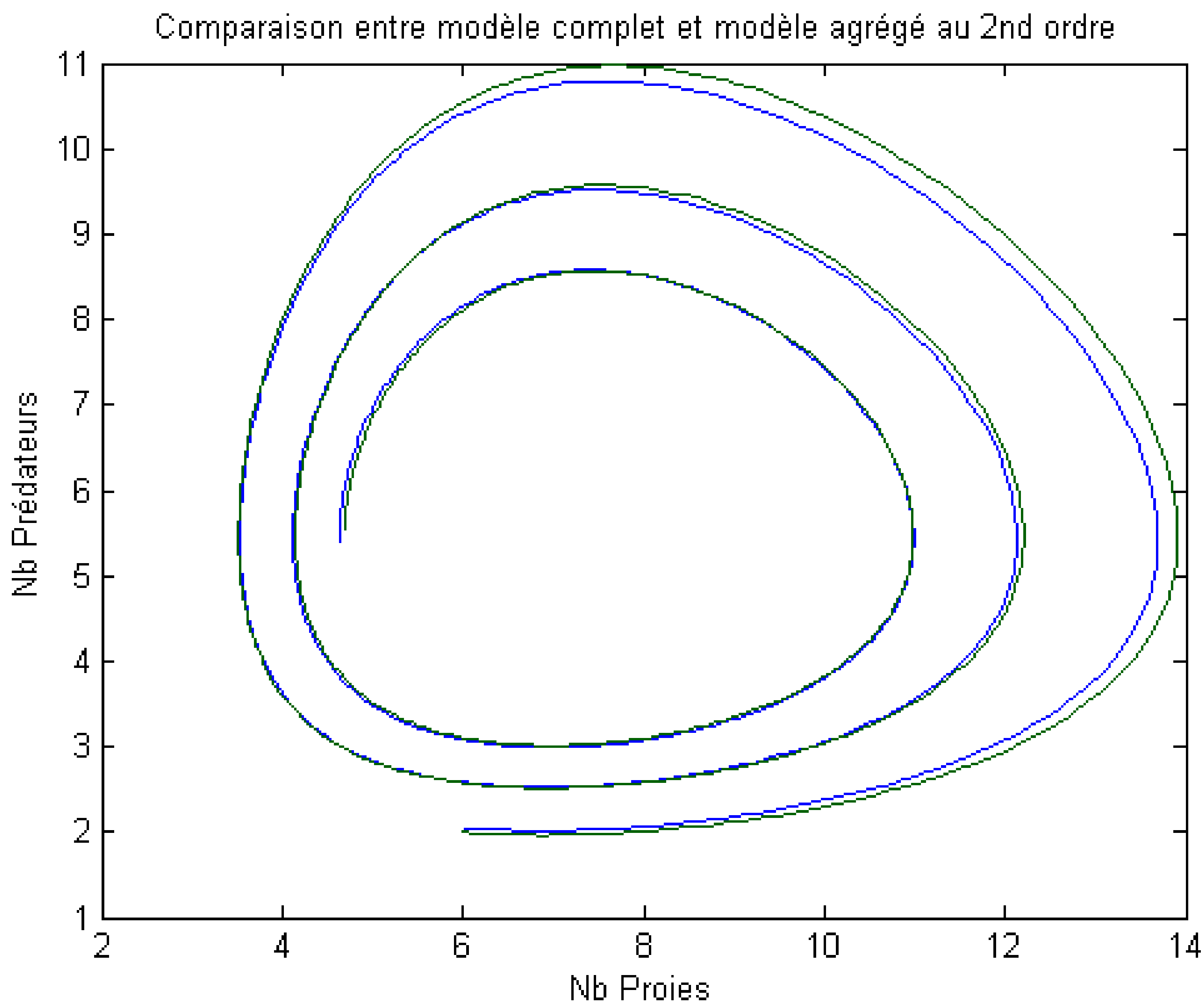
$$x = h(y;\varepsilon)$$

$$\begin{cases} \dfrac{dy}{dt} = g(h(y;\varepsilon);y;\varepsilon) \\ \qquad = G(y;\varepsilon) \approx G(y;0) + O(\varepsilon) \end{cases}$$

⌘ Fenichel center manifold theorem

$$\begin{cases} \dfrac{dN}{dt} = rN - aNP + \varepsilon N\omega_1(N;P)(r_1 - r_2 - a_1 P) \\ \dfrac{dP}{dt} = eaNP - \mu P + \varepsilon NPea_1\omega_1(N;P) \end{cases}$$

$$\omega_1(N;P) = \frac{N_1{}^* N_2{}^* (r_1 - r_2 - a_1 P)}{N^2 (m_{12} + m_{21})}$$


Comparaison entre modèle complet et modèle agrégé au 2nd ordre
Nb Prédateurs
Nb Proies
11
10
9
8
7
6
5
4
3
2
1
2
4
6
8
10
12
14

⌘ The « fast derivation » method is valid :

- ⌘ If $\varepsilon \ll 1$
- ⌘ If the « aggregated » model is structurally stable
- ⌘ If the « aggregated » model is not structurally stable, it is needed to calculate the next term of the Taylor expansion
- ⌘ Fast limit cycle…

⌘ References on aggregation methods

⌘ « Perfect and approximate aggregation » :

Y. Iwasa, V. Andreasen, S.A. Levin. Aggregation in model ecosystems I. Perfect aggregation. Ecol Model. 37 (1987) 287.

Y. Iwasa Y., S.A. Levin, V. Andreasen. Aggregation in model ecosystems II. Approximate aggregation. IMA. J. Math. Appl. Med. Bio. 6 (1989) 1.

⌘ ODE’s, JC Poggiale, PhD thesis (1994) :

P. Auger et R. Roussarie, Complex ecological models with simple dynamics : From individuals to populations, Acta Biotheoretica, 42 (1994) 111.

P. Auger & J.C. Poggiale. Aggregation and Emergence in Systems of Ordinary Differential Equations. Math. Computer Modelling. Special issue "Aggregation and Emergence in Population Dynamics". P. Antonelli & P. Auger guest-Editors. 27 (1998) 1.

P. Auger and R. Bravo de la Parra. Methods of aggregation of variables in population dynamics. Comptes-Rendus de l’Académie des Sciences, Sciences de la Vie, 323 (2000) 665.

P. Auger, R. Bravo de la Parra, J.-C. Poggiale, E. Sanchez, L. Sanz, T. Nguyen Huu, Chapter in a book, Le Havre Conference, Lecture notes in Mathematics, Mathematical Biosciences sub-series, Springer, to appear.

⌘ Time discrete systems : L. Sanz, PhD thesis (1998) and A. Blasco, PhD thesis (2000) :

R. Bravo de la Parra, P. Auger & E. Sanchez, Aggregation methods in discrete models, Journal of Biological Systems, (1995), 3(2), 603-612.

E. Sanchez, R. Bravo de la Parra & P. Auger. Linear Discrete Models with Different Time Scales. Acta Biotheoretica, 43, pp. 465-479, 1995.

R. Bravo de la Parra, E. Sanchez, O. Arino and P. Auger. A discrete model with density dependent fast migration. Mathematical Biosciences, 157, 91-109, 1999.

⌘ PDE’s et DDE’s :

O. Arino, E. Sanchez, R. Bravo de la Parra and P. Auger. A model of an age-structured population with two time scales. SIAM J Appl. Math., 60, 408-436, 1999.

Sanchez E., Bravo de la Parra R., Auger P. and Gomez-Mourelo P. Time scales in linear delayed differential equations. Journal of Mathematical Analysis and Applications, 323, pp. 680-699, 2006.

D-D dispersal in a patchy environment

- P. Amarasekare. Interactions between Local Dynamics and Dispersal: Insights from Single Species Models. *Theoretical Population Biology*, 53 (1998) 44.
- P. Amarasekare. Spatial variation and density-dependent dispersal in competitive coexistence. *Proc. R. Soc. Lond.* B 271 (2004) 1497.
- P. Amarasekare. The role of density-dependent dispersal in source–sink dynamics. *Journal of Theoretical Biology*, 226 (2004) 159.

- **Density dependent migration of predators**

$$\frac{dx_1}{d\tau} = kx_2 - k'x_1 + \varepsilon\left(r_1x_1\left(1-\frac{x_1}{K_1}\right)-a_1x_1p_1\right)$$

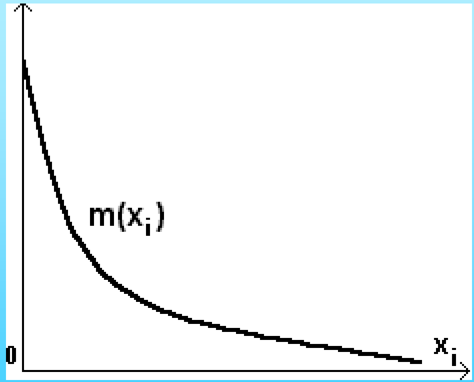
$$\frac{dx_2}{d\tau} = k'x_1 - kx_2 + \varepsilon\left(r_2x_2\left(1-\frac{x_2}{K_2}\right)-a_2x_2p_2\right)$$

$$\frac{dp_1}{d\tau} = m(x_2)p_2 - m'(x_1)p_1 + \varepsilon\left(b_1x_1p_1 - d_1p_1\right)$$

$$\frac{dp_2}{d\tau} = m'(x_1)p_1 - m(x_2)p_2 + \varepsilon\left(b_2x_2p_2 - d_2p_2\right)$$

$$m'(x_1) = \frac{1}{\alpha x_1 + \alpha_0}$$

$$m(x_2) = \frac{1}{\beta x_2 + \alpha_0}$$



R. Mchich, P. Auger, R. Bravo de la Parra and N. Raïssi, 2002. Ecological Modelling.

Fast and stable equilibrium

$$x_1^* = \frac{kx}{k+k'} = \nu_1 x$$

$$x_2^* = \frac{k'x}{k+k'} = \nu_2 x$$

$$p_1^* = \frac{(\alpha\nu_1 x + \alpha_0)\,p}{(\alpha\nu_1 x + \beta\nu_2 x + 2\alpha_0)} = \eta_1(x)\,p$$

$$p_2^* = \frac{(\beta\nu_2 x + \alpha_0)\,p}{(\alpha\nu_1 x + \beta\nu_2 x + 2\alpha_0)} = \eta_2(x)\,p$$

Aggregated model

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - a(x)xp$$

$$\frac{dp}{dt} = b(x)xp - d(x)p$$

$$r = r_1\nu_1 + r_2\nu_2$$

$$a(x) = a_1\eta_1(x)\nu_1 + a_2\eta_2(x)\nu_2$$

$$b(x) = b_1\eta_1(x)\nu_1 + b_2\eta_2(x)\nu_2$$

$$d(x) = d_1\eta_1(x) + d_2\eta_2(x)$$

$$K = \frac{r}{\dfrac{r_1(\nu_1)^2}{K_1} + \dfrac{r_2(\nu_2)^2}{K_2}}$$

- **Emergence**

⌘ The complete model

$$\frac{dx_1}{d\tau} = kx_2 - k'x_1 + \varepsilon\left(r_1x_1\left(1-\frac{x_1}{K_1}\right) - a_1x_1p_1\right)$$

$$\frac{dx_2}{d\tau} = k'x_1 - kx_2 + \varepsilon\left(r_2x_2\left(1-\frac{x_2}{K_2}\right) - a_2x_2p_2\right)$$

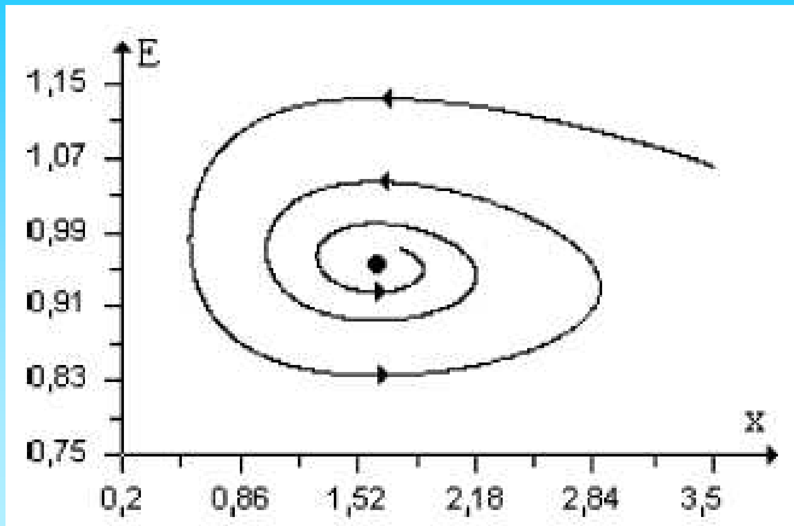
$$\frac{dp_1}{d\tau} = m(x_2)p_2 - m'(x_1)p_1 + \varepsilon\left(b_1x_1p_1 - d_1p_1\right)$$

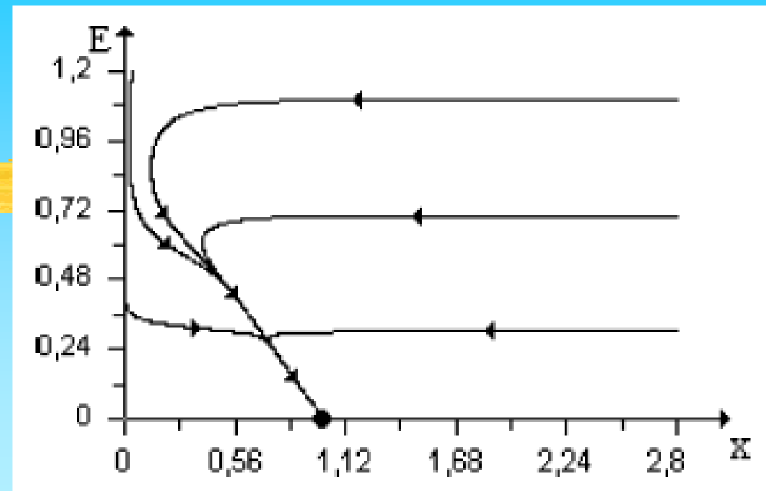
$$\frac{dp_2}{d\tau} = m'(x_1)p_1 - m(x_2)p_2 + \varepsilon\left(b_2x_2p_2 - d_2p_2\right)$$

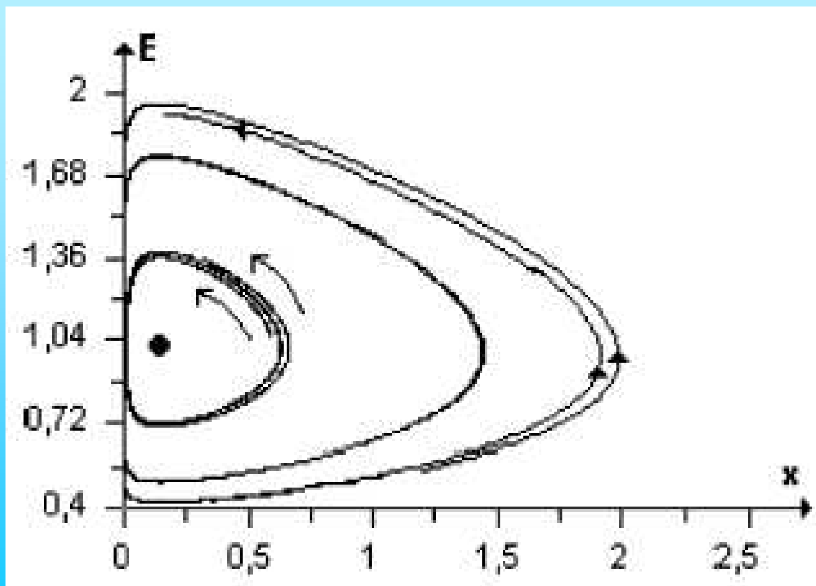
⌘ The aggregated model

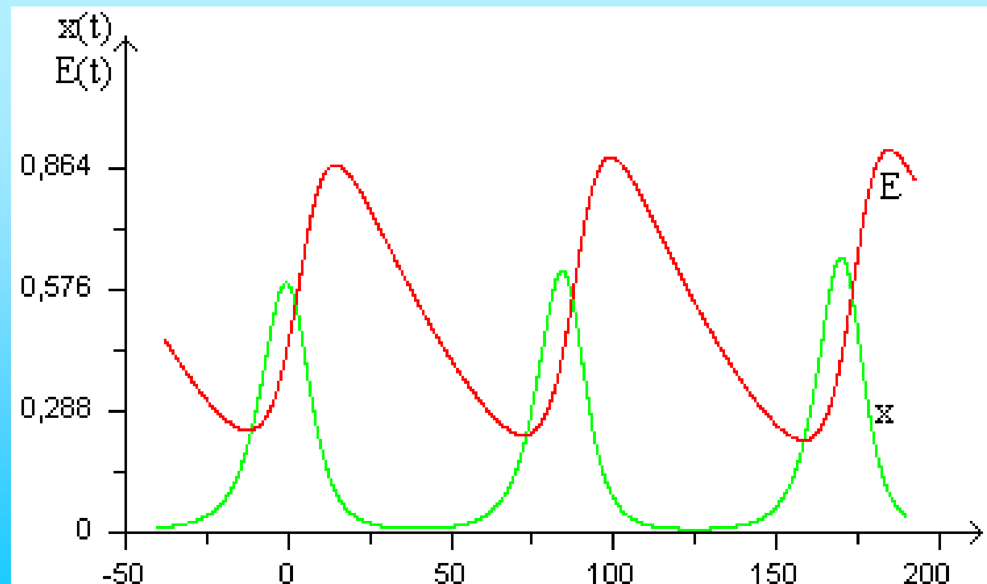
$$\frac{dx}{dt} = rx\left(1-\frac{x}{K}\right) - a(x)xp$$

$$\frac{dp}{dt} = b(x)xp - d(x)p$$


E
1,15
1,07
0,99
0,91
0,83
0,75
x
0,2
0,86
1,52
2,18
2,84
3,5


E
1,2
0,96
0,72
0,48
0,24
0
x
0
0,56
1,12
1,68
2,24
2,8


E
2
1,68
1,36
1,04
0,72
0,4
x
0
0,5
1
1,5
2
2,5


x(t)
E(t)
0,864
0,576
0,288
0
E
x
-50
0
50
100
150
200

• Emergence

- **Functional emergence** : The mathematical functions of the aggregated and local models are different

- **Dynamical emergence** : The dynamics of the aggregated model is qualitatively different from the dynamics of the local model

The predator-prey model with prey D-D predator dispersal and predator D-D prey dispersal

$$
\begin{cases}
\dfrac{dn_1}{d\tau} = (\alpha_2 p_2 + \alpha_0)n_2 - (\alpha_1 p_1 + \alpha_0)n_1 + \varepsilon\left[r_1 n_1\left(1 - \dfrac{n_1}{K_1}\right) - a_1 n_1 p_1\right] \\
\dfrac{dn_2}{d\tau} = (\alpha_1 p_1 + \alpha_0)n_1 - (\alpha_2 p_2 + \alpha_0)n_2 + \varepsilon\left[r_2 n_2\left(1 - \dfrac{n_2}{K_2}\right) - a_2 n_2 p_2\right] \\
\dfrac{dp_1}{d\tau} = \left(\dfrac{p_2}{\beta_2 n_2 + \beta_0} - \dfrac{p_1}{\beta_1 n_1 + \beta_0}\right) + \varepsilon[-\mu_1 p_1 + b_1 n_1 p_1] \\
\dfrac{dp_2}{d\tau} = \left(\dfrac{p_1}{\beta_1 n_1 + \beta_0} - \dfrac{p_2}{\beta_2 n_2 + \beta_0}\right) + \varepsilon[-\mu_2 p_2 + b_2 n_2 p_2]
\end{cases}
$$

ELABDELLAOUI A., AUGER P., BRAVO DE LA PARRA R., KOOI B. & MCHICH R. Mathematical Biosciences, (2007).

