Mathematical formulation of ecological processes : a problem of scale
Mathematical approach and ecological consequences

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Outline

Introduction

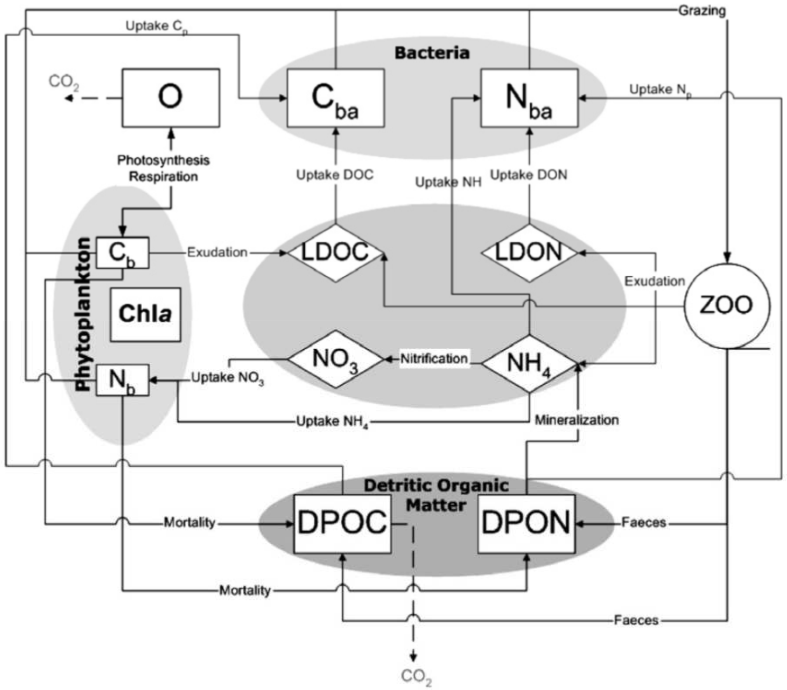


Fig. 1. The biogeochemical model, including the microbial loop.

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

ELSEVIER

Marine Pollution Bulletin 61 (2010) 465–479

Modelling the spatial and temporal variability of the SW lagoon of New Caledonia I: A new biogeochemical model based on microbial loop recycling

Vincent Faure[a,*], Christel Pinazo[a], Jean-Pascal Torréton[b], Séverine Jacquet[b,1]

State variables (except Chl.*a* which is a diagnostic variable).

	Variables	Definition	Units
1	C_B	Phytoplankton carbon	µmol l^{-1}
2	N_B	Phytoplankton nitrogen	µmol l^{-1}
3	Chl.*a*	Phytoplankton chlorophyll *a*	µg Chl.*a* l^{-1}
4	C_{BA}	Bacterial carbon	µmol l^{-1}
5	N_{BA}	Bacterial nitrogen	µmol l^{-1}
6	DPOC	Detrital particulate organic carbon	µmol l^{-1}
7	DPON	Detrital particulate organic nitrogen	µmol l^{-1}
8	LDOC	Labile dissolved organic carbon	µmol l^{-1}
9	LDON	Labile dissolved organic nitrogen	µmol l^{-1}
10	NH_4	Ammonium	µmol l^{-1}
11	NO_3	Nitrates + nitrites	µmol l^{-1}
12	O	Oxygen	µmol l^{-1}

The carbon specific uptake rate of nitrogen:

$$V_N^C = V_{NH_4}^C + V_{NO_3}^C$$

$$V_{NH_4}^C = \max V_{NH_4}^C \cdot \left[\frac{\max Q_C^N - Q_C^N}{\max Q_C^N - \min Q_C^N}\right] \cdot \left(\frac{NH_4}{NH_4 + K_{NH_4}}\right)$$

$$V_{NO_3}^C = \max V_{NO_3}^C \cdot \left[\frac{\max Q_C^N - Q_C^N}{\max Q_C^N - \min Q_C^N}\right] \cdot \left(\frac{NO_3}{NO_3 + K_{NO_3}}\right)$$

Introduction

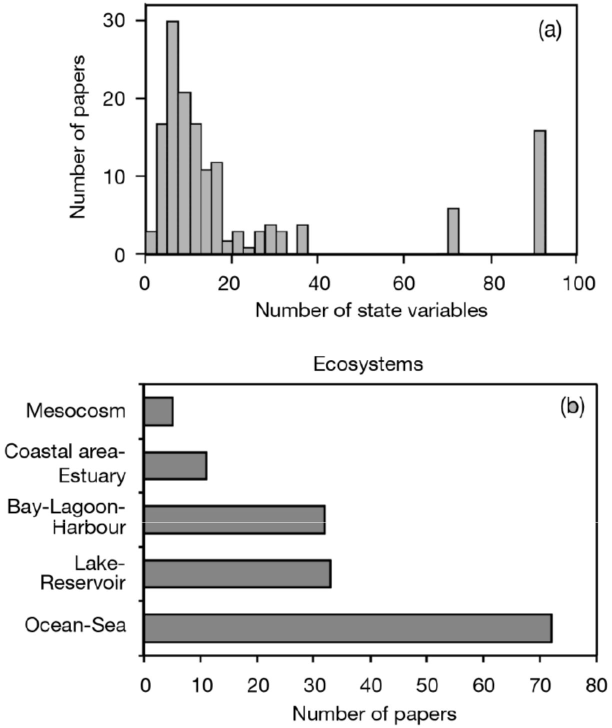


Fig. 1. Frequency histograms of (a) aquatic biogeochemical model complexity based on number of state variables and (b) types of ecosystems modeled

Vol. 271: 13–26, 2004 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published April 28

Evaluation of the current state of mechanistic aquatic biogeochemical modeling

George B. Arhonditsis[1,2,*], Michael T. Brett[1]

[1]Department of Civil & Environmental Engineering, More Hall, Box 352700, University of Washington, Seattle, Washington 98195, USA

[2]*Present address:* Nicholas School of the Environment and Earth Sciences, Duke University, Durham, North Carolina 27708, USA

153 studies published from 1990 to 2002

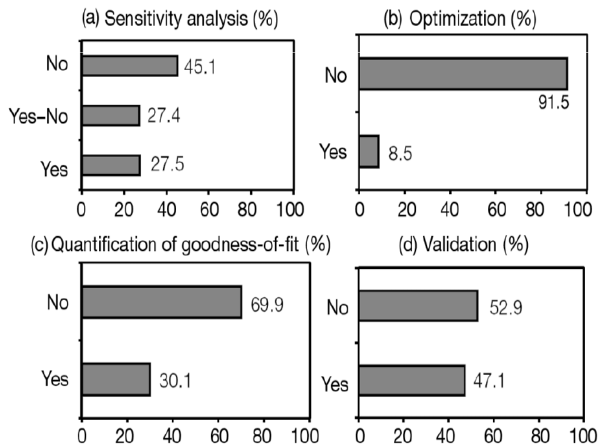
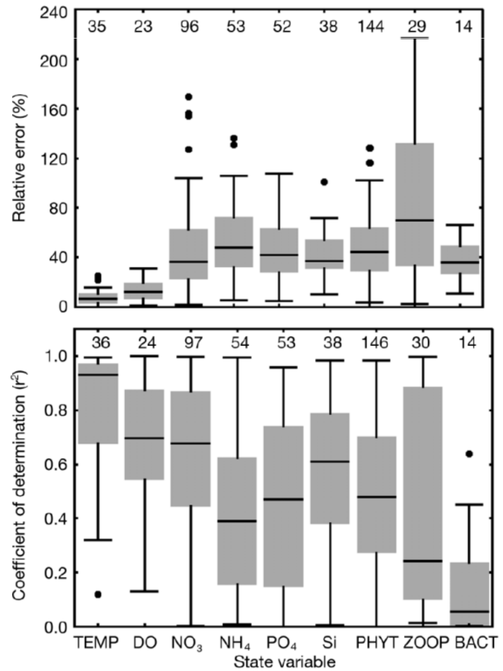


Fig. 2. Proportion of aquatic biogeochemical modeling studies that (a) performed sensitivity analyses, (b) used optimization techniques for model calibration, (c) quantified fit between simulated and field data, and (d) validated models (see first subsection of 'Results'). In (a) category 'YES–NO' indicates qualitative approaches (see first subsection of 'Results' for further explanation)



mio Institut Méditerranéen d'Océanologie

Introduction

• Complex systems **dynamics** (high number of entities interacting in nonlinear way, networks, loops and feed-back loops, etc.) - **Ecosystems**

• **Response of the complete network** to a given perturbation (contamination, exploitation, global warming, …) on a particular part of the system? (amplified, damped, how and why?)