Fast equilibrium

$$\begin{cases} (\alpha_2 p_2 + \alpha_0)n_2 = (\alpha_1 p_1 + \alpha_0)n_1 \\ \dfrac{p_2}{\beta_2 n_2 + \beta_0} = \dfrac{p_1}{\beta_1 n_1 + \beta_0} \end{cases}$$

$$\begin{cases} (\alpha_2 (p - p_1) + \alpha_0)(n - n_1) = (\alpha_1 p_1 + \alpha_0)n_1 \\ (p - p_1)(\beta_1 n_1 + \beta_0) = p_1(\beta_2 (n - n_1) + \beta_0) \end{cases}$$

Fast equilibrium

$$n_1^* = \frac{AD+B}{\Delta},\ p_1^* = \frac{CD+E}{\Delta},\ n_2^* = n - n_1^*,\ p_2^* = p - p_1^*,$$

$$\Delta = -(2\alpha_0 + \alpha_2 p)(2\beta_0 + \beta_2 n) - \alpha_2 \beta_1 np$$

with

$$A = \alpha_2 n(\beta_2 - \beta_1) - (2\beta_0 + \beta_2 n)(\alpha_2 - \alpha_1)$$

$$B = \beta_0 \alpha_2 np - (2\beta_0 + \beta_2 n)(\alpha_0 + \alpha_2 p)n$$

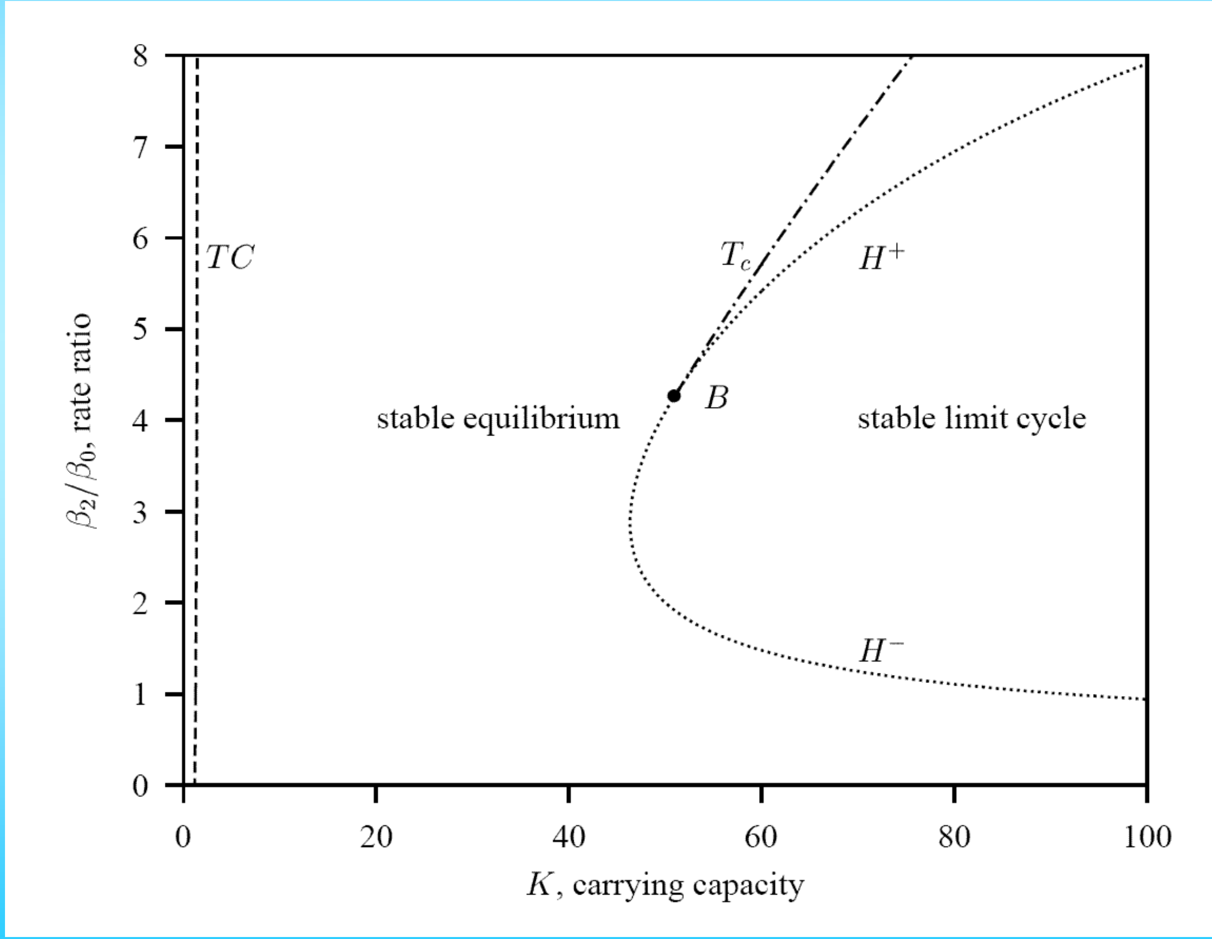
$$C = (2\alpha_0 + p\alpha_2)(\beta_1 - \beta_2) - \beta_1 p(\alpha_2 - \alpha_1)$$

$$E = -\beta_0 p(2\alpha_0 + p\alpha_2) - \beta_1 np(\alpha_0 + \alpha_2 p)$$

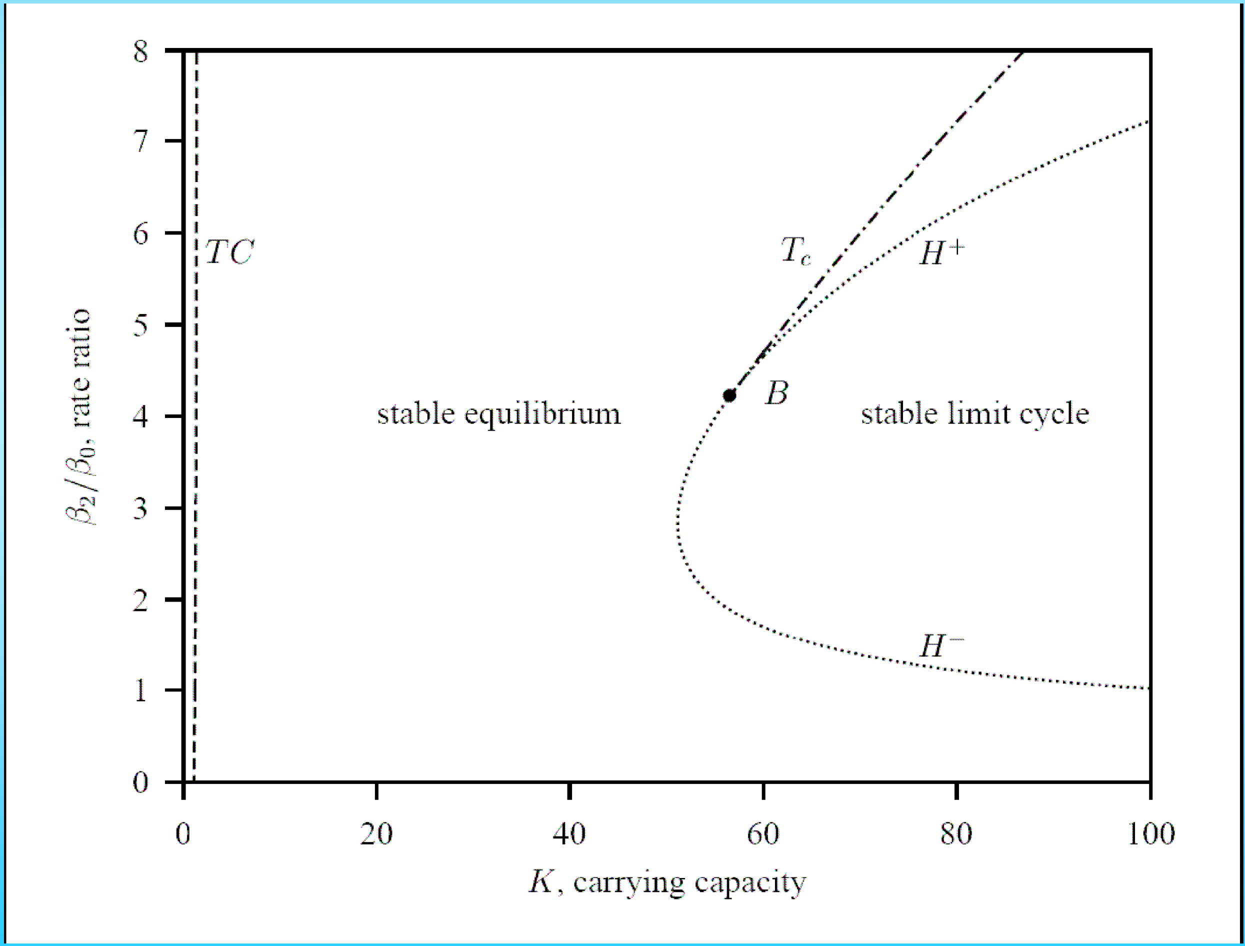
⌘ The aggregated model

$$\begin{cases} \dfrac{dn}{dt} = r_1 n_1^* \left(1 - \dfrac{n_1^*}{K_1}\right) + r_2 (n - n_1^*)\left(1 - \dfrac{n - n_1^*}{K_2}\right) - (a_1 n_1^* p_1^* + a_2 (n - n_1^*)(p - p_1^*)) \\ \dfrac{dp}{dt} = -(\mu_1 p_1^* + \mu_2 (p - p_1^*)) + b_1 n_1^* p_1^* + b_2 (n - n_1^*)(p - p_1^*) \end{cases}$$

⌘ Bifurcation analysis (aggregated)

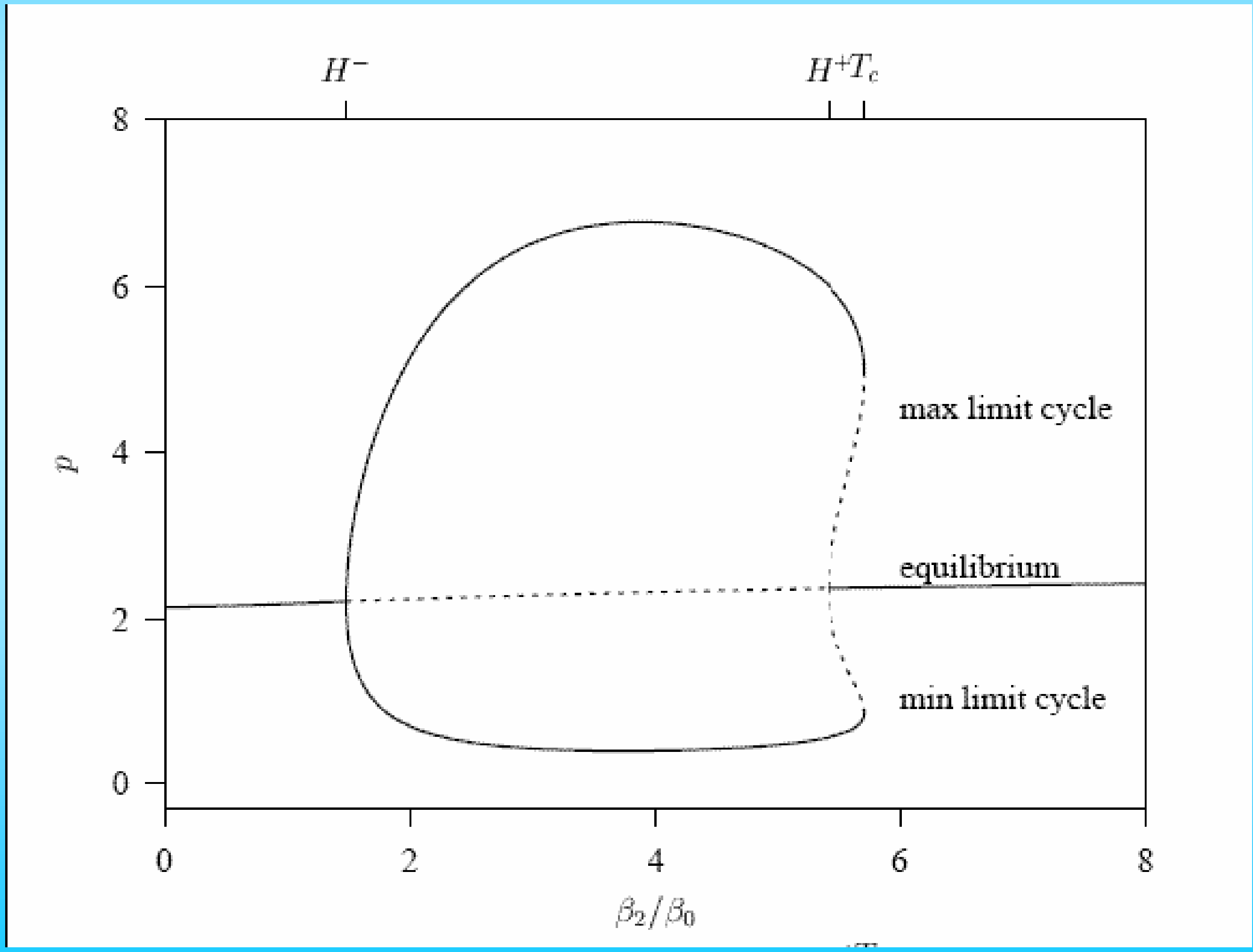


⌘ Bifurcation analysis (complete model)