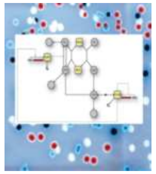
- processes intensities and variations;
- the whole system dynamics;
- from **individuals** to **communities** and back;

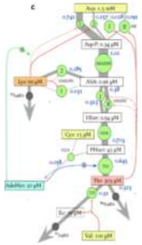
MODELLING:

• How does the **formulation** of a process in a complex system affect the whole system dynamics? How to **measure** the impacts of a perturbation?

Introduction

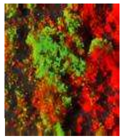
Information - Data





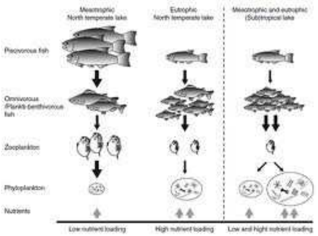
Individuals

Bioenergetics – Genetic properties – Metabolism – Physiology - Behaviours



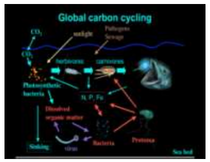
Functional groups

Activities – Genetic and Metabolic expressions



Communities

Biotic interactions – Trophic webs



Ecosystems

Environmental forcing – – Energy assessments – Human activities

Complexity

Introduction

How can we used data got in laboratory experiments to field models? How can we take benefit of the large amount of data obtained at small scales to understand global system functioning?

Can we link different data sets obtained at different scales?

For a given process in a complex system, what is the effect of its mathematical formulation on the whole dynamics? Does it matter if it is well quantitatively validated?

For a given process, we often use functions even if we know that it is a bad representation, because it is simpler : is there a simple alternative?

For an given ecosystem, many models can be developed. How to choose? One of them can be valid during a given time period while another will be efficient for another period : how do we know the sequence of the models to use?

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STRUCTURE SENSITIVITY

Structure sensitivity

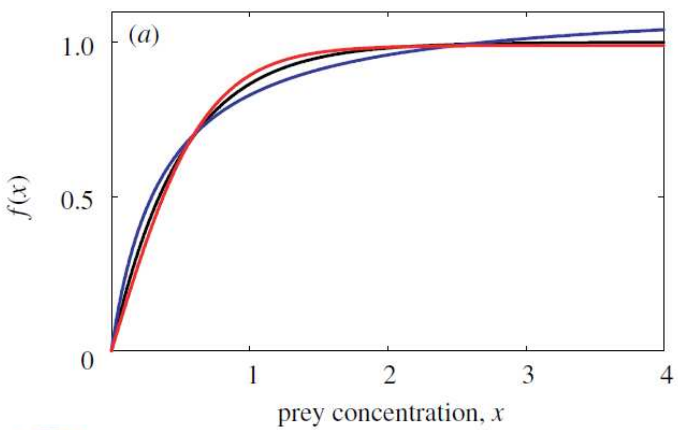
biology letters
Biol. Lett. (2005) **1**, 9–12
doi:10.1098/rsbl.2004.0246
Published online 29 November 2004

Community response to enrichment is highly sensitive to model structure

Gregor F. Fussmann[1,†,*] and Bernd Blasius[2]

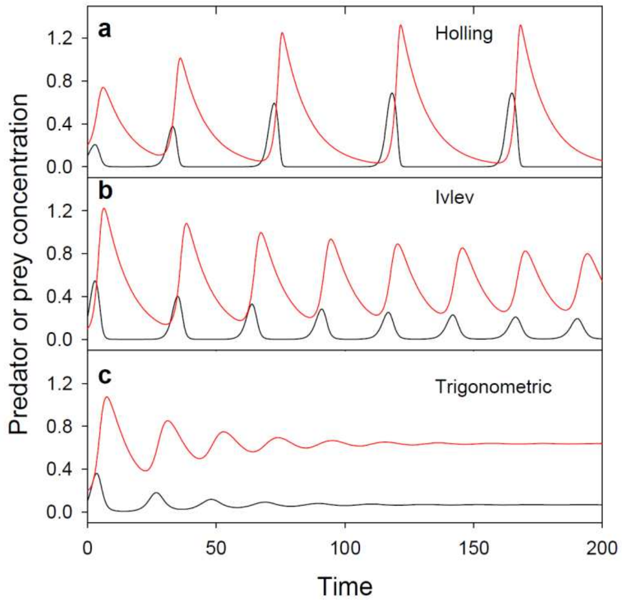
$$dx/dt = g(x) - f(x)y,$$

$$dy/dt = f(x)y - my.$$



Myerscough, M. R., Darwen, M. J. & Hogarth, W. L. 1996 Stability, persistence and structural stability in a classical predator–prey model. *Ecol. Model.* **89**, 31–42.

level of enrichment	Holling $f_H(x) = a_H x/(1+b_H x)$	Ivlev $f_I(x) = a_I(1-\exp(-b_I x))$	trigonometric $f_T(x) = a_T \tanh(b_T x)$
$K < 0.45$	stable	stable	stable
$0.45 < K < 1.08$	unstable	stable	stable
$1.08 < K < 2.65$	unstable	unstable	stable
$2.65 < K < 10.12$	unstable	unstable	multi-stable[a]
$K > 10.12$	unstable	unstable	unstable



Structure sensitivity

$$\frac{dx}{dt} = rx(1-\frac{x}{K}) - g(x)y$$
$$\frac{dy}{dt} = eg(x)y - my$$

Sensitivity to function *g* ?

g_R : Reference model = M_R

g_P : Perturbed model = M_P

$$d_M(M_R,M_P) = \int_D |g_R(X) - g_P(X)|\, dX$$

$$d_H(K_1,K_2) = \max\left\{ \max_{y\in K_2}\{d(K_1,y)\}, \max_{x\in K_1}\{d(K_2,x)\} \right\}$$

with $d(A,y) = \min_{x\in A}\{d(x,y)\}$ for any compact set A.

Structure sensitivity

Let us consider two fixed positive numbers σ and ρ and a reference model (M_R). We denote by $B_\rho(M_R)$ the set of models (M) such that $d_M(M_R,M) < \rho$. For a given initial condition $X \in \mathbb{R}^n$, we denote by $K_R(X)$ its ω-limit with the model (M_R) and by $K(X)$ its ω-limit with the model (M).