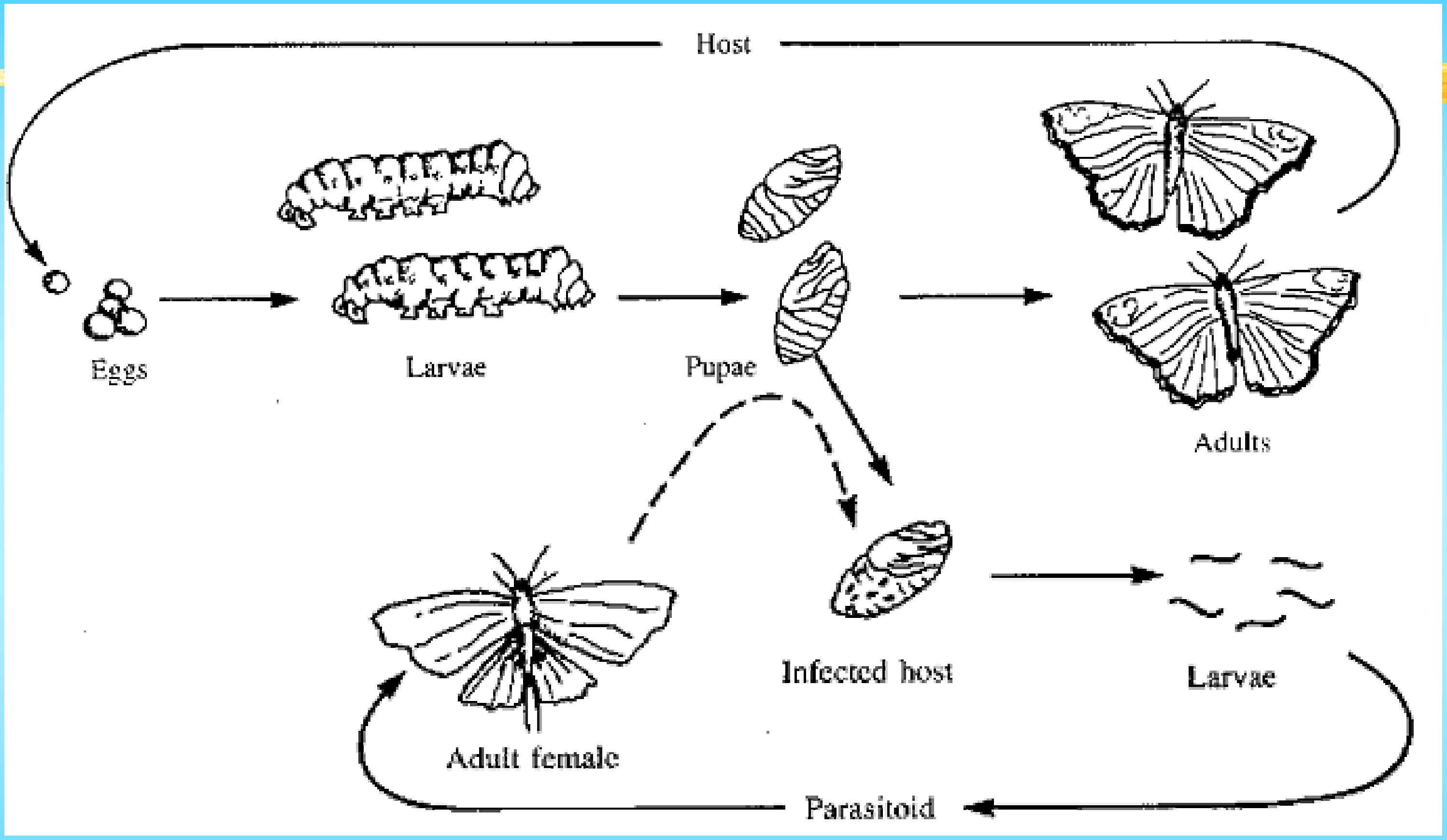


ε = 0.01

⌘ Bifurcation analysis (aggregated)



Système hôte-parasitoïde



Edelstein-Keshet, 1989

- Population d'hôtes à l'instant t : N_t
- Population de parasitoïdes à l'instant t : P_t

Modèle de Nicholson Bailey classique

- Modèle

$$N_{t+1} = \lambda \cdot N_t \cdot \exp\left(-a \cdot P_t\right)$$

$$P_{t+1} = c \cdot N_t \cdot \left(1 - \exp\left(-a \cdot P_t\right)\right)$$

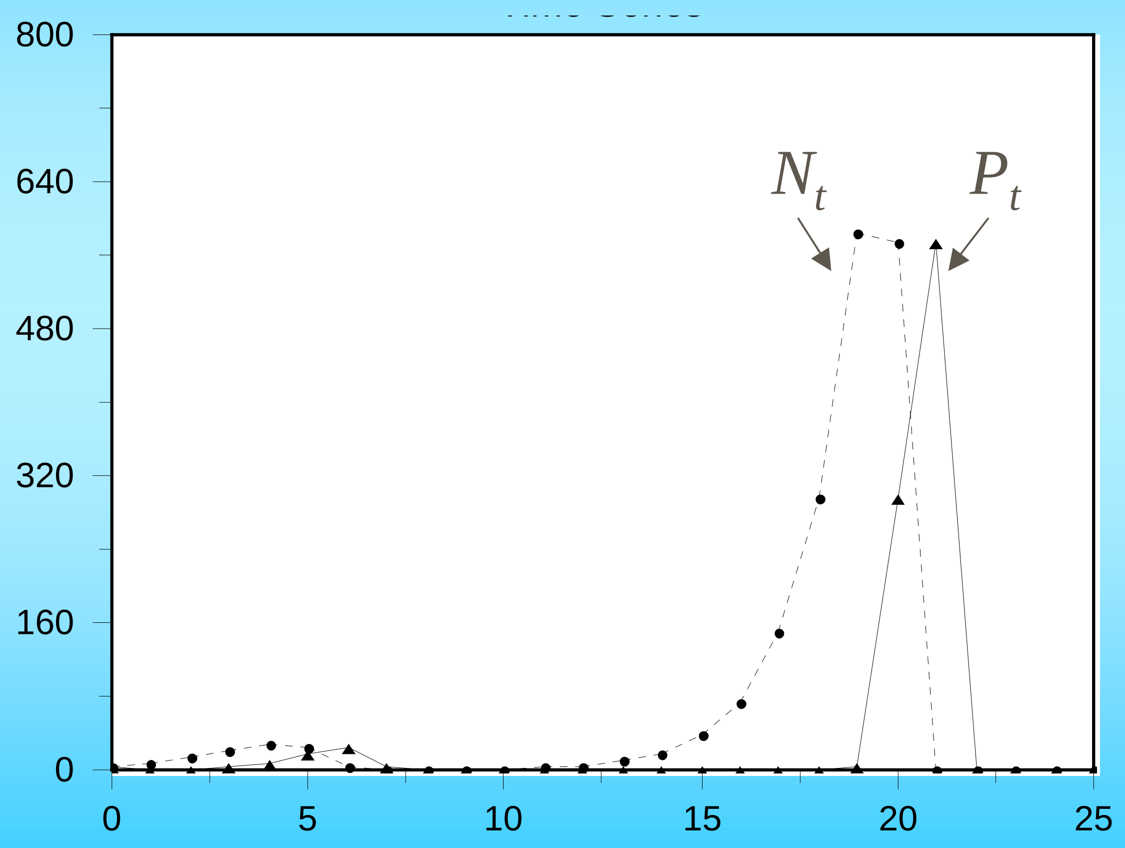
- Un point d'équilibre positif …

$$N^* = \frac{\lambda \cdot \ln\left(\lambda\right)}{a \cdot c \cdot \left(\lambda - 1\right)}$$

$$P^* = \frac{\ln\left(\lambda\right)}{a}$$

$\lambda > 1$ … instable !

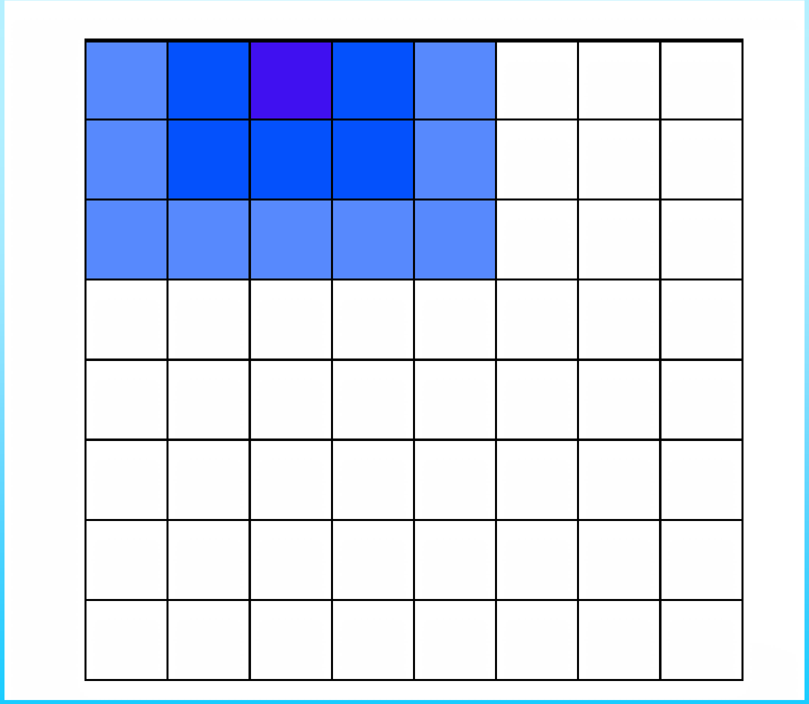
Simulations numériques



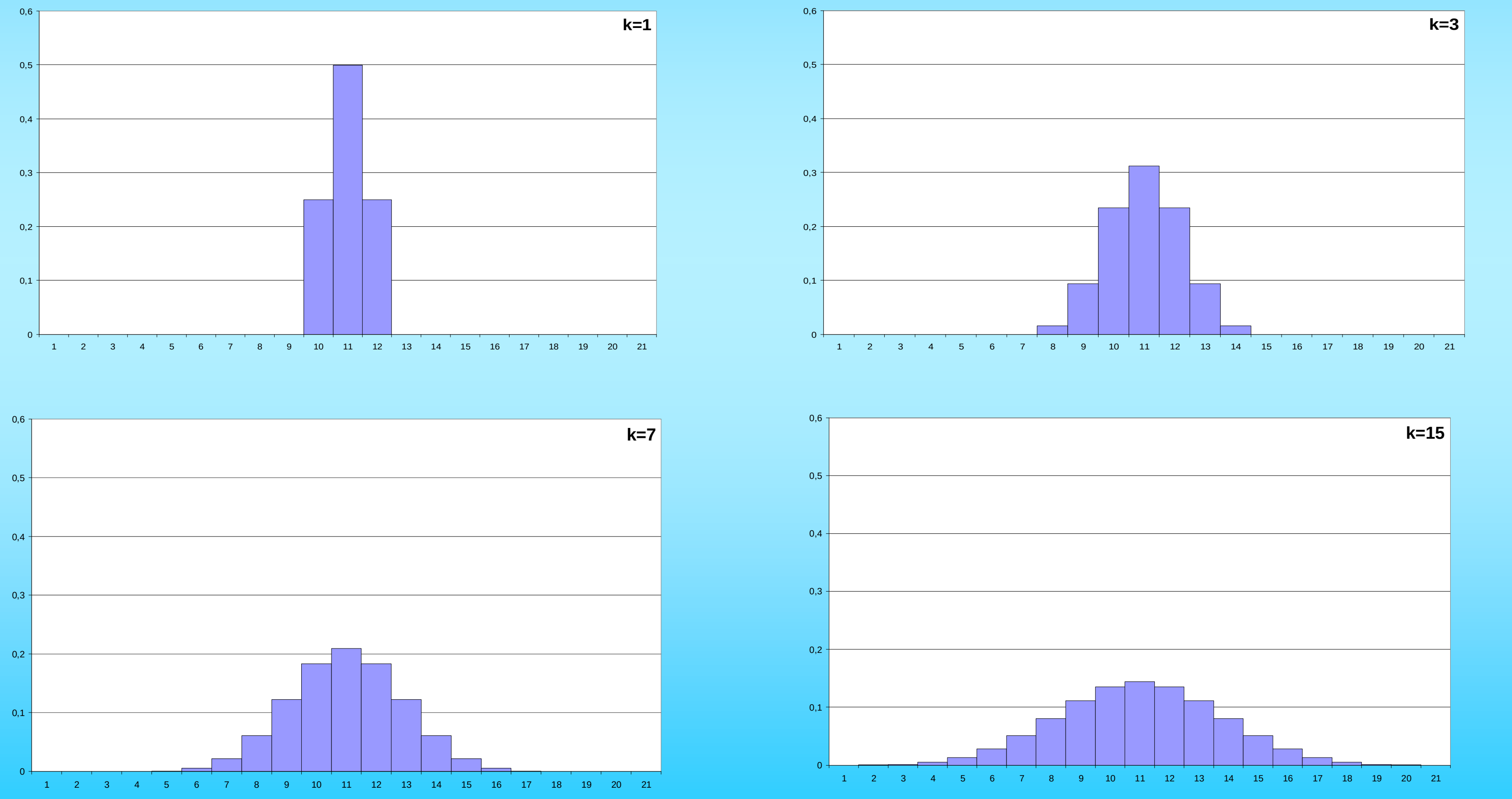
$a = 0.15,\ c = 1,\ \lambda = 2$

Modèle spatialisé

- Grille de dimension *A* x *A*:
  - Dynamique locale
  - Phase de déplacement: k événements de dispersion



Effet du paramètre k



μ = 0.5

Dynamique locale de Nicholson-Bailey

$$N_{t+1} = \lambda N_t \exp(-aP_t)$$
$$P_t = cN_t\left(1-\exp(-aP_t)\right)$$

Migration

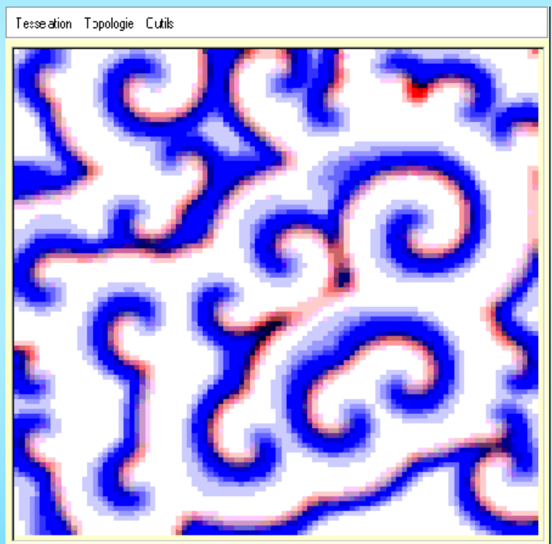
$$N_{t+1} = (1-\mu_H)N_t + \frac{\mu_H}{8}\sum_{\text{voisins}} N_t$$
$$P_{t+1} = (1-\mu_P)P_t + \frac{\mu_P}{8}\sum_{\text{voisins}} P_t$$

μ_H Mobilité des hôtes

μ_P Mobilité des parasites

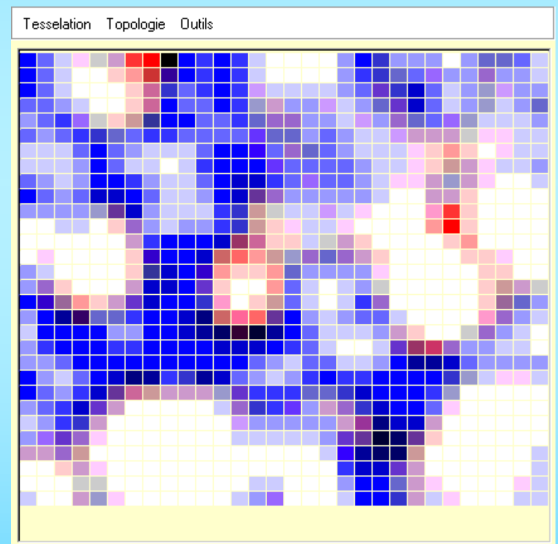
Dynamique spatiale

- Spirales



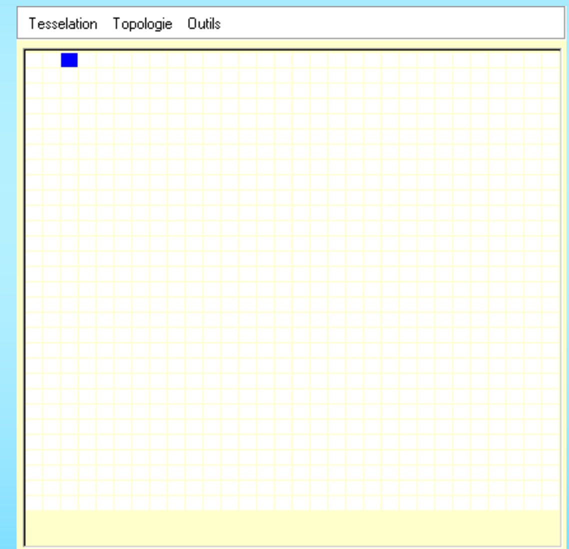
μ_H=1, μ_P=0.89, a=1, λ=2, c=1

- Chaos spatial



μ_H=0.2, μ_P=0.89, a=1, λ=2, c=1

- Structures cristallines



μ_H=0.05, μ_P=1, a=1, λ=2, c=1

k >> 1: agrégation spatiale

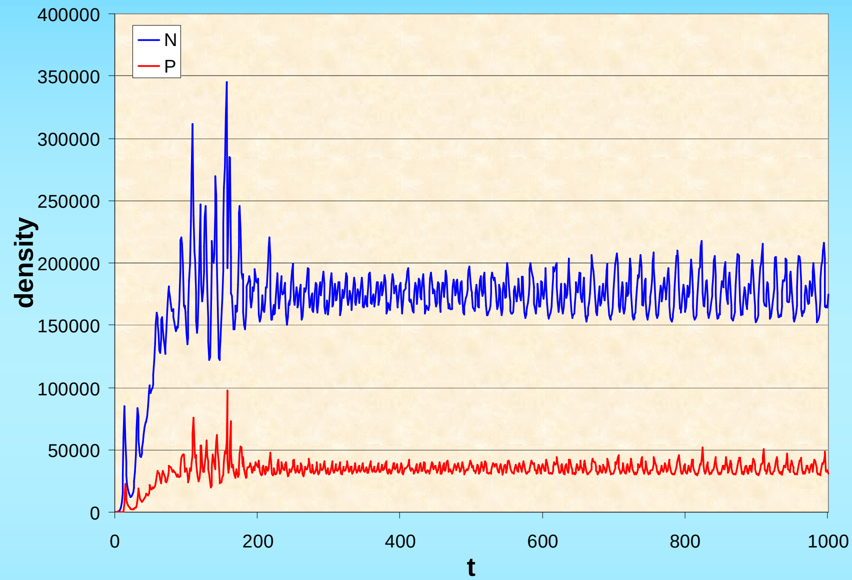
- Modèle agrégé: répartition spatiale uniforme à chaque génération:

$$\nu_i^* = \mu_i^* = \frac{1}{A^2}$$

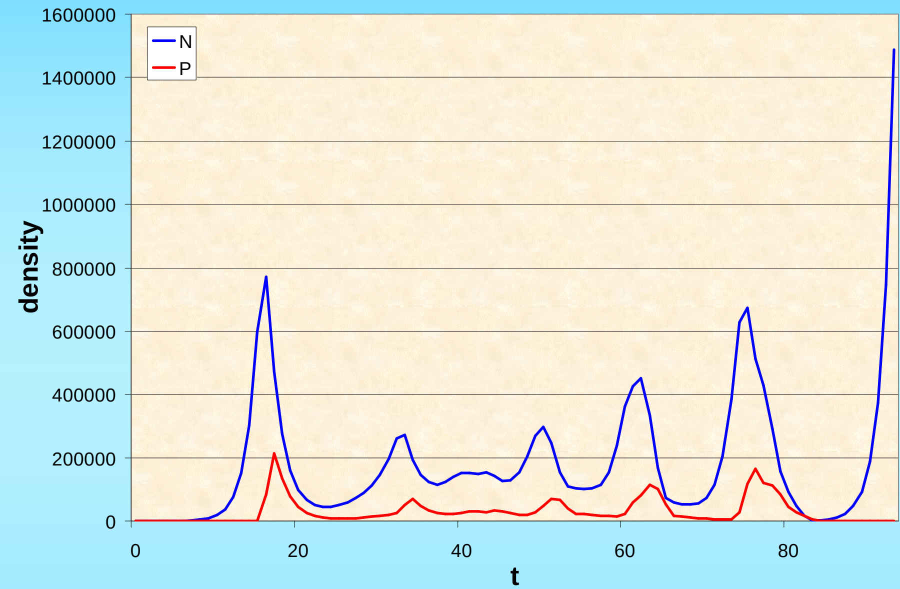
- Modèle obtenu: même forme, paramètres différents

$$\begin{cases} N_{t+1} = \lambda N_t e^{-a\frac{P_t}{A^2}} \\ P_{t+1} = cN_t(1 - e^{-a\frac{P_t}{A^2}}) \end{cases}$$

Simulations numériques



k=1, A=50



k=4, A=50

- ⌘ k faible : persistence
- ⌘ k fort : instabilité
- ⌘ Le modèle agrégé est valide pour de faibles valeurs de k

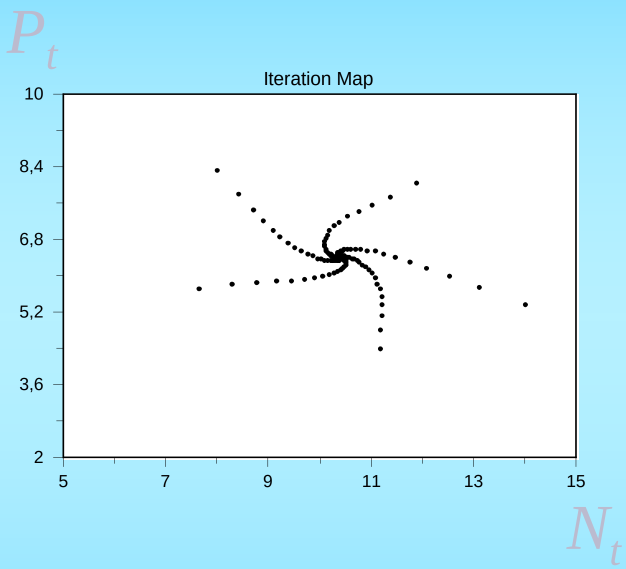
Modèle de Nicholson Bailey avec équation logistique

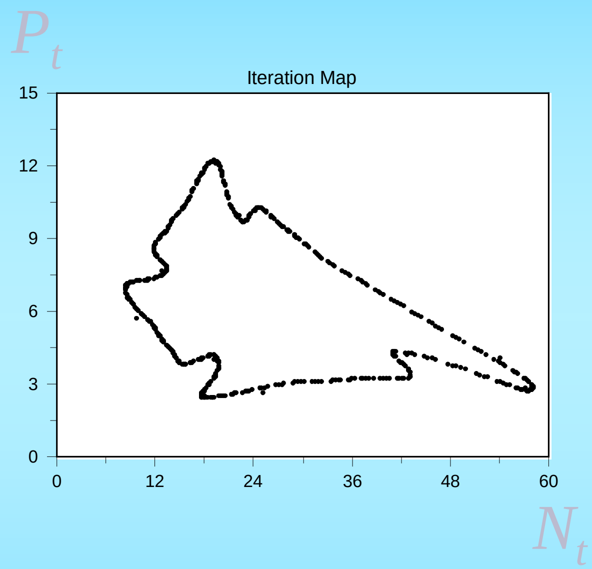
- Population d'hôtes à l'instant t : N_t
- Population de parasitoïdes à l'instant t : P_t

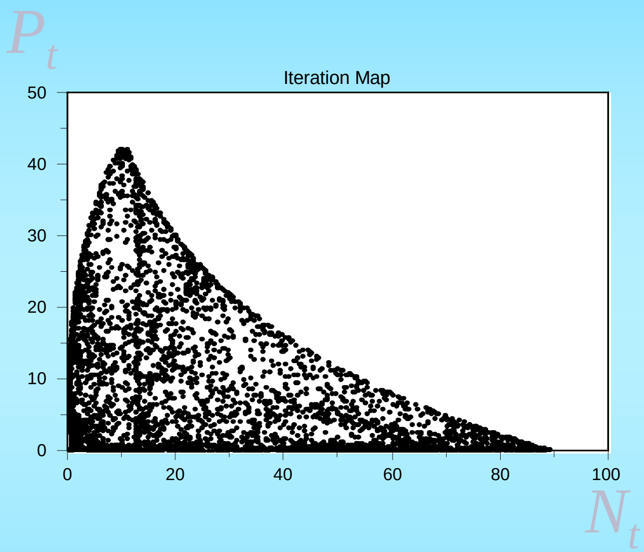
$$N_{t+1} = \exp\left(r\left(1 - N_t / K\right)\right)\exp\left(-aP_t\right)$$

$$P_{t+1} = cN_t\left(1 - \exp\left(-aP_t\right)\right)$$

Types de dynamique







Point d'équilibre stable

a=0.15, r=2, K=20, c=1

Courbe invariante

a=0.2, r=2.6, K=50, c=0.4

Attracteur chaotique

a=0.15, r=2.5, K=50, c=1

- Dynamique locale: modèle de Nicholson-Bailey avec croissance logistique des hôtes

$$N_{t+1} = N_t \exp\left(r\left(1 - \frac{N_t}{K}\right)\right) \exp(-aP_t)$$

$$P_{t+1} = cN_t\left(1 - \exp(-aP_t)\right)$$

- Migration (répétée k fois)

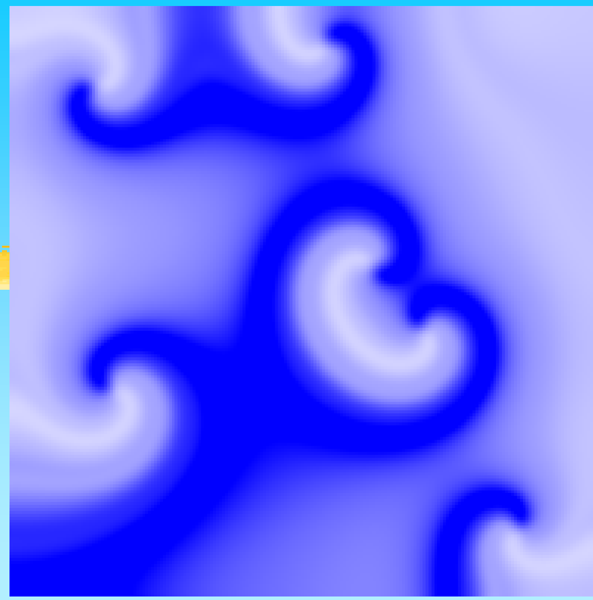
$$N_{t+1} = (1-\mu_H) N_t + \frac{\mu_H}{8} \sum_{\text{voisins}} N_t$$

$$P_{t+1} = (1-\mu_P) P_t + \frac{\mu_P}{8} \sum_{\text{voisins}} P_t$$

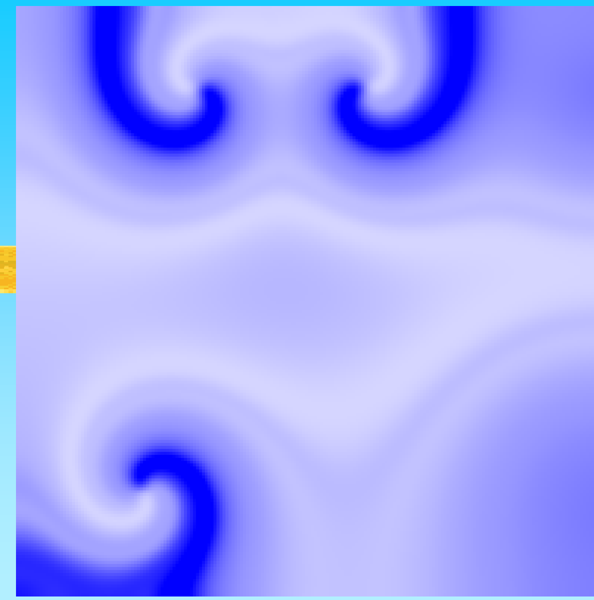
μ_H Mobilité des hôtes

μ_P Mobilité des parasitoïdes

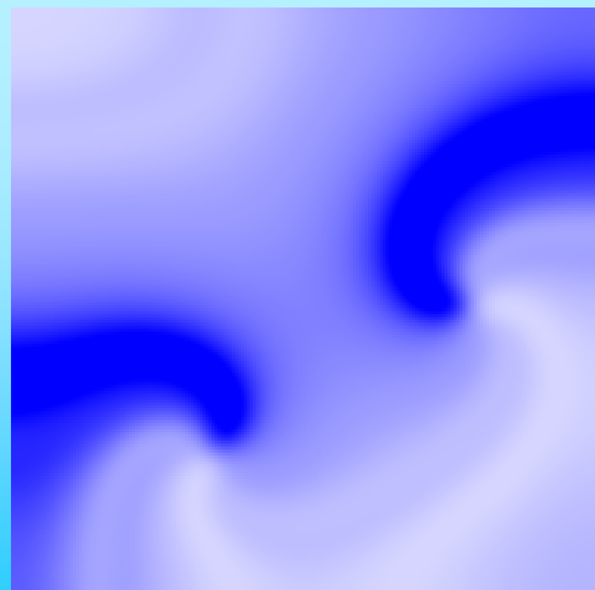
Modèle complet. La densité des hôtes est représentée en bleu.



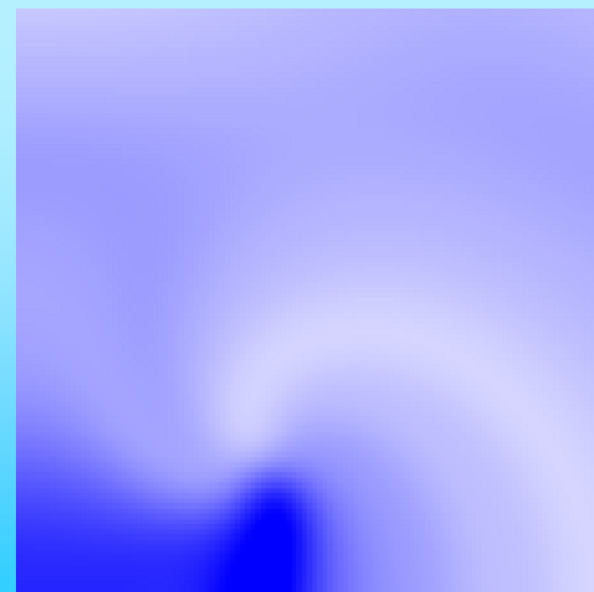
k=1



k=2



k=3



k=4

a = 0.2, r = 2.6, K = 50,

c = 0.4,

$\mu_n = \mu_p$ = 1 et A = 200.

$k >> 1$: agrégation spatiale

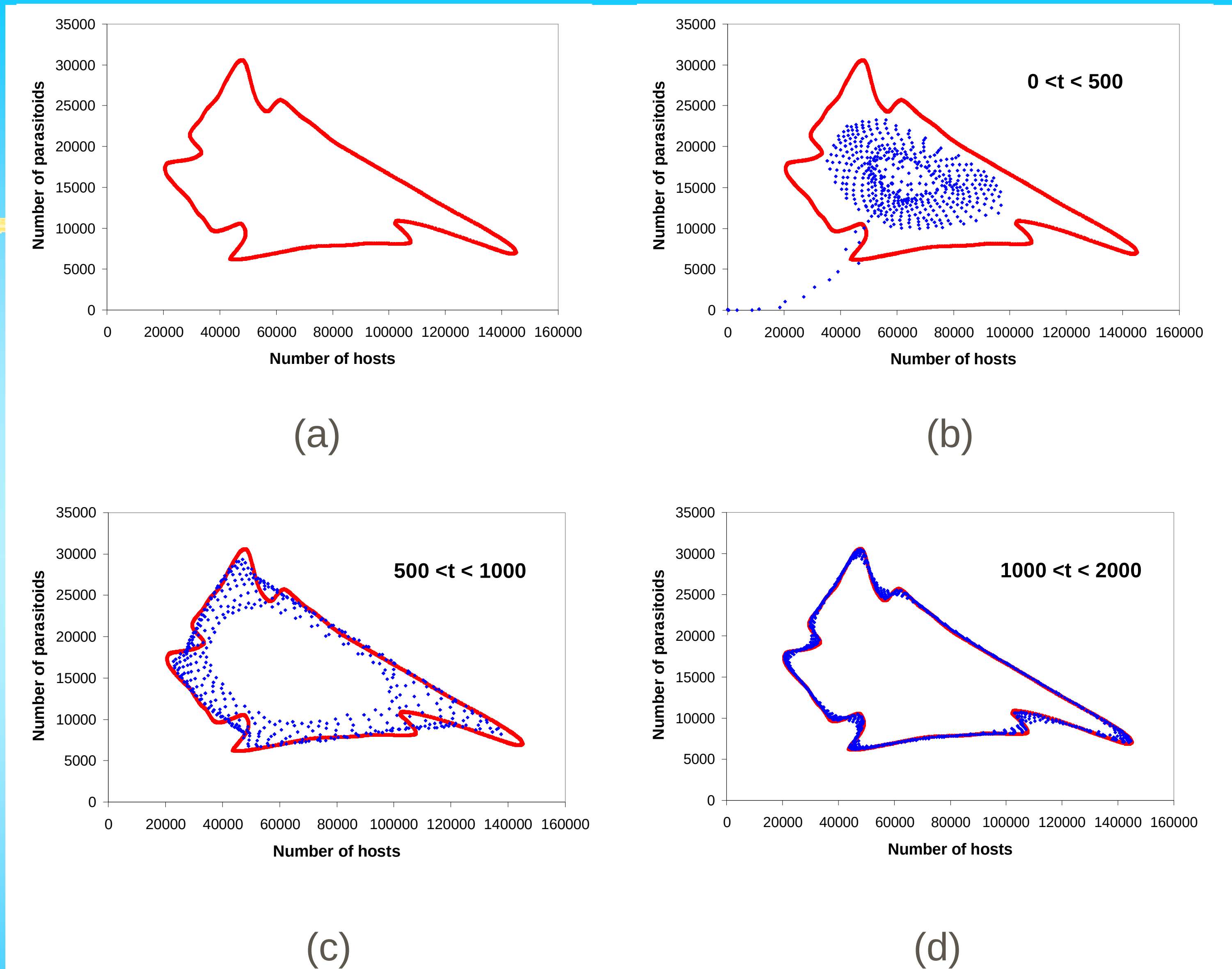
- Modèle agrégé: répartition spatiale uniforme à chaque génération:

$$\nu_i^* = \mu_i^* = \frac{1}{A^2}$$

- Modèle obtenu: même forme, paramètres différents

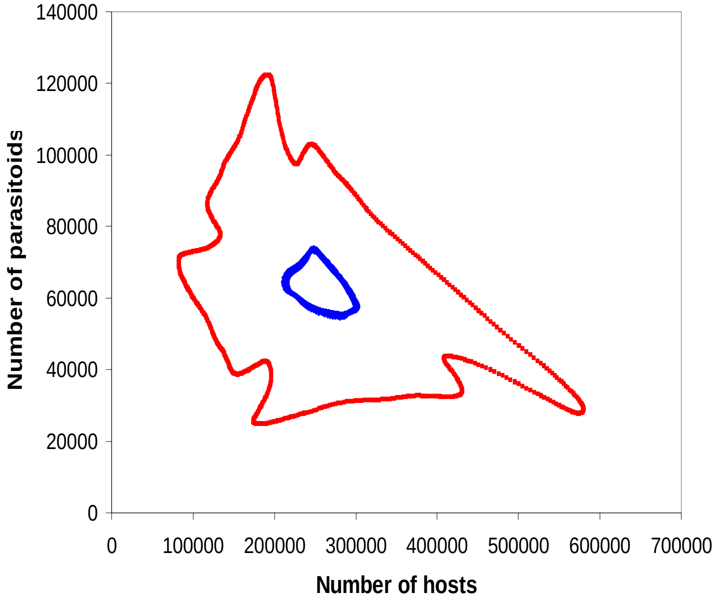
$$N_{t+1} = N_t \exp\left(r\left(1-\frac{N_t}{KA^2}\right)\right)\exp\left(-\frac{aP_t}{A^2}\right)$$

$$P_t = cN_t\left(1-\exp\left(-\frac{aP_t}{A^2}\right)\right)$$

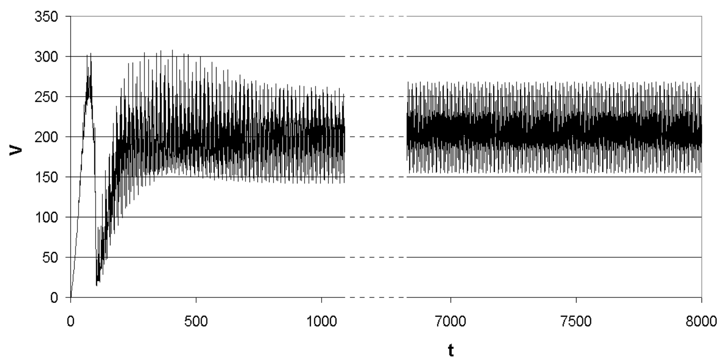


⌘ ***a=0.2, r=2.6, K=50, c=0.4, $\mu_n=\mu_p=1$ et A=50*. (b)-(c)-(d) Modèle agregé (a) en rouge, et le modèle complet pour *k*=1 en bleu pour 0<*t*<500 (b), 500<*t*<1000 (c) et 1000<*t*<2000 (d).**