Journal of Theoretical Biology 283 (2011) 82–91

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Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Journal of Theoretical Biology

Structural sensitivity of biological models revisited

Cordoleani Flora [a,*], Nerini David [a], Gauchon Mathias [a], Morozov Andrew [b], Poggiale Jean-Christophe [a]

Marseille (COM), Université de la Méditerranée, UMR LMGEM 6117 CNRS, Campus de Luminy, Case 901, 13288 Marseille Cedex 09, France

ıtics, University of Leicester, University Road, Leicester LE1 7RH, United Kingdom

Structure sensitivity

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We say that (M_R) is ρ-structurally σ-sensitive if there exists $M \in B_\rho(M_R)$ such that one of the following conditions is fulfilled:

(i) (M) is not structurally stable;
(ii) there exists an initial condition $X_0 \in \mathbf{R}^n$ such that for all X satisfying $K_R(X) = K_R(X_0)$, then $d_H(K_R(X), K(X)) \geq \sigma$.

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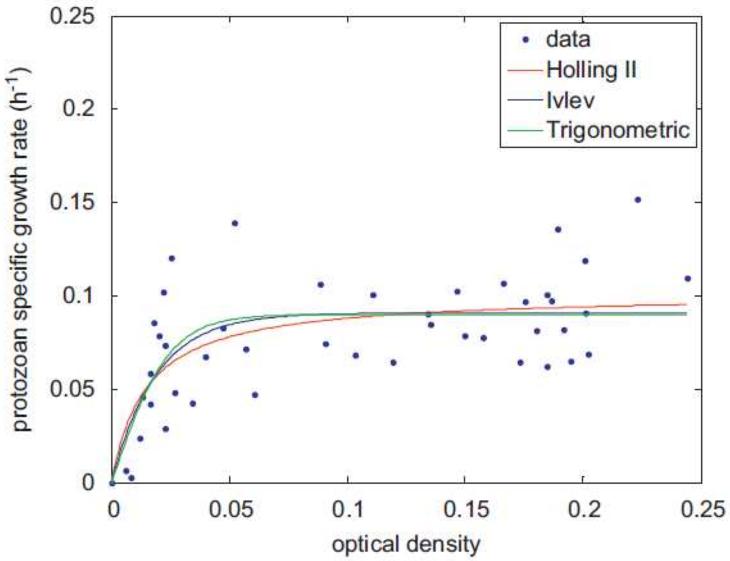
Structure sensitivity

$$\begin{cases} \frac{dx}{dt} = D(x_{in}-x)-f(x)y \\ \frac{dy}{dt} = e_1 f(x)y-g(y)z-Dy \\ \frac{dz}{dt} = e_2 g(y)z-Dz \end{cases}$$

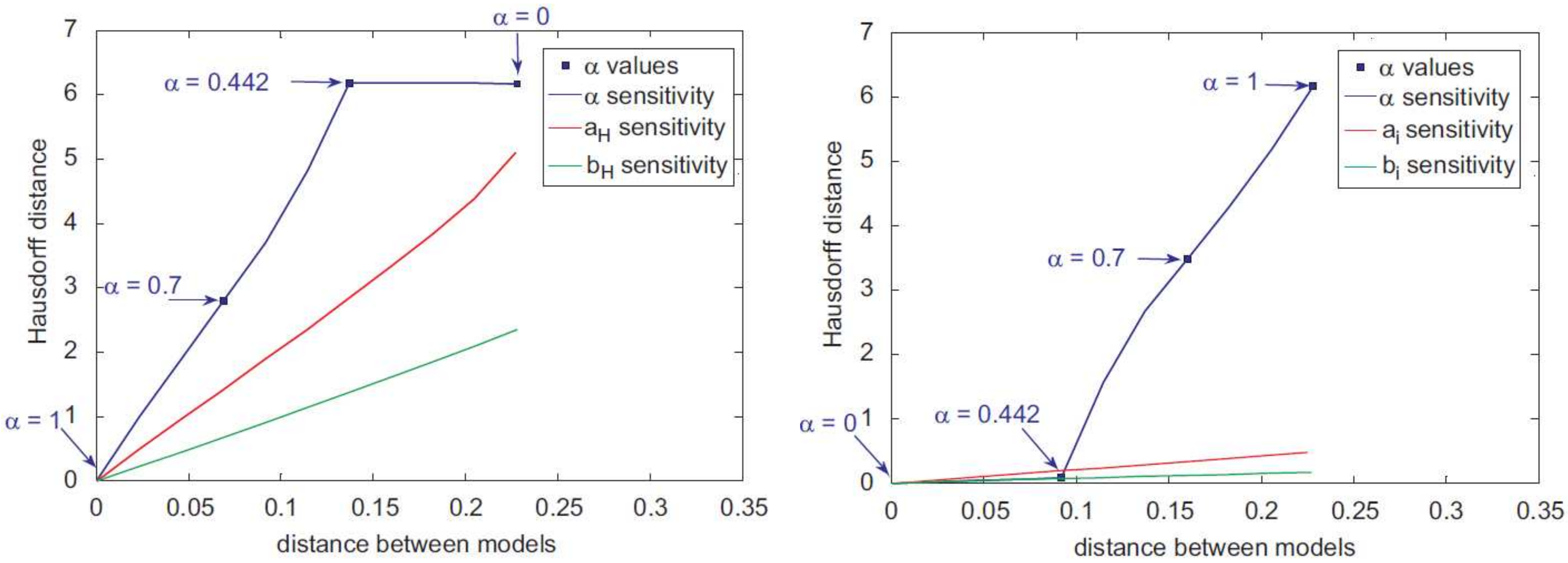
$$f(x) = v_{max}x/(k+x)$$

Functional response	Formulation
Holling (Holling 1959b)	$g_h(y) = \frac{a_h y}{1+b_h y}$
Ivlev (Ivlev, 1961)	$g_i(y) = \frac{a_i}{b_i}(1-\exp(-b_i y))$
Trigonometric	$g_t(y) = \frac{a_t}{b_t}\tanh(b_t y)$

$$G_\alpha = \alpha\hat{g}_h + (1-\alpha)\hat{g}_i, \quad \alpha \in [0,1]$$



Structure sensitivity



$$d_M(M_R, M_P) = \int_D |g_R(X) - g_P(X)| \, dX$$

$$d_H(K_1, K_2) = \max\left\{ \max_{y \in K_2}\{d(K_1, y)\}, \max_{x \in K_1}\{d(K_2, x)\} \right\}$$

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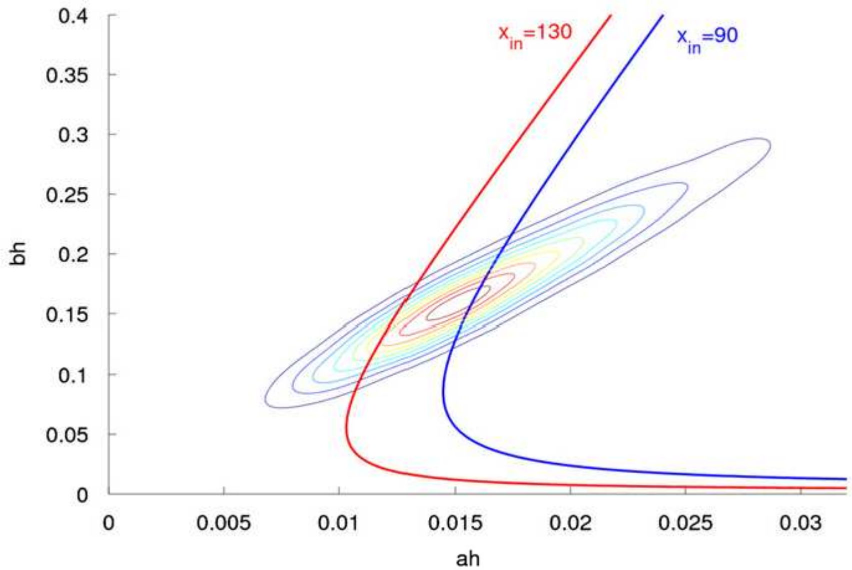
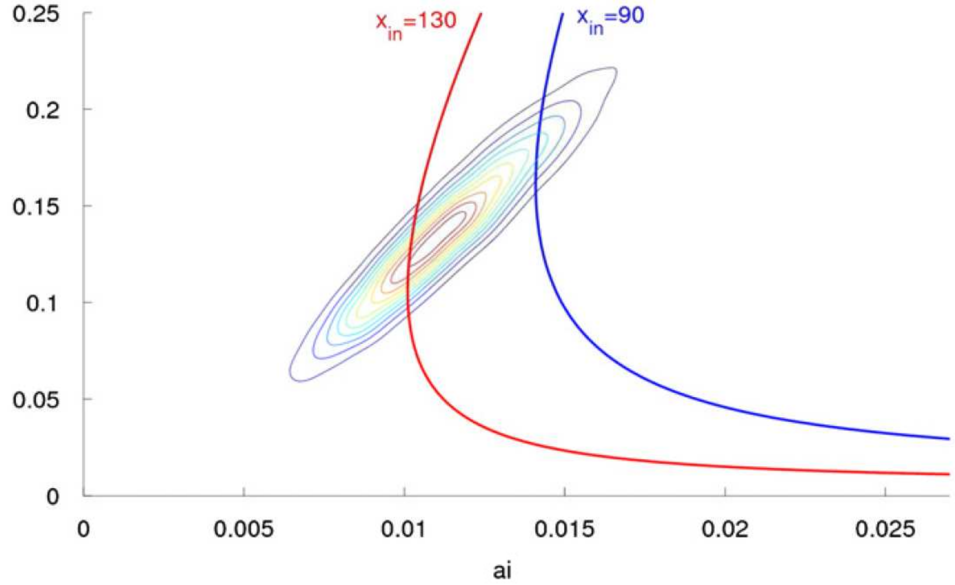
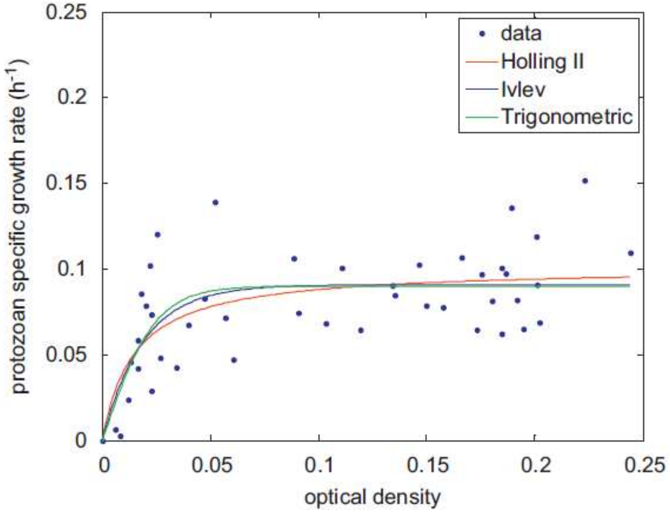
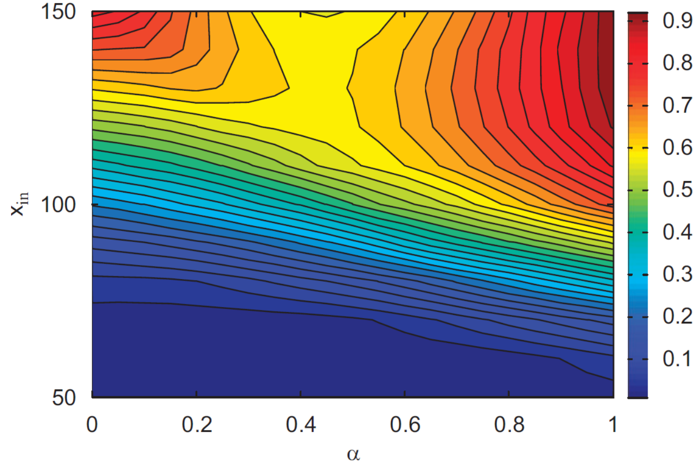
Structure sensitivity