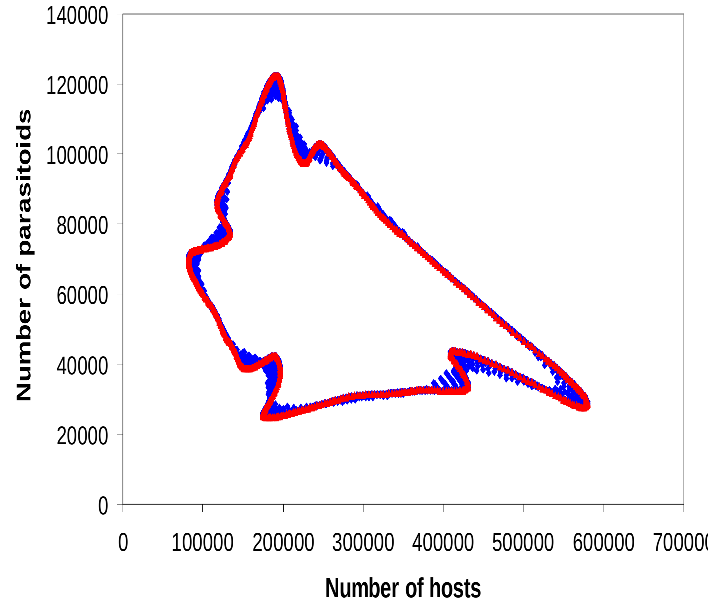
(a)



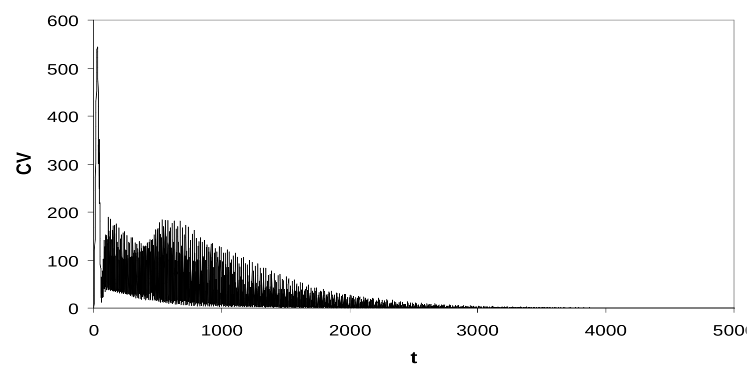
(b)



(c)



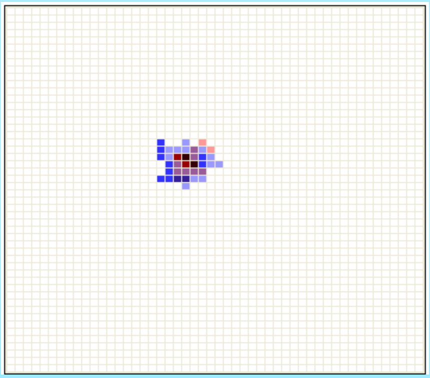
(d)



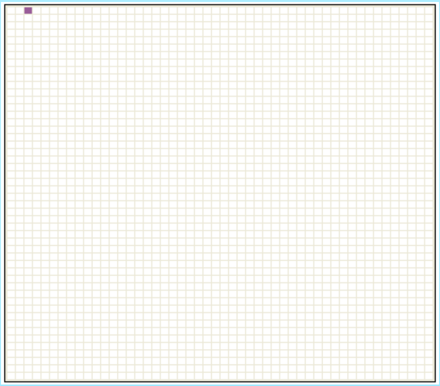
Modèle agrégé (rouge) avec *k*=1, *A*=100 (a) pour 1000<*t*<8000. Somme des variances des hôtes et des parasitoïdes *(b)*.

Modèle agrégé (rouge) avec *k*=3, *A*=100 (*c*) pour 1000<*t*<8000. Somme des variances des hôtes et des parasitoïdes *(d)*.

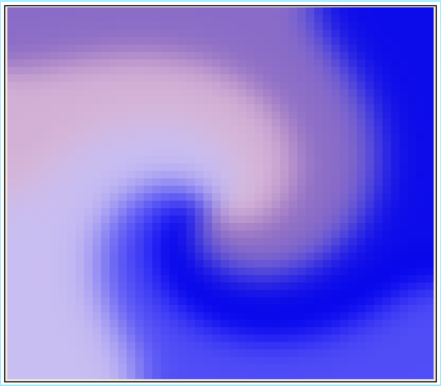
Sensibilité aux conditions initiales



(a)



(b)



(c)

⌘ Effet du paramètre *k* : A=100

k	1	2	4	7	8	9
CI(a)	-	+	+	+	+	+
CI(b)	-	+	+	+	+	+
CI(c)	-	-	-	-	+	+

a=0.2, r=2.6, K=50, c=0.4, A=100 and μ_n=μ_p=1, “+”(resp. “-”) : la distribution des hôtes et des parasitoïdes tend (resp. ne tend pas) vers l’uniformité spatiale

⌘ Valeur seuil de *k*

A	30	50	100	200
$\tilde{k}$	2	3	8	10

Résultats

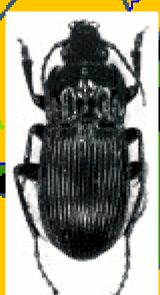
- Le modèle agrégé est utilisable pour de faibles valeurs de k

  $\rightarrow$ méthodes d'agrégation des variables utilisables sur des modèles appliqués

- Pas d'émergence

- Le synchronisme spatial peut être dû à la dispersion des individus (alternative à effet Moran)

Un modèle de dynamique d'une population de carabe forestier en milieu fragmenté

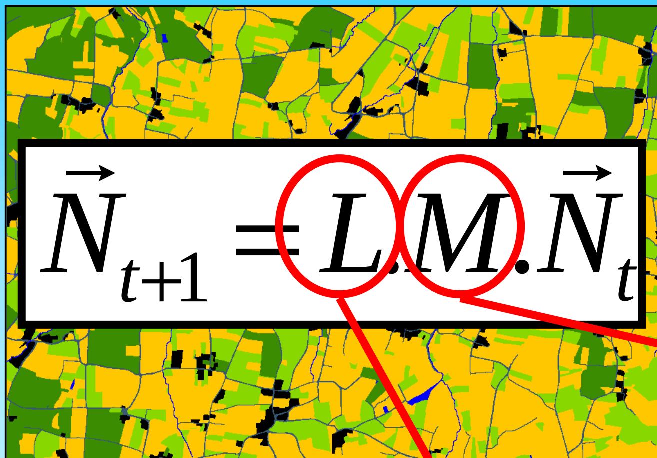


Pierre Auger*, Françoise Burel, Jean-Baptiste Pichancourt****
***IRD UR Geodes, Centre d'île de France**
****UMR CNRS Ecobio, Université de Rennes**

Les coléoptères carabiques: indicateurs du fonctionnement des paysages agricoles

- Ce sont des insectes dont la biologie et l'écologie sont relativement bien connues
- De nombreuses espèces prédatrices des ennemis des cultures et sont utilisées en lutte intégrée
- Certaines espèces, spécialistes des habitats semi-naturels (prairies, bois, lande, zone humide…), ont une valeur patrimoniale

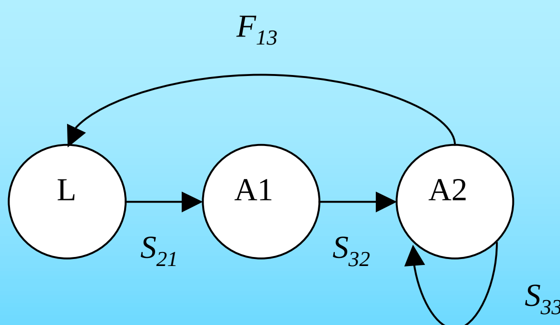
A.Modèle de Leslie spatialisé



$$\vec{N}_{t+1} = L.M.\vec{N}_t$$

- B — Bois, Forêt, bosquets
- CC — chemin creux bordé de haies
- H — Haies de bords de champs
- M — Matrice agricole : Maïs

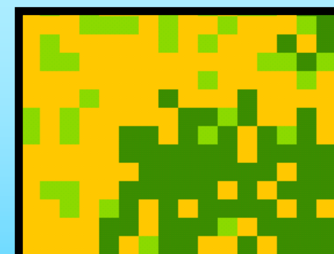
Matrice démographique de Leslie



Fécondité (f) : f(B) et f(CC)

Survie (s): s(B)=s(CC) > s(H) > s(M)

Matrice de diffusion (stepping stone)

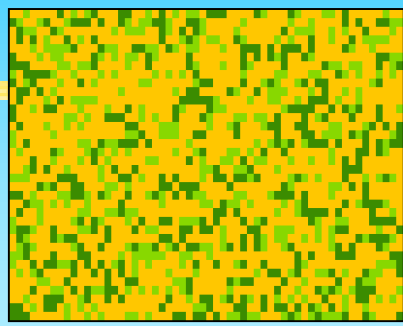


Fuit M $\rightarrow$ B, CC ou H

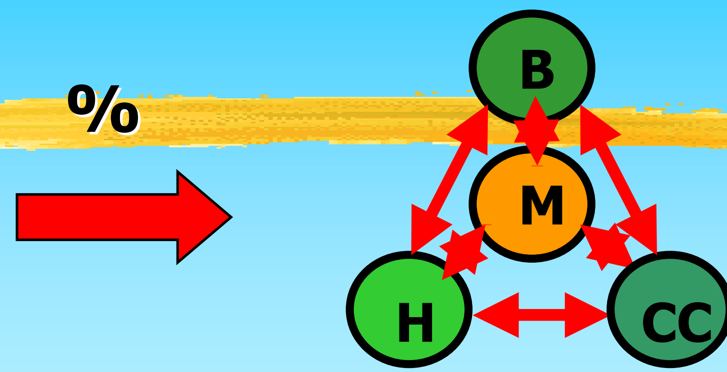
Quitte peu B

Ne distingue pas B et CC

B. Modèle de paysage & modèle de mouvement



paysage en grille



Paysage en diagramme

Simplification du modèle de mouvement

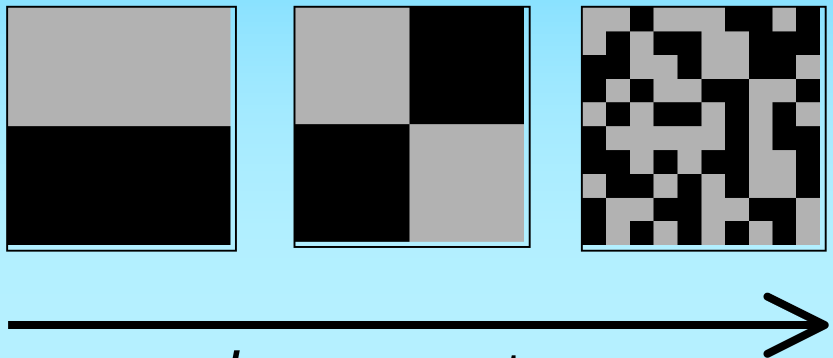
$$m_{ij} = p_j \,.\, q_{ij}$$

Martin (2001); Pichancourt et al. Ecological Modelling (2006)

transitions entre éléments (q_{ij})

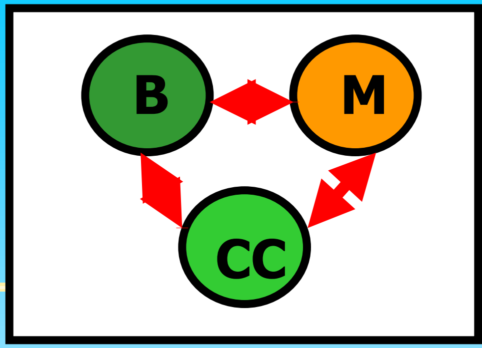
Eléments	B	CC	H	M
B	1	0.5	0.5	0.05
CC	0.5	1	0.5	0.1
H	0.5	0.5	1	0.2
M	1	1	0.2	1

<u>Fragmentation</u> = diminution de la quantité d'habitat favorable (exemple : bois) + évolution des grandes taches vers des taches plus petites et éloignées

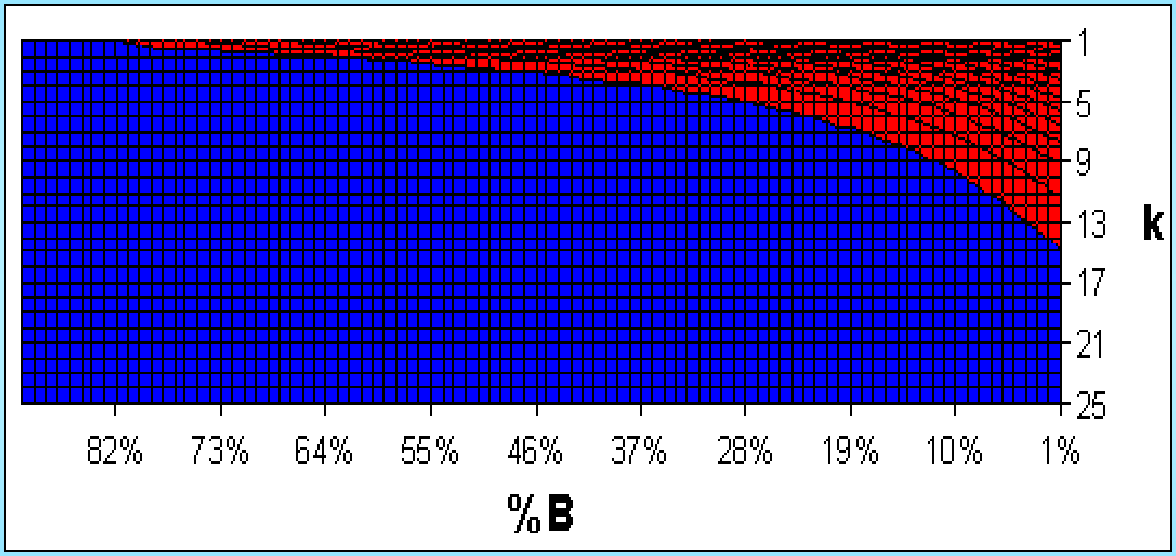


k augmente

$$\vec{N}_{t+1} = LM^{k}\vec{N}_t$$



Agrégation de variables (10% CC)

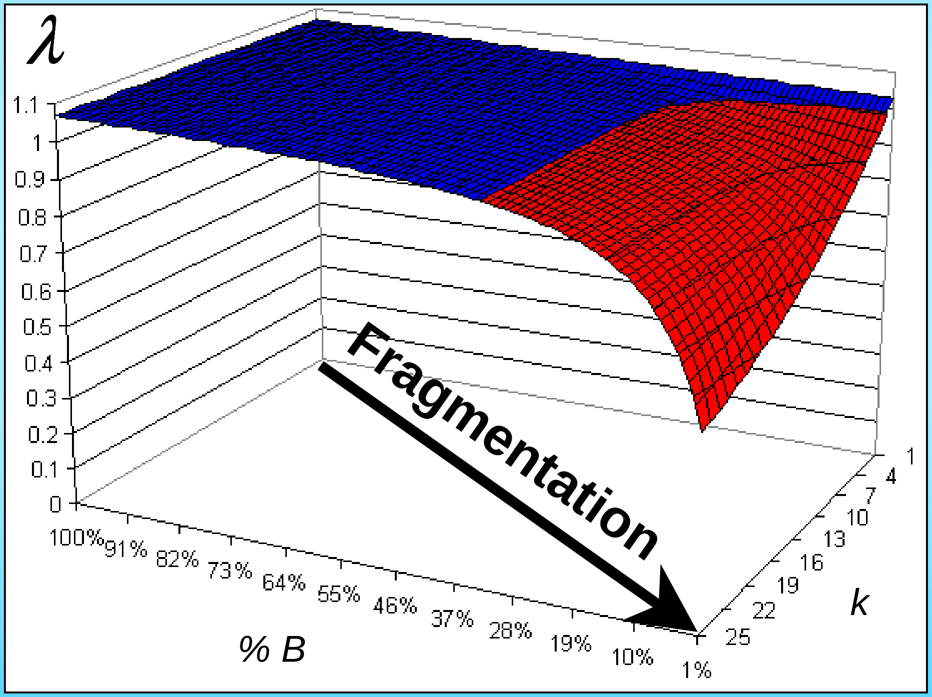


- (rouge) $\lambda_{agrégé} / \lambda_{complet} < 95\%$ $\Rightarrow$ On utilise le Modèle complet
- (bleu) $95\% < \lambda_{agrégé} / \lambda_{complet} < 100\%$ $\Rightarrow$ On utilise le Modèle agrégé

Effet des bois sur λ (seuil à 33%)

$\lambda < 1$

$\lambda > 1$



Perspectives and conclusion

- Incorporate individual behaviour in population and community models, like IBM : Auger et al. (1998, 2002, 2005), realistic games, Lett and Auger TPB, 2004.