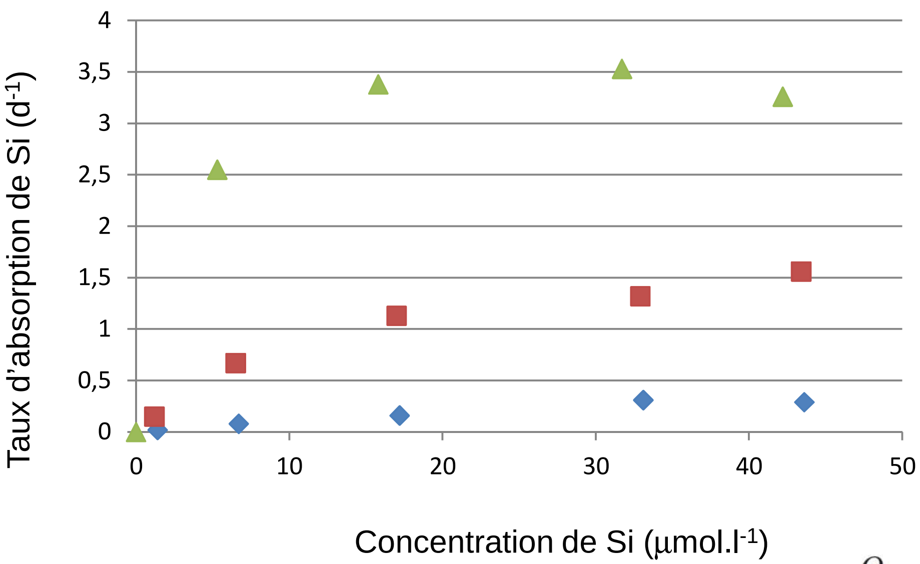




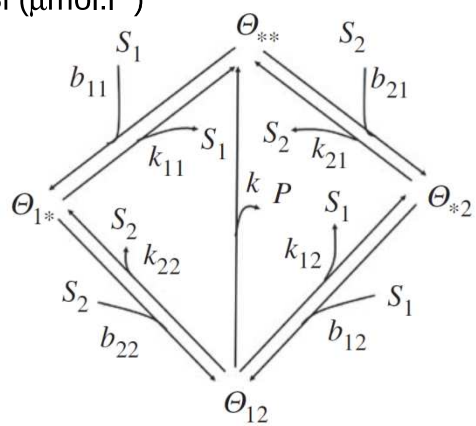


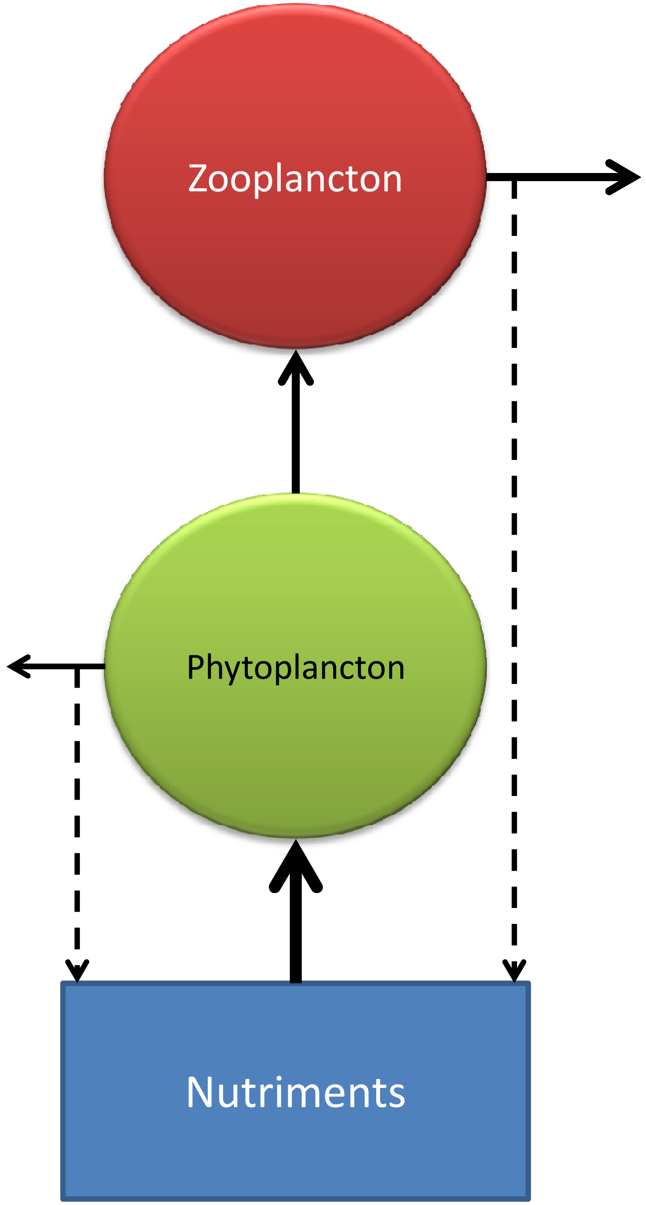
$$V = \frac{1}{2m^2}\sum_i\sum_j d_H^2(A_i,A_j)$$

Structure sensitivity



$$V = \frac{V_{\max}(Fe)Si}{K_S(Fe) + Si}$$





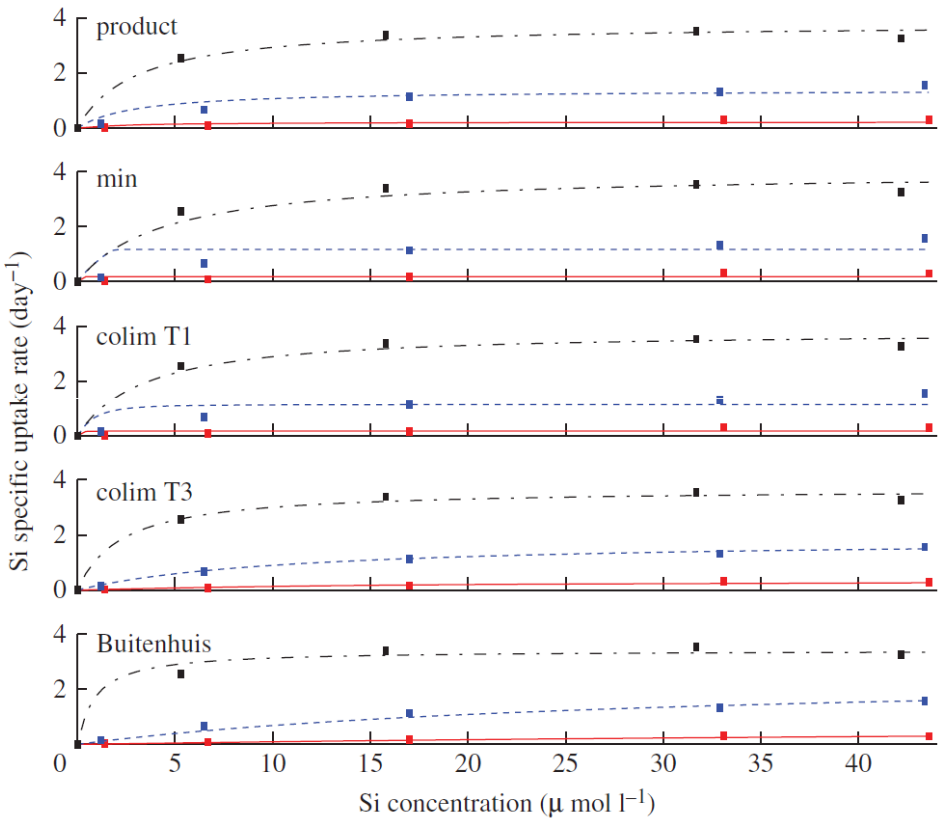
How far details are important in ecosystem modelling: the case of multi-limiting nutrients in phytoplankton –zooplankton interactions

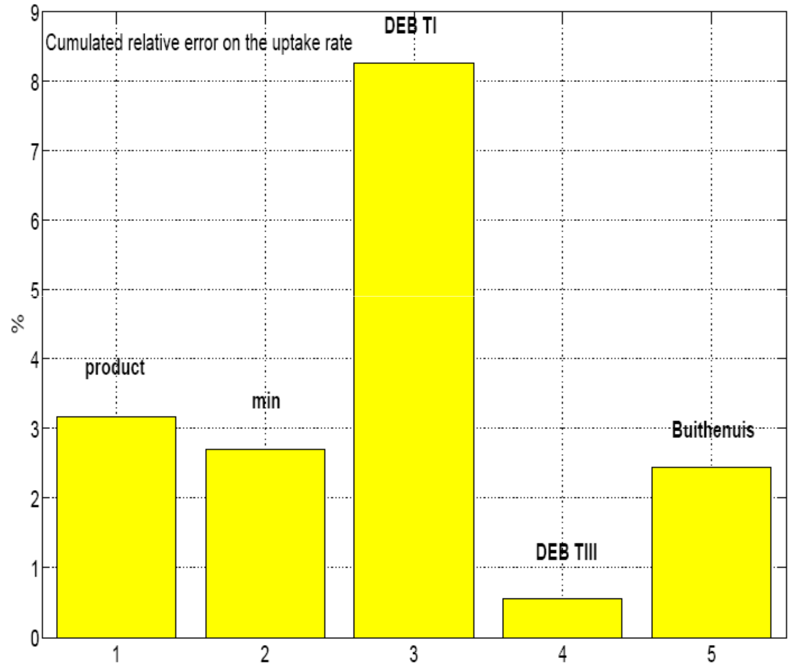
J.-C. Poggiale, M. Baklouti, B. Queguiner and S. A. L. M. Kooijman

Phil. Trans. R. Soc. B 2010 **365**, 3495-3507

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Structure sensitivity





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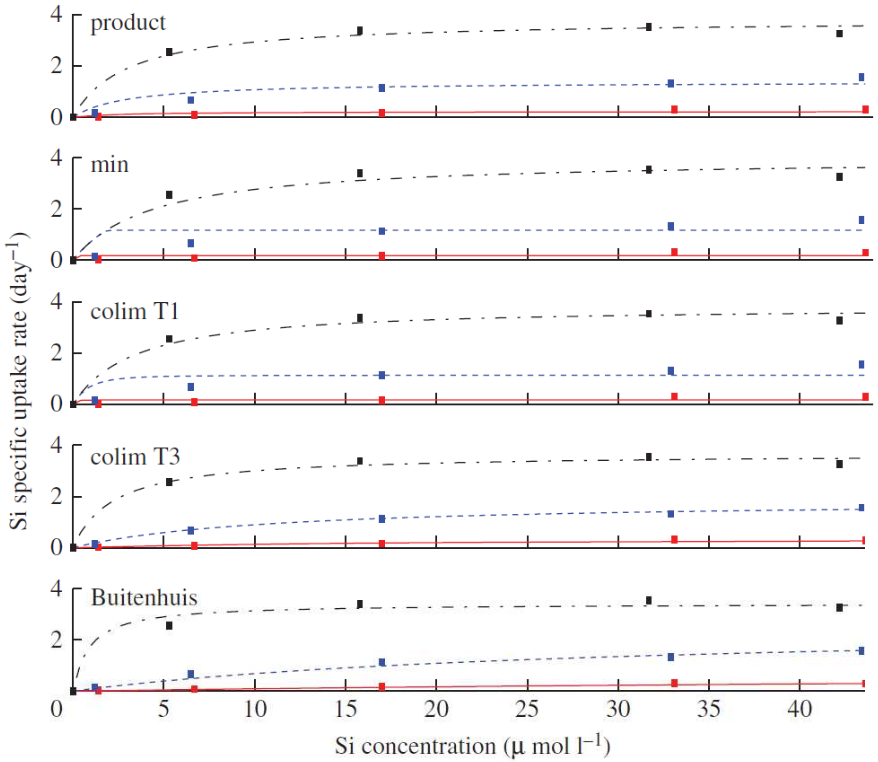

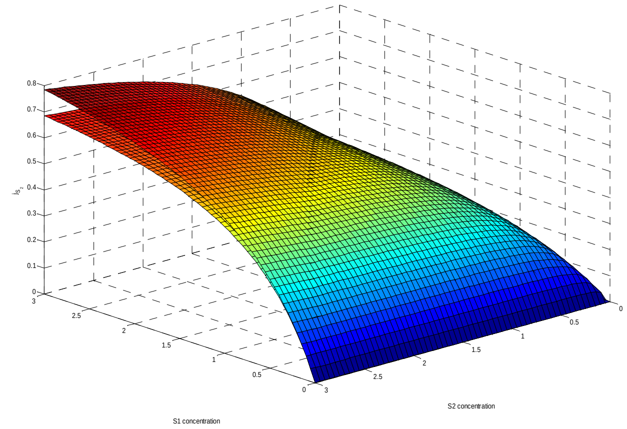

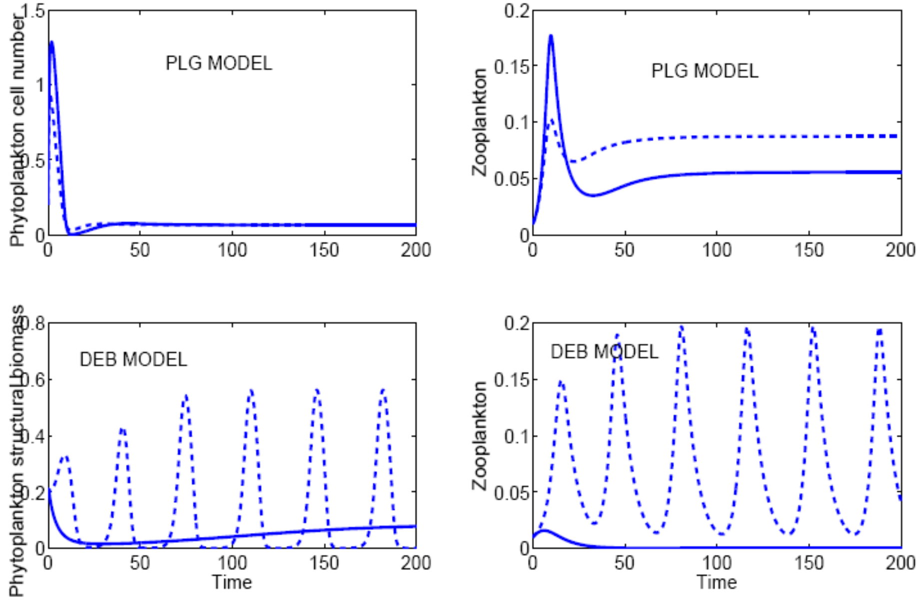

PROCESS FORMULATION : FUNCTIONAL RESPONSE

Functional response

How should we formulate the functional response? At which scale?

Process which describes the **biomass flux from a trophic level to another one** : the functional response aims to describe this process at the **population level**.

However, it results from many individual properties :

- **behavior** (interference between predators, optimal foraging, ideal free distribution, etc.)

- **physiology** (satiation, starvation, etc.)

And population properties as well:

- **population densities** (density-dependence effects)

- **populations distribution** (encounter rates, etc.)

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Current ecosystem models are sensitive to the functional response formulation.

Functional response

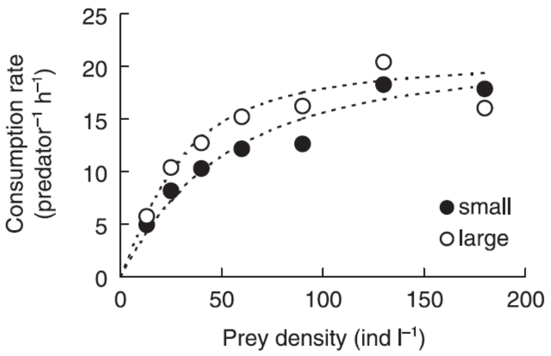


Fig. 1. The mean prey consumption rate of *Neomysis* preying on *Polyphemus* in small and large containers. The hatched lines show the fitted type II functional response functions.

Journal of Animal Ecology 2004
73, 487–493

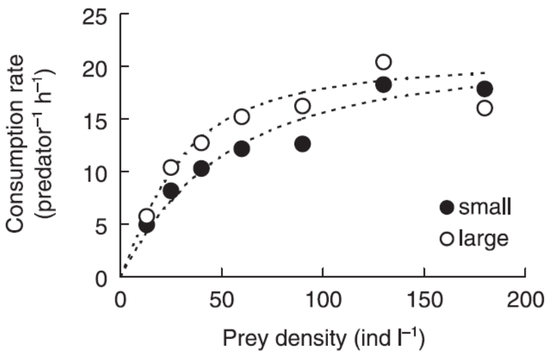
Spatial scale, heterogeneity and functional responses

ULF BERGSTRÖM and GÖRAN ENGLUND

Small scale : experiments

Large scale : integrate spatial variability and individuals displacement (behavior, …)

Functional response



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Ecology, 87(6), 2006, pp. 1478–1488
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Small scale : experiments

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THE SCALE TRANSITION: SCALING UP POPULATION DYNAMICS WITH FIELD DATA

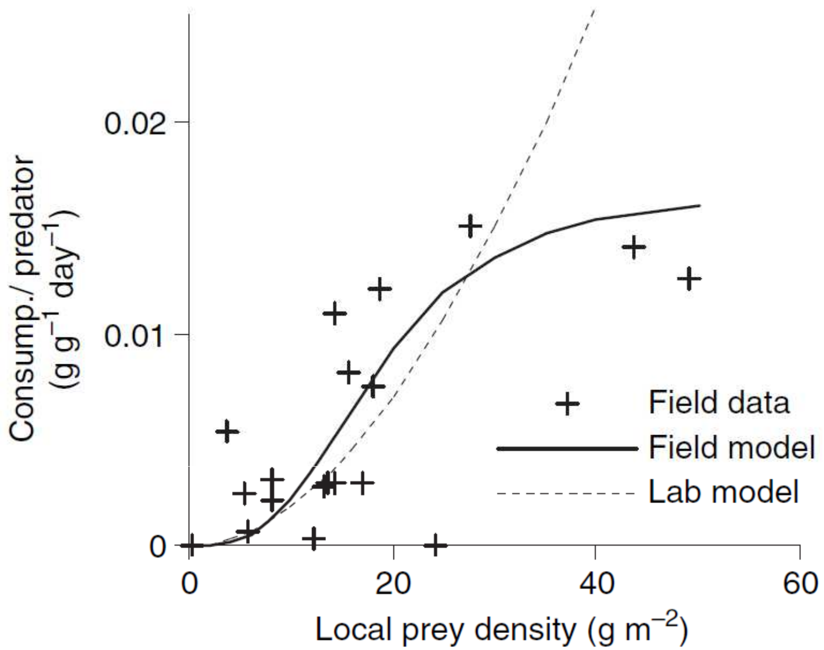
BRETT A. MELBOURNE[1,3] AND PETER CHESSON[2]