- Several practical applications (Abax ater in Brittany landscape, fisheries in Morocco, epidemiology, …), 2D patch network…

Collaborations

- Eva Sanchez (ETSI, Madrid)
- Nadia Raïssi (SIANO, Kenitra Univ.)
- Rafael Bravo de la Parra (Alcala de Henares Univ.)
- Hassan Hbid (LMDP, Marrakech Univ.)
- Mohamed Khaladi (LMDP, Marrakech Univ.)
- Bob Kooi (Amsterdam Free Univ.)
- Christophe Lett (IRD, Lyon)
- Rachid Mchich (ENCG, Tanger)
- Jean-Christophe Poggiale (COM, Marseille)
- Luis Sanz (ETSI, Madrid)

Chemin creux

Fast hawk-dove game dynamics

Slow predator-prey dynamics

Contest for resource and aggressiveness

Dominique Allainé, Lyon 1

Hawk-dove game

- Payoff matrix

$$A = \begin{array}{cc} & \begin{array}{cc} H & D \end{array} \\ & \begin{pmatrix} \frac{G-C}{2} & G \\ 0 & \frac{G}{2} \end{pmatrix} \begin{array}{c} H \\ D \end{array} \end{array}$$

- Gain G

- Cost C

Replicator equations

$$\frac{dx}{dt} = x(1-x)\left((1,0)A\begin{pmatrix} x \\ 1-x \end{pmatrix} - (0,1)A\begin{pmatrix} x \\ 1-x \end{pmatrix}\right)$$

- G<C, mixed equilibrium $x^* = \frac{G}{C}$

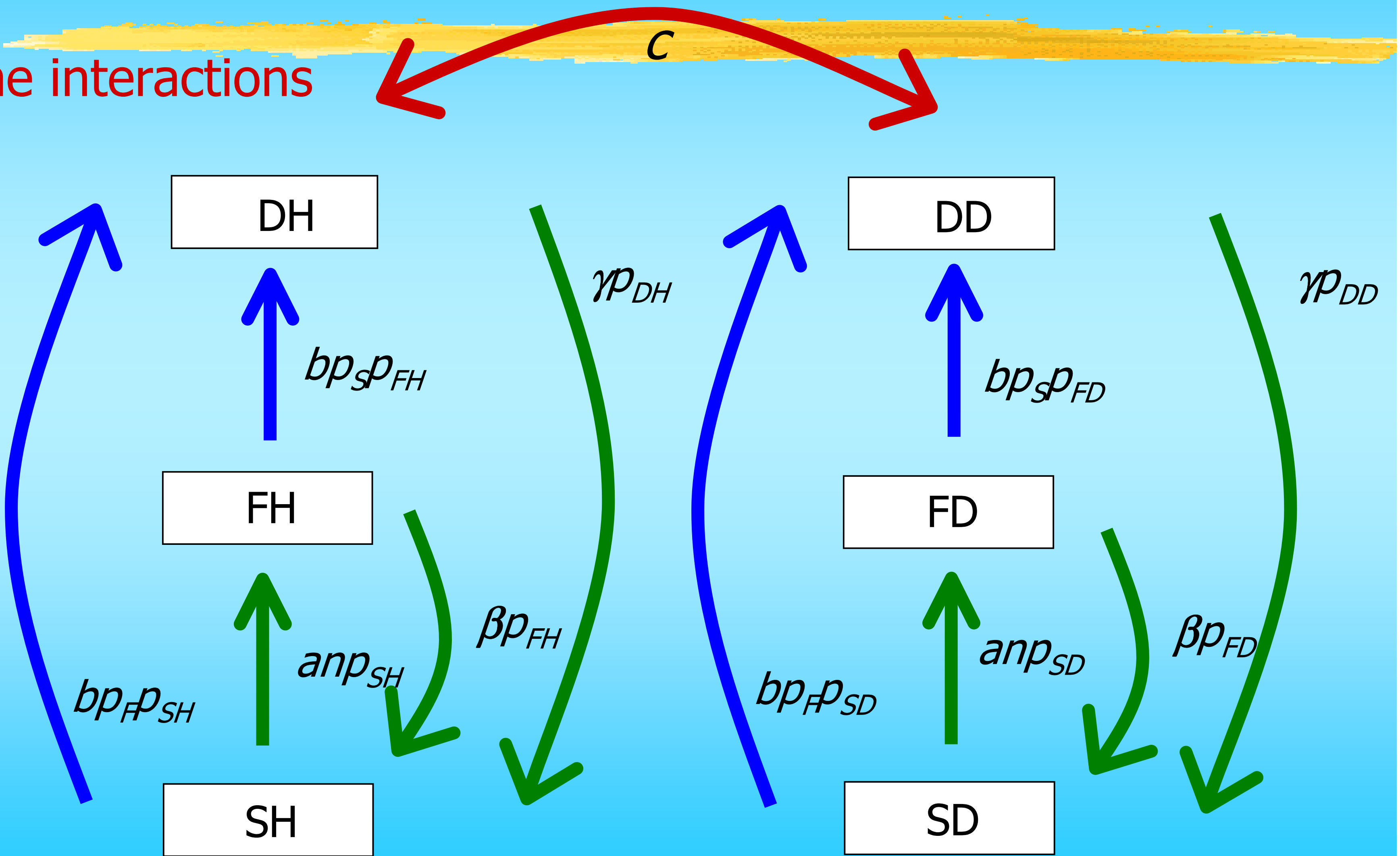
- G>C, pure hawk $x^* = 1$

Hofbauer, J., Sigmund, K., 1988. The Theory of Evolution and Dynamical Systems. Cambridge University Press, Cambridge.

Trophic interactions

Interactions between predators

Game interactions



AUGER P., KOOI B., BRAVO DE LA PARRA R. and POGGIALE J.-C. Journal of Theoretical Biology. 2006.

The complete model : 7 equations

$$\frac{dn}{d\tau} = \varepsilon\left(rn\left(1 - \frac{n}{K}\right) - anp \right)$$

$$\begin{cases}
\dfrac{dp_{SD}}{d\tau} = -bp_F\, p_{SD} - anp_{SD} + \beta p_{FD} + \gamma p_{DD} + \varepsilon\left(\alpha\left(\beta p_{FD} + (Au)_D\, p_{DD} - \mu p_{SD}\right)\right) \\
\dfrac{dp_{FD}}{d\tau} = -bp_S\, p_{FD} + anp_{SD} - \beta p_{FD} - \varepsilon\mu p_{FD} \\
\dfrac{dp_{DD}}{d\tau} = bp_F\, p_{SD} + bp_S\, p_{FD} - \gamma p_{DD} + cp_{DD}\left((Au)_D - u^T Au\right) - \varepsilon\mu p_{DD} \\
\dfrac{dp_{SH}}{d\tau} = -bp_F\, p_{SH} - anp_{SH} + \beta p_{FH} + \gamma p_{DH} + \varepsilon\left(\alpha\left(\beta p_{FH} + (Au)_H\, p_{DH} - \mu p_{SH}\right)\right) \\
\dfrac{dp_{FH}}{d\tau} = -bp_S\, p_{FH} + anp_{SH} - \beta p_{FH} - \varepsilon\mu p_{FH} \\
\dfrac{dp_{DH}}{d\tau} = bp_F\, p_{SH} + bp_S\, p_{FH} - \gamma p_{DH} + cp_{DH}\left((Au)_H - u^T Au\right) - \varepsilon\mu p_{DH}
\end{cases}$$

Fast model : adding H and D

$$\begin{cases} \dfrac{dp_S}{d\tau} = -bp_F\,p_S - anp_S + \beta p_F + \gamma p_D \\ \dfrac{dp_F}{d\tau} = -bp_S\,p_F + anp_S - \beta p_F \\ \dfrac{dp_D}{d\tau} = 2bp_F\,p_S - \gamma p_D \end{cases}$$

with $p = p_S + p_F + p_D$ **constant**

Fast equilibrium : S, F and D

$$
\begin{cases}
p_F^* = \dfrac{anp_S^*}{\beta + bp_S^*} \\[2ex]
p_S^* = \dfrac{\gamma(bp-\beta-an)+\sqrt{\gamma^2(bp-\beta-an)^2+8ab\gamma\beta np+4\gamma\beta^2 bp}}{2(2abn+b\gamma)}
\end{cases}
$$

The aggregated model

- Substituting the fast equilibrium into the complete model
- Reduction of the dimension from 7 to 2 variables

Two aggregated models

Dimorphic

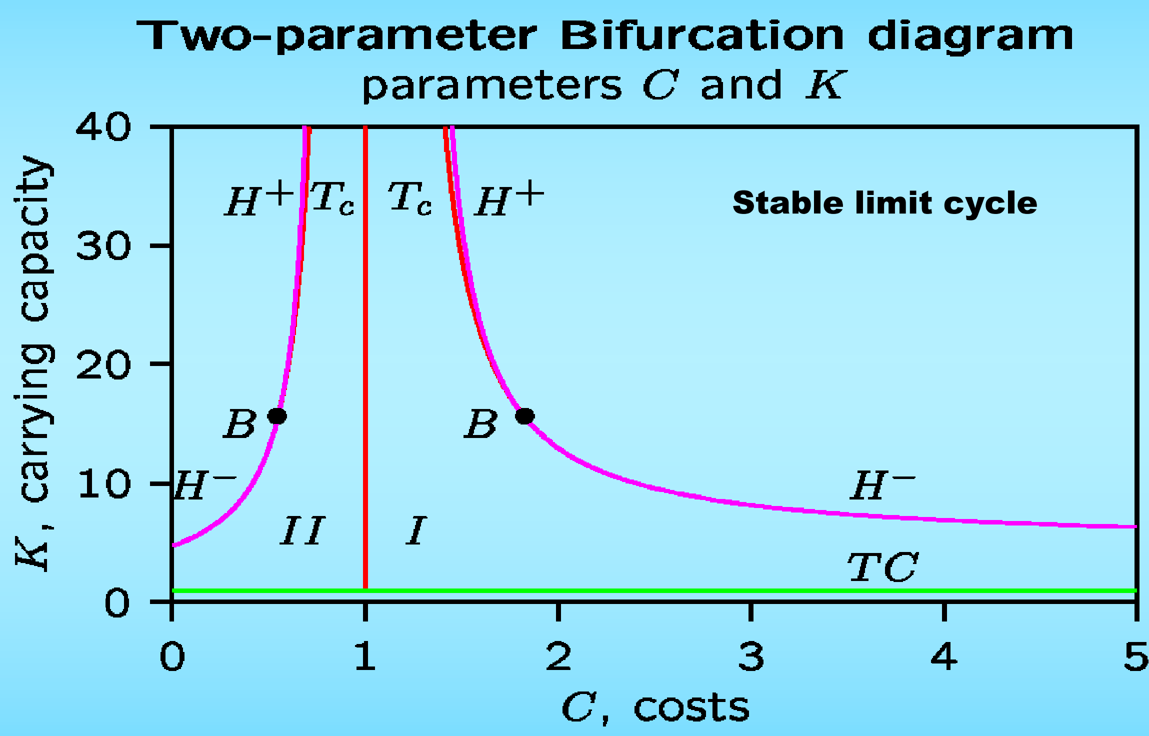
$$\begin{cases} \dfrac{dn}{dt} = rn\left(1-\dfrac{n}{K}\right) - anp_S^* + o(\varepsilon) \\ \dfrac{dp}{dt} = -\mu p + \alpha\left(\beta p_F^* + \dfrac{\gamma}{2}\left(1-\dfrac{\gamma}{C}\right)p_D^*\right) + o(\varepsilon) \end{cases}$$

Hawk

$$\begin{cases} \dfrac{dn}{dt} = rn\left(1-\dfrac{n}{K}\right) - anp_S^* + o(\varepsilon) \\ \dfrac{dp}{dt} = -\mu p + \alpha\left(\beta p_F^* + \dfrac{\gamma}{2}\left(1-\dfrac{C}{\gamma}\right)p_D^*\right) + o(\varepsilon) \end{cases}$$

Aggregated model

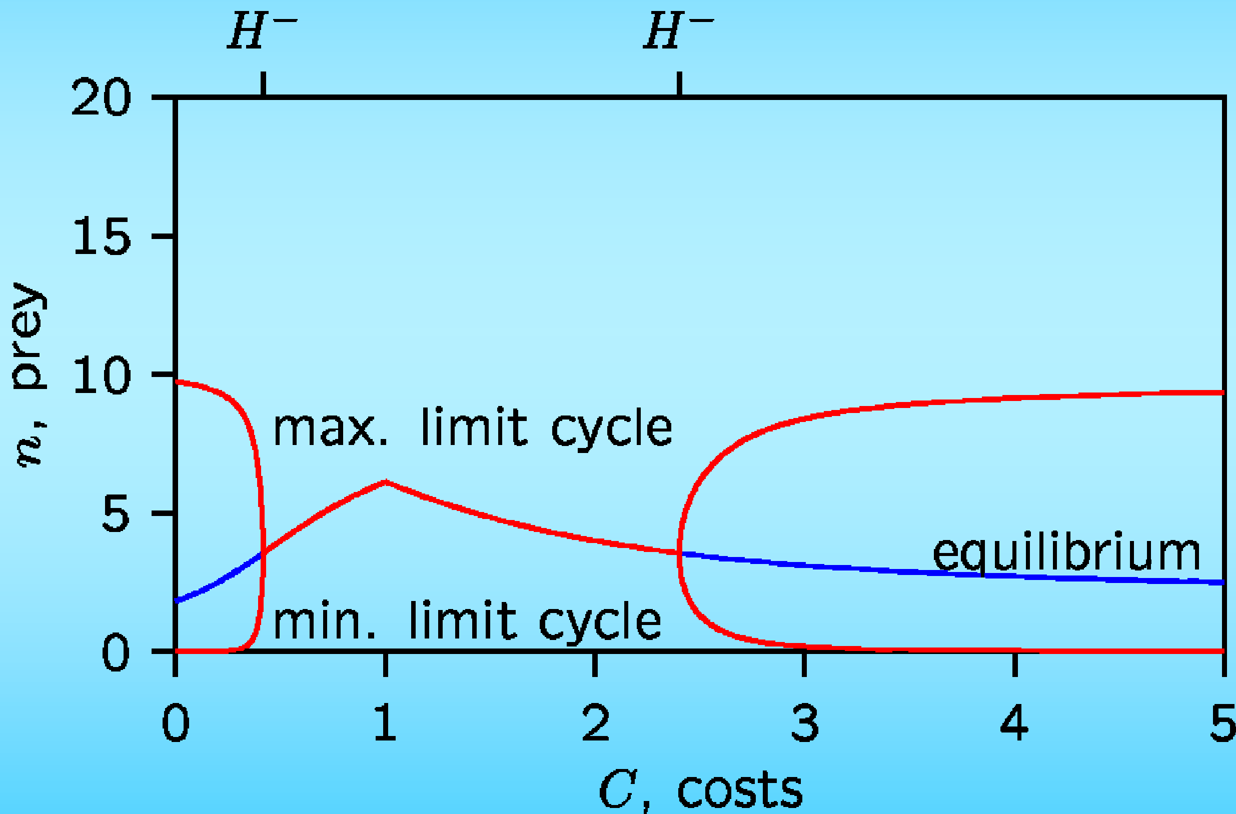
- When b=0 : Holling type II model
- General case : bifurcation analysis



H^+: Subcritical Hopf, H^-: Supercritical Hopf
TC : Transcritical
T_c : Tangent (saddle-node) for limit cycle
B : codim-two Bautin point
II : monomorphic case (only hawk predators)
I : dimorphic case (hawks and doves)

One-parameter Bifurcation diagram for Prey

$K = 10$: stable, unstable



H^-: Supercritical Hopf

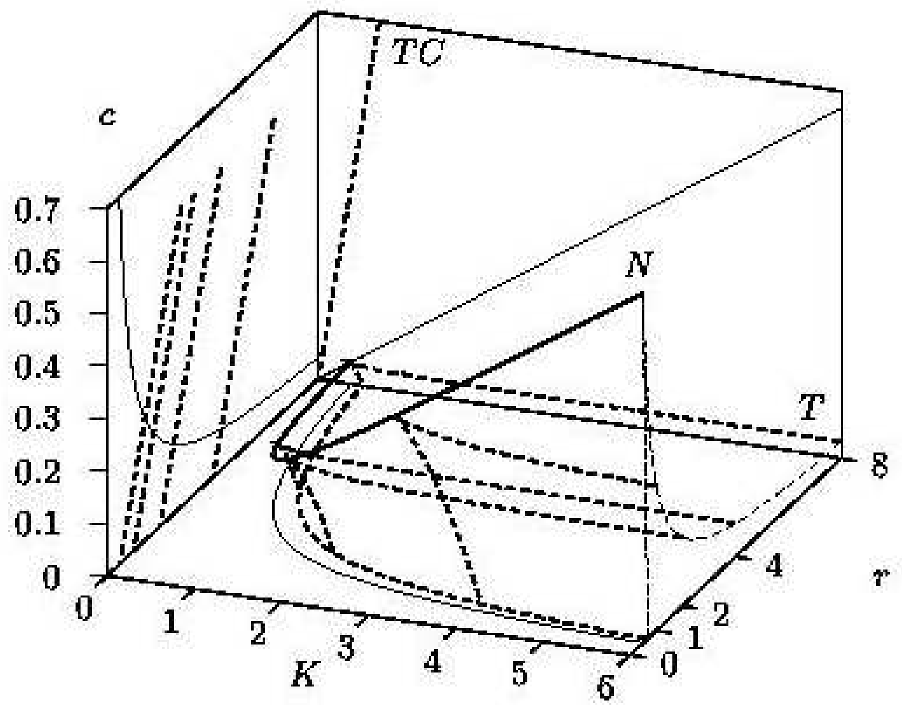


Figure 4: The three-dimensional bifurcation diagram for the aggregated system using K, r and c as bifurcation parameters. Fixed parameters: $A = 1$ and $q = 1$. N is a codim-2 cusp-bifurcation, TC the transcritical bifurcation where the fish population is at carrying capacity and the fish efforts is positive and T is a tangent (saddle-node) bifurcation where two positive equilibria collide. Of the cusp bifurcation N (thick solid curve) also the projections on the three planes are shown as thin solid curves.