$$\frac{dR_x}{dt} = g(R_x) - f(R_x)C_x + I_{R,x} - E_{R,x}$$

$$\frac{dC_x}{dt} = \big(cf(R_x) - m\big)C_x + I_{C,x} - E_{C,x}$$

$$\frac{d\overline{R}}{dt} \approx \underbrace{g(\overline{R}) - f(\overline{R})\overline{C}}_{\text{mean-field model}} + \underbrace{\tfrac{1}{2}g''(\overline{R})\mathrm{Var}(R)}_{a} - \underbrace{\tfrac{1}{2}f''(\overline{R})\mathrm{Var}(R)\overline{C}}_{b} \underbrace{- f'(\overline{R})\mathrm{Cov}(R,C)}_{c}$$

Functional response



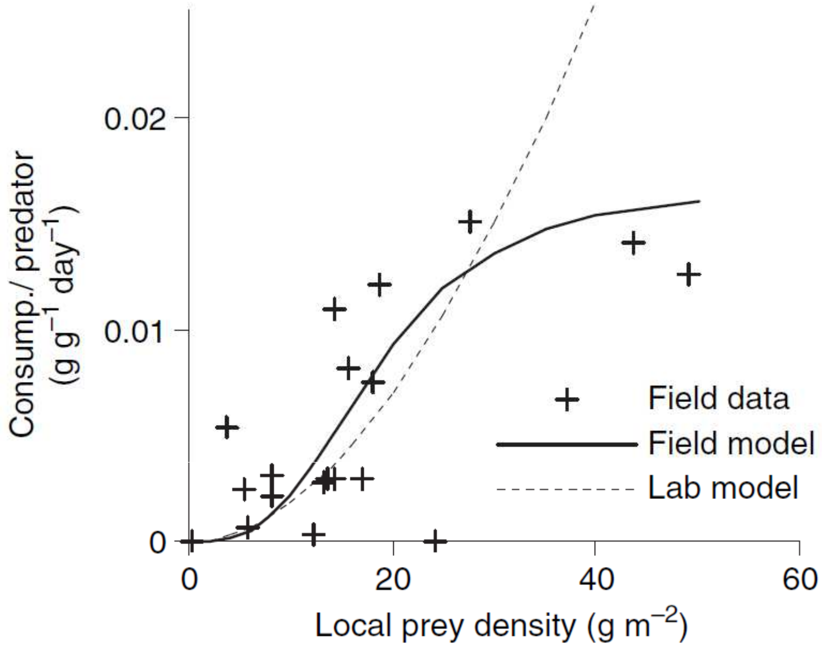
LETTER

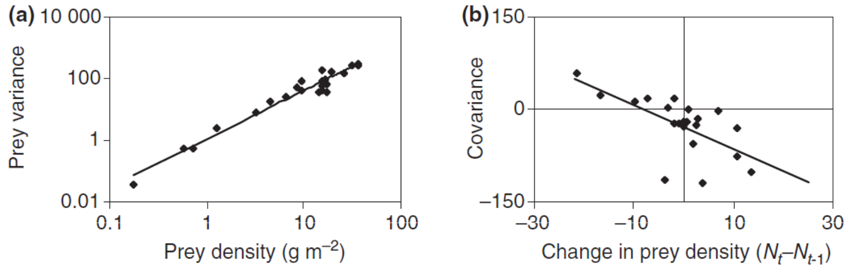
Scaling up the functional response for spatially heterogeneous systems

Ecology Letters, (2008) **11**

Göran Englund* and Kjell Leonardsson

Functional response





$$\frac{d\bar{N}}{dt} = g(\bar{N}) - f(\bar{N})\bar{P} + g''(\bar{N})\sigma_N^2/2 - f''(\bar{N})\bar{P}\sigma_N^2/2 - f'(\bar{N})\sigma_{N,P}$$

$$\frac{d\bar{P}}{dt} = q[f(\bar{N})\bar{P} + f''(\bar{N})\bar{P}\sigma_N^2/2 + f'(\bar{N})\sigma_{N,P}] - d\bar{P}$$

LETTER

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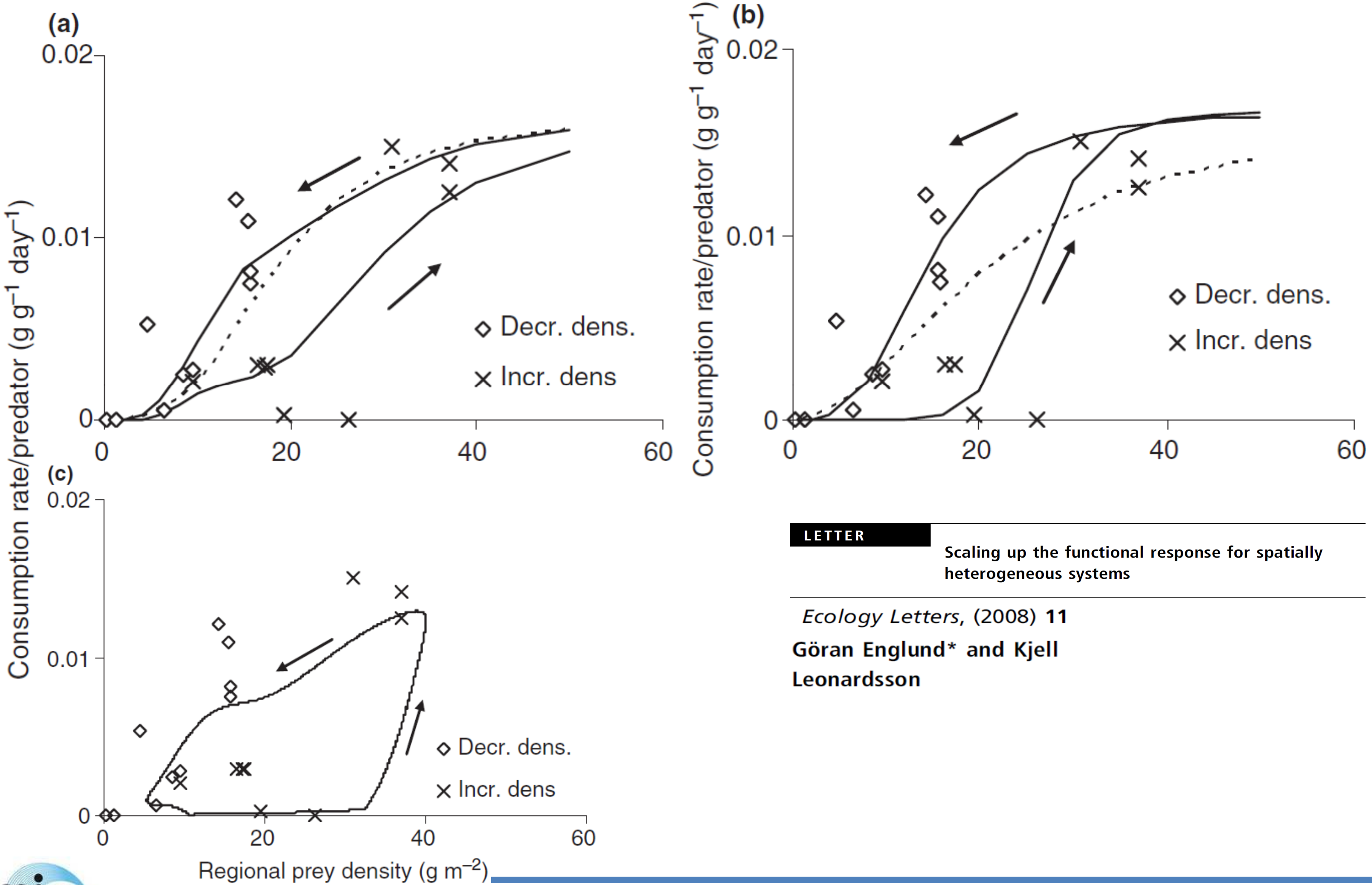
Göran Englund* and Kjell Leonardsson