Théorème de Fénichel (1971) :

On suppose que X est un champ de vecteurs C^r sur R^n avec r>1.

Soit $\overline{M} = M \cup \partial M$ une variété compacte C^r connexe et débordante pour X.. Supposons de plus que :

pour tout $p \in M$, $\nu(p) < 1$ et $\sigma(p) < 1/r$.

Alors pour tout champ C^r, Y, dans un C^1 voisinage de X assez petit, il y a une variété M' proche de M, débordante pour Y et C^r, difféomorphe à M.

$$\begin{cases} \dfrac{dx}{d\tau} = f(x; y; \varepsilon) \\ \dfrac{dy}{d\tau} = \varepsilon g(x; y; \varepsilon) \\ \dfrac{d\varepsilon}{d\tau} = 0 \end{cases}$$

$$x \in R^{k_1}; y \in R^{k_2}$$

$$S = \{(x; y); f(x; y; 0) = 0\}$$

HYP : S contient M_{0},variété compacte normalement hyperbolique

Théorème de Fénichel :

Si $\varepsilon > 0$ est assez petit, il existe M_ε dans un ε - voisinage de M_0 qui lui est difféomorphe et qui est localement invariante sous l'action du flot défini par le système différentiel.

Si f est C^k, alors M_ε est C^k.

Bifurcation diagram

- Cost window for stability
- Stability for models I and II
- Domain with two limit cycles

Prey-predator model with predator density dependent migration of prey

$$\frac{dn_1}{d\tau} = (\beta p_2 + \alpha_0)n_2 - (\alpha p_1 + \alpha_0)n_1 + \varepsilon(r_1 n_1 - a_1 n_1 p_1)$$

$$\frac{dn_2}{d\tau} = (\alpha p_1 + \alpha_0)n_1 - (\beta p_2 + \alpha_0)n_2 + \varepsilon(r_2 n_2 - a_2 n_2 p_2)$$

$$\frac{dp_1}{d\tau} = mp_2 - m' p_1 + \varepsilon(-\mu_1 n_1 + b_1 n_1 p_1)$$

$$\frac{dp_2}{d\tau} = m' p_1 - mp_2 + \varepsilon(-\mu_2 n_2 + b_2 n_2 p_2)$$

⌘ MCHICH R., AUGER P. and POGGIALE J-C. Effect of predator density dependent dispersal of prey on stability of a predator-prey system. Mathematical Biosciences. 206(2), pp. 343-356, 2007.

Prey-predator model with predator density dependent migration of prey

- The aggregated model :

$$\frac{dn}{dt} = \frac{1}{\delta p + 2\alpha_0}\left(rn + anp - \bar{b}np^2\right)$$

$$\frac{dp}{dt} = -Mp + \frac{1}{\delta p + 2\alpha_0}\left(bnp + cnp^2\right)$$

$$\delta = \alpha\nu_1 + \beta\nu_2$$

Prey-predator model with predator density dependent migration of prey

- Similar Patches : Coexistence $\alpha = \beta \quad \mu_1 \neq \mu_2$

- General case : $\alpha \neq \beta$

  - **Coexistence** $2\alpha_0 c < \delta b$
  - **Center** $2\alpha_0 c = \delta b$
  - **Non persistence** $2\alpha_0 c > \delta b$

Fast equilibrium : adding S, D and F

$$\begin{cases} \dfrac{dp_H}{d\tau} = cp_{DH}\left((Au)_H - u^T Au\right) \\ \dfrac{dp_D}{d\tau} = cp_{DD}\left((Au)_D - u^T Au\right) \end{cases}$$

Replicator equations

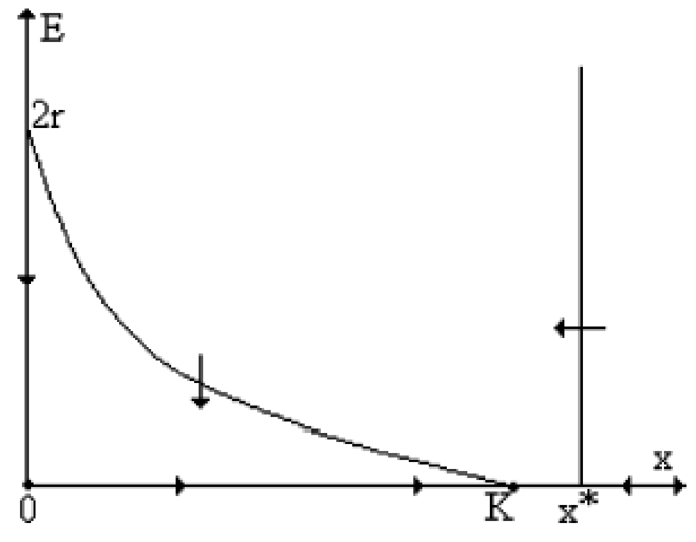


Fig. 1. Nullclines in the case $2\tau_2 > \tau_1$ and $x^* > K$. (x^*, E^*) does not belong to the positive quadrant and $(K, 0)$ is a stable node.

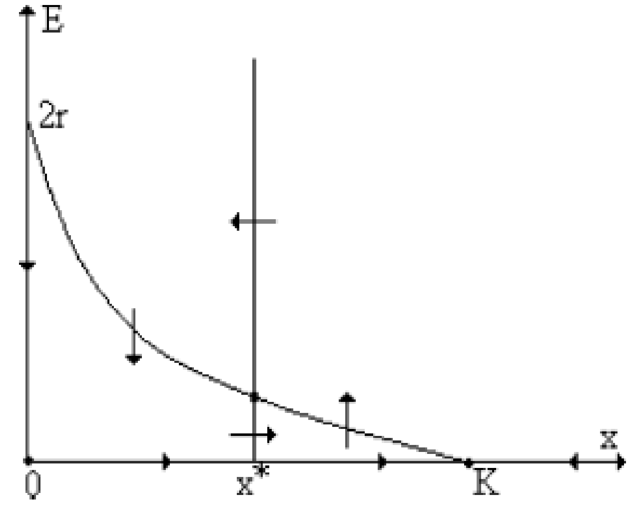


Fig. 2. Nullclines in the case $2\tau_2 > \tau_1$ and $x^* < K$. (x^*, E^*) belongs to the positive quadrant and is globally asymptotically stable while $(K, 0)$ is a saddle.

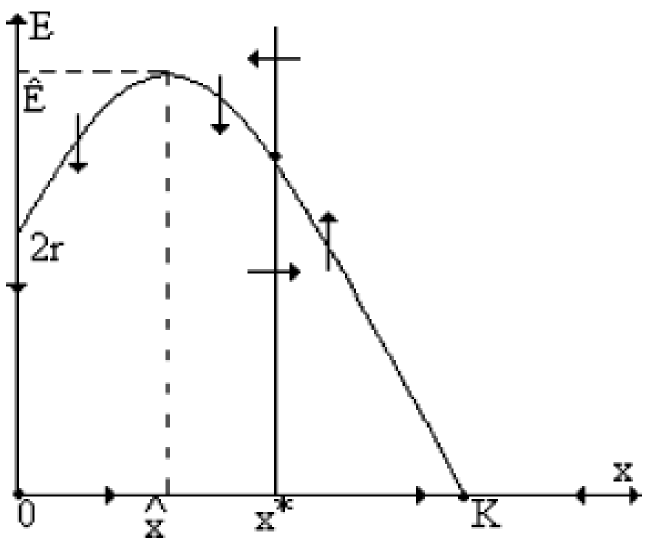


Fig. 4. Nullclines in ths case $2\tau_2 < \tau_1$ and $\hat{x} < x^* < K$. (x^*, E^*) belongs to the positive quadrant and is globally asymptotically stable while $(K, 0)$ is a stable node.

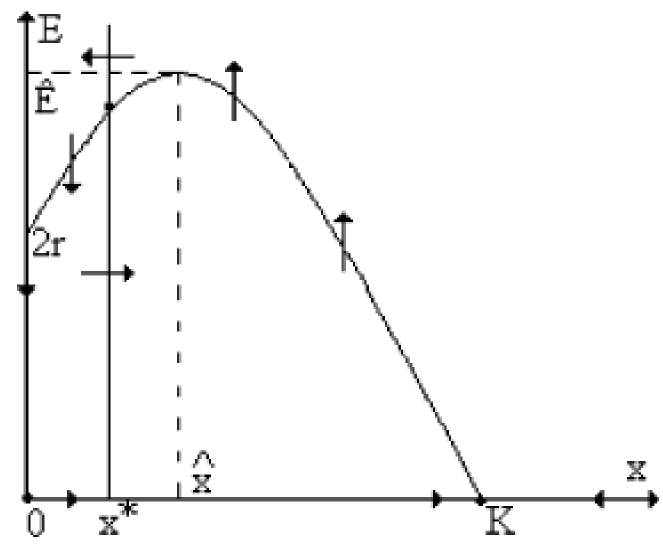


Fig. 5. Nullclines in the case $2\tau_2 < \tau_1$ and $x^* < \hat{x} < K$. (x^*, E^*) belongs to the positive quadrant and is unstable. $(K, 0)$ is a stable node.

Game dynamics and time scales

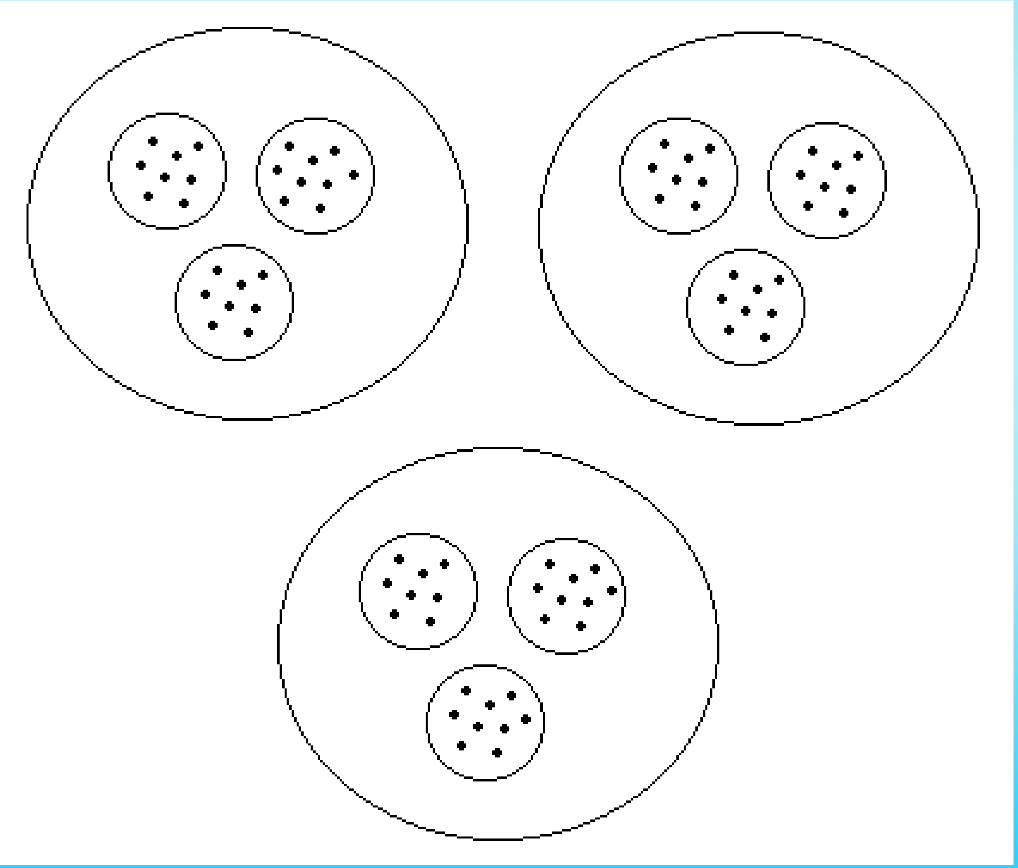
⌘ Game dynamics : evolutionary time scales

⌘ Behavioural plasticity : fast time scale

⌘ Domestic cats

P. AUGER & D. PONTIER. Mathematical Biosciences, 1998.
D. PONTIER, P. AUGER, R. BRAVO DE LA PARRA, E. SANCHEZ. Ecological Modelling, 2000.

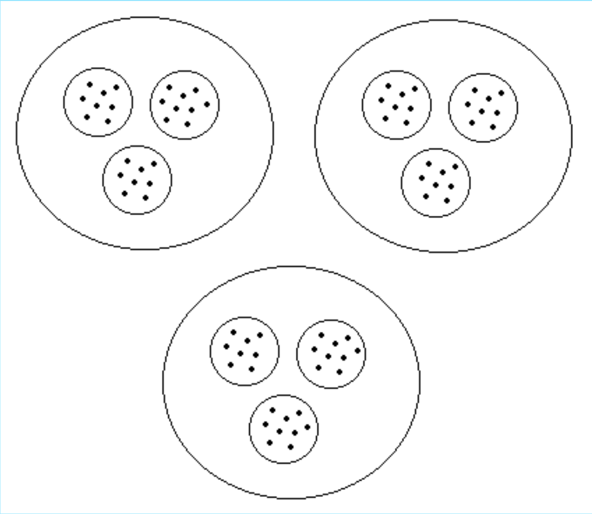
Hierarchical structure



Fast intra-group dynamics

Slow inter-group dynamics

Complete model



$$\varepsilon << 1$$

$$x_i^{\alpha}(\tau)$$

A groups and N sub-groups

$$\frac{dx_i^{\alpha}}{d\tau} = f_i^{\alpha}\left(x_1^{\alpha}, x_2^{\alpha}, \ldots, x_N^{\alpha}\right) \quad + \varepsilon \sum_{\beta \neq \alpha} f_i^{\alpha\beta}\left(x_1^{\alpha}, x_2^{\alpha}, \ldots, x_N^{\alpha}, x_1^{\beta}, x_2^{\beta}, \ldots, x_N^{\beta}\right)$$

Fast part

Slow part

Which global variables ?

A groups and N sub-groups

- Conservative fast dynamics $\varepsilon = 0$

$$\frac{dx_i^\alpha}{d\tau} = f_i^\alpha\left(x_1^\alpha, x_2^\alpha, \ldots, x_N^\alpha\right)$$

Y^α First integral

$$\tau = \frac{t}{\varepsilon}$$ Fast time

$$Y^\alpha = \sum_i x_i^\alpha$$

Aggregated variables

Building an « aggregated » model

- Fast stable equilibrium

$$\frac{dx_i^\alpha}{d\tau} = f_i^\alpha\left(x_1^\alpha, x_2^\alpha, \ldots, x_N^\alpha\right) = 0 \qquad\qquad x_i^{\alpha *}\left(Y^\alpha\right)$$

- Substitution of the fast equilibrium

$$\frac{dY^\alpha}{dt} = \sum_{\beta \neq \alpha} \sum_i f_i^{\alpha\beta}\left(x_1^{\alpha *}\left(Y^\alpha\right), \ldots, x_N^{\alpha *}\left(Y^\alpha\right), x_1^{\beta *}\left(Y^\beta\right), \ldots, x_N^{\beta *}\left(Y^\beta\right)\right)$$

The dynamics of the aggregated model is an approximation of the dynamics of the complete model

Two models

Complete model

$$\frac{dx_i^\alpha}{d\tau} = f_i^\alpha\left(x_1^\alpha, x_2^\alpha, \dots, x_N^\alpha\right) \quad + \varepsilon \sum_{\beta\neq\alpha} f_i^{\alpha\beta}\left(x_1^\alpha, x_2^\alpha, \dots, x_N^\alpha, x_1^\beta, x_2^\beta, \dots, x_N^\beta\right)$$

Aggregated model

$$\frac{dY^\alpha}{dt} = \sum_{\beta\neq\alpha}\sum_i f_i^{\alpha\beta}\left(x_1^{\alpha*}\left(Y^\alpha\right), \dots, x_N^{\alpha*}\left(Y^\alpha\right), \dots, x_1^{\beta*}\left(Y^\beta\right), \dots, x_N^{\beta*}\left(Y^\beta\right)\right) \ + O(\varepsilon)$$

• Effet du prix variable : contexte pêcherie

$$\begin{cases} \dfrac{dn}{d\tau} = \varepsilon[rn(1-\dfrac{n}{K}) - qnE] \\ \\ \dfrac{dE}{d\tau} = \varepsilon E(pqn - c) \\ \\ \dfrac{dp}{d\tau} = \alpha[D(p) - qnE] \end{cases}$$

$$D(p) = A - p(t)$$

α : paramètre positif décrivant la rapidité de l'ajustement du prix sur le marché

A : capacité limite du marché >0

<u>Equilibre rapide:</u> $$p^* = A - qnE$$

R. Mchich, P. Auger, N. Raïssi & B. Koii, 2008. « Stability of a fishery bio-economic model with price equation». Theoretical Population Biology. Submitted.

- # Modèle agrégé

$$\begin{cases} \dfrac{dn}{dt} = n(r(1-\dfrac{n}{K}) - qE) \\ \\ \dfrac{dE}{dt} = E(-c + qn(A - qnE)) \end{cases}$$

<u>Points d'équilibre:</u>

- (0,0): E_0 point selle
- (K,0): E_K stable si **K<(c/Aq)** ou point selle sinon
- $E_1(n^*,E^*)$, $E_2(n^*,E^*)$ et $E_3(n^*,E^*)$ si **r>(3A/K)**

- **Changement de variables**

$$\nu = \sqrt{q}n \,, \quad \epsilon = \frac{\sqrt{q}}{A}E \,, \quad \tau = \sqrt{q}At$$

$$\rho = \frac{r}{A\sqrt{q}} \,, \quad \gamma = \frac{c}{A\sqrt{q}} \,, \quad \kappa = \sqrt{q}K$$

$$\begin{cases} \dfrac{d\nu}{d\tau} = \nu(\rho(1 - \dfrac{\nu}{\kappa}) - \epsilon) \\ \\ \dfrac{d\epsilon}{d\tau} = \epsilon(-\gamma + \nu(1 - \nu\epsilon)) \end{cases}$$

LOCBIF & DsTool

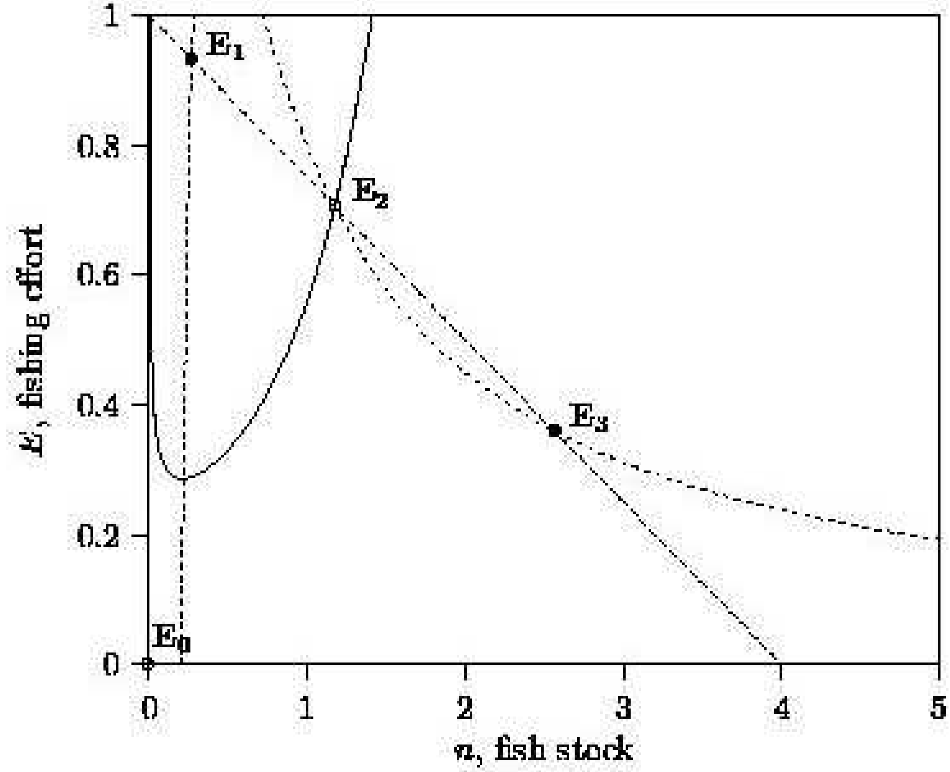


Figure 3: Phase-plane plot for $r = 1$, $c = 0.2$ and $K = 4$. The solid line is the separatrix between the two stable equilibria $\mathbf{E}_1$ and $\mathbf{E}_3$. It is the stable manifold of the saddle $\mathbf{E}_2$. The dashed straight line is the isocline for the Eqn. (3.2_1) and the short dashed curve that of Eqn. (3.2_2).

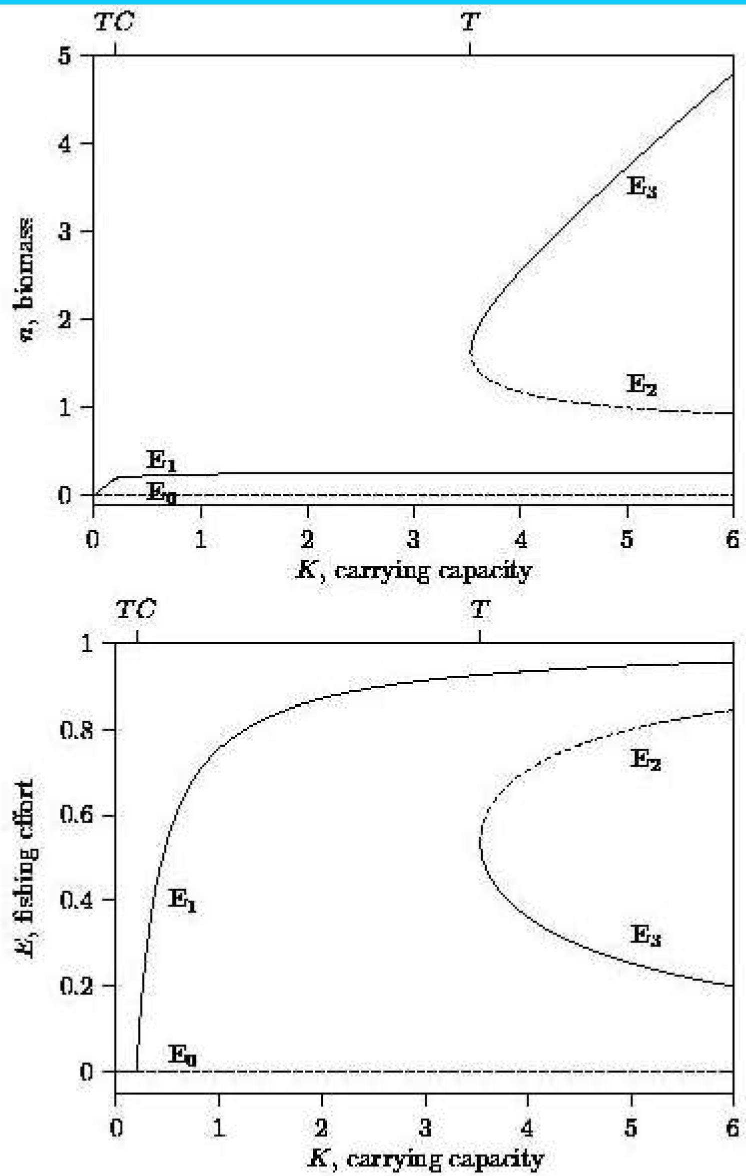


Figure 2: One-parameter diagram of the fish biomasses and fishing efforts, n and E respectively, with carrying capacity K as bifurcation parameter where $r = 1$ and $c = 0.2$. Of the cusp bifurcation N (thick solid curve) also the projections on the three planes are shown as thin solid curves.

Comparaison des prix des deux équilibres

$$r > \frac{3A}{K}$$

$$\begin{cases} E_1^* = \dfrac{1}{qn_1^*}(A - \dfrac{c}{qn_1^*}) \\ \\ E_3^* = \dfrac{1}{qn_3^*}(A - \dfrac{c}{qn_3^*}) \end{cases}$$

$$\begin{cases} p_1^* = A - qn_1^* E_1^* \\ \\ p_3^* = A - qn_3^* E_3^* \end{cases}$$

$$p_1^* - p_3^* = \frac{c}{q} \frac{(n_3^* \text{-} n_1^*)}{n_1^* n_3^*}$$

$$\Rightarrow \begin{cases} n_3^* > n_1^* \\ E_3^* < E_1^* \\ p_3^* < p_1^* \end{cases} \Rightarrow$$

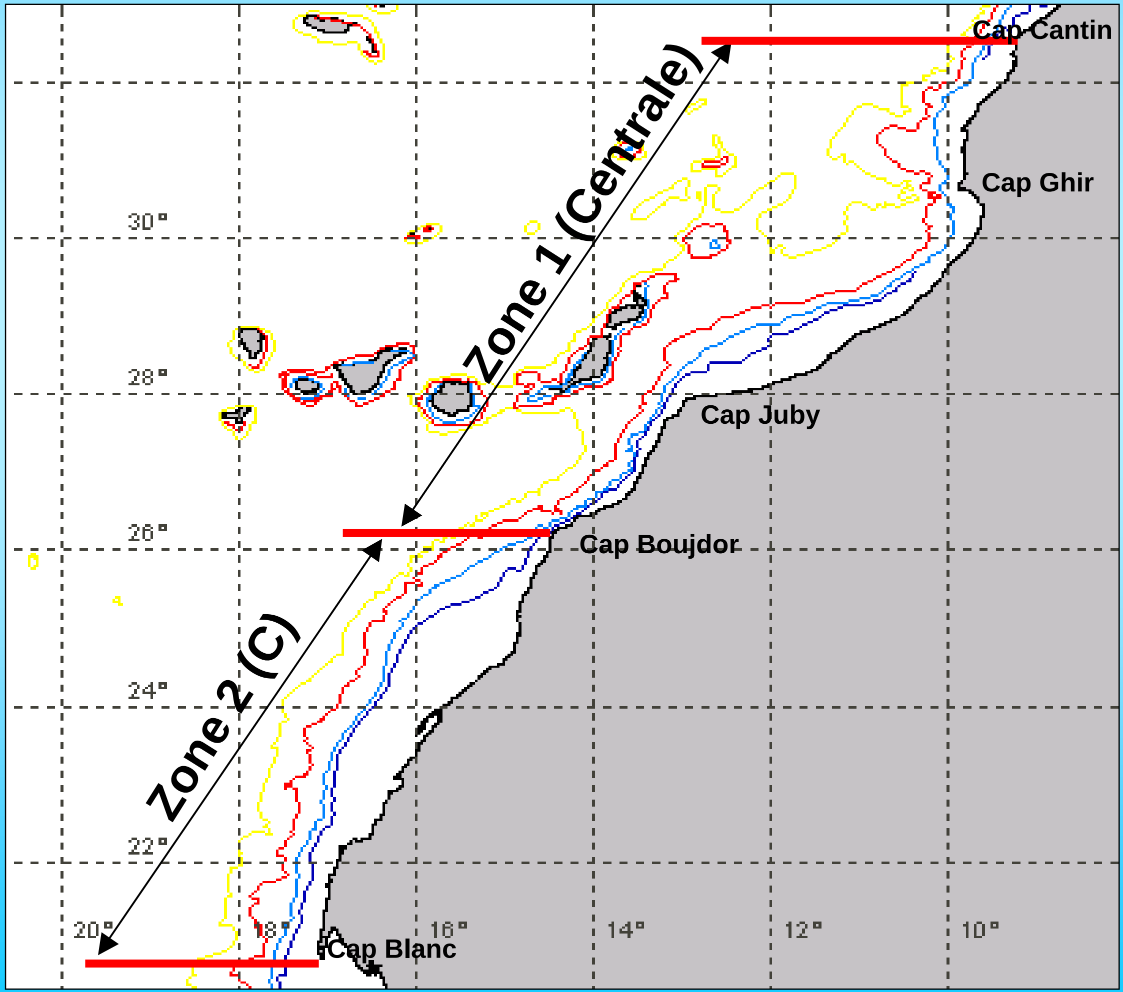
<u>Surexploitation:</u> (n1,E1)

<u>Pêcherie durable:</u> (n3,E3)

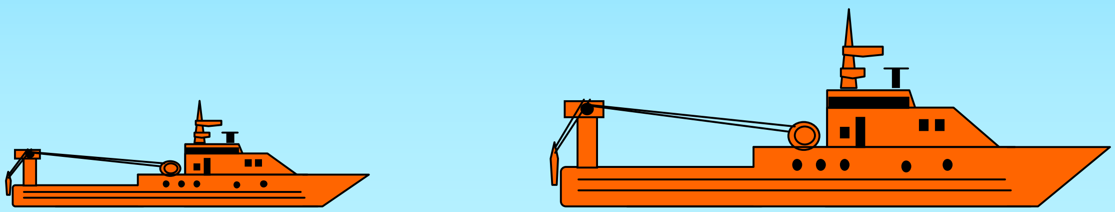
Two fisheries

- **An over exploited fishery** : The fishery allows a large fishing effort at a satisfying market price but the fish density is maintained at a low level with extinction risk.
- **A « traditional » fishery** : The fishery maintains the fish stock at a desirable level far from extinction but with small fishing effort and market price.

Zones des pêcheries de la sardine en atlantique marocain



Deux flottes de pêche



	Classe 1 (E)	Classe 2 (e)
T.J.B	[25-70]	[70-120]
Puissance Moyenne (CV)	284	396

Un modèle avec deux flottes sur deux zones

$$\frac{dn_1}{d\tau} = \varepsilon\left(r_1 n_1\left(1-\frac{n_1}{K_1}\right) - a_1 n_1 e_1 - a_1 n_1 E_1\right)$$

$$\frac{dn_2}{d\tau} = \varepsilon\left(r_2 n_2\left(1-\frac{n_2}{K_2}\right) - a_2 n_2 e_2 - a_2 n_2 E_2\right)$$

$$\frac{dE_1}{d\tau} = \varepsilon\left(-c_1 E_1 + p a_1 n_1 E_1\right)$$

$$\frac{dE_2}{d\tau} = \varepsilon\left(-c_2 E_2 + p a_2 n_2 E_2\right)$$

$$\frac{de_1}{d\tau} = \left(m e_2 - \tilde{m} e_1\right) + \varepsilon\left(-c_1 e_1 + p a_1 n_1 e_1\right)$$

$$\frac{de_2}{d\tau} = \left(\tilde{m} e_1 - m e_2\right) + \varepsilon\left(-c_2 e_2 + p a_2 n_2 e_2\right)$$

- E1, E2 : efforts de pêche des petits vaisseaux
- n_1, n_2 : densité de poissons sur les deux zones
- e_1, e_2 : efforts de pêche des petits vaisseaux

Paramètres à estimer :

Paramètres relatifs à la dynamique et l'exploitation du stock :

	Zone (Centrale)	**Zone C**
Taux de croissance **r**	1.53	1.14
Capacité de charge **K**	1703	5723
Coefficient de capturabilité **q**	0.025	0.0035

Informations utilisées pour l'estimation :

- Séries de biomasses de la sardines de 1995 à 2005
  (Rapports de campagnes acoustiques Dr Fridtjof Nansen)

- Séries de captures de la sardine dans les ports de 1995 à 2005
  (Statistiques de l'Office National de Pêche)

- Séries des efforts de pêche de 1995 à 2005
  (Données de la FAO)

Paramètres relatifs à l’exploitation et à la commercialisation de la sardine:

Destinations de la sardine pêchée:

Destination	Proportion annuelle
Sous produits	47%
Consommation locale	22%
Conserve+Congélation	29%
Appâts	2%

Prix par unité de poisson (Kg) et coût par unité d’effort (Jours de pêche) :

	Classe 1	Classe 2
Prix moyen (Dh/Kg)	1.08	
Coût par unité d’effort	7237	11014

*Source: D’après **A. Kamili** (2006); Mémoire de master intilulé: BIO-ECONOMIE ET GESTION DE LA PECHERIE DES PETITS PELAGIQUES: Cas de l’Atlantique Centre Marocain*