Functional response



LETTER

Scaling up the functional response for spatially heterogeneous systems

Ecology Letters, (2008) **11**

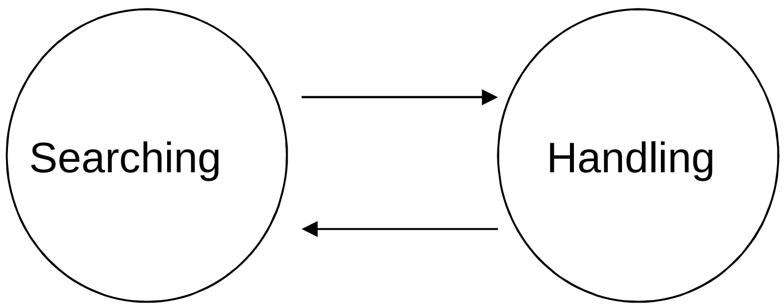
Göran Englund* and Kjell Leonardsson

Functional response

$$\frac{dx}{d\tau} = rx\left(1 - \frac{x}{K}\right) - \frac{ax}{1+bx}y$$

$$\frac{dy}{d\tau} = \varepsilon y\left(e_1 \frac{ax}{1+bx} - \mu_1\right)$$

Holling idea:



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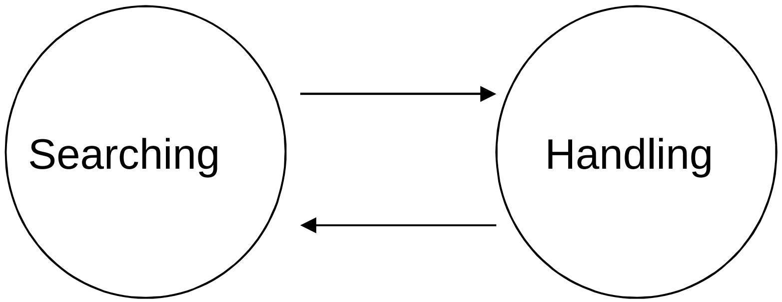

$$\Delta t = \Delta t_s + \Delta t_h$$

$$\Delta x = ax\Delta t_s$$

$$\Delta t_h = T_h \Delta x = T_h ax \Delta t_s$$

$$\frac{\Delta x}{\Delta t} = \frac{ax\Delta t_s}{\Delta t_s + T_h ax \Delta t_s} = \frac{ax}{1 + T_h ax}$$

Functional response

$$\frac{dx}{d\tau} = rx\left(1 - \frac{x}{K}\right) - \frac{ax}{1+bx}y$$

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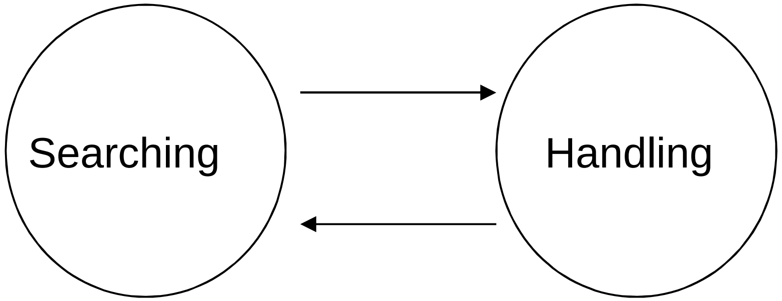


$$\Delta t = \Delta t_s + \Delta t_h$$

$$\Delta x = ax\Delta t_s$$

$$\Delta t_h = T_h \Delta x = T_h a x \Delta t_s$$

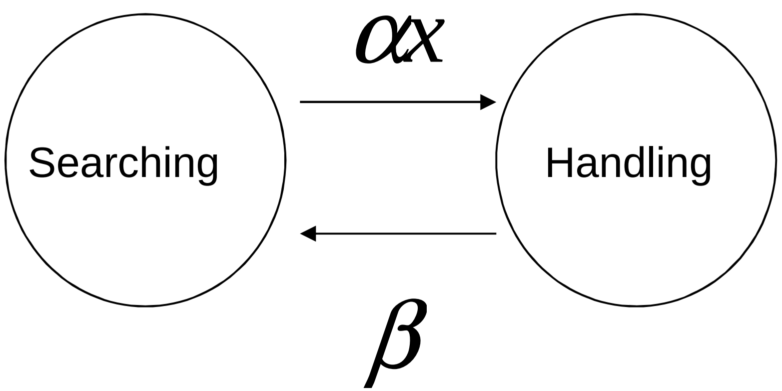
x is assumed constant at this scale of description

$$\frac{\Delta x}{\Delta t} = \frac{ax\Delta t_s}{\Delta t_s + T_h a x \Delta t_s} = \frac{ax}{1 + T_h a x}$$

Functional response

$$g(x) = \frac{ax}{1+bx}$$

Holling type II (Disc equation – Holling 1959)



Functional response

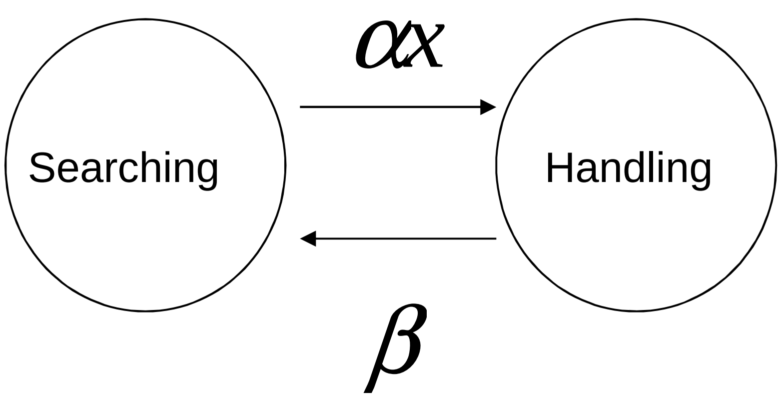
$$g(x) = \frac{ax}{1+bx}$$

Holling type II (Disc equation – Holling 1959)

$$\frac{dx}{d\tau} = \varepsilon\left(xr(x) - axy_r\right)$$

$$\frac{dy_r}{d\tau} = -\alpha x y_r + \beta y_o + \varepsilon\left(eaxy_r - \mu y_r\right)$$

$$\frac{dy_o}{d\tau} = \alpha x y_r - \beta y_o - \varepsilon \mu y_o$$



$$y = y_r + y_o$$

Functional response

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Holling type II (Disc equation – Holling 1959)

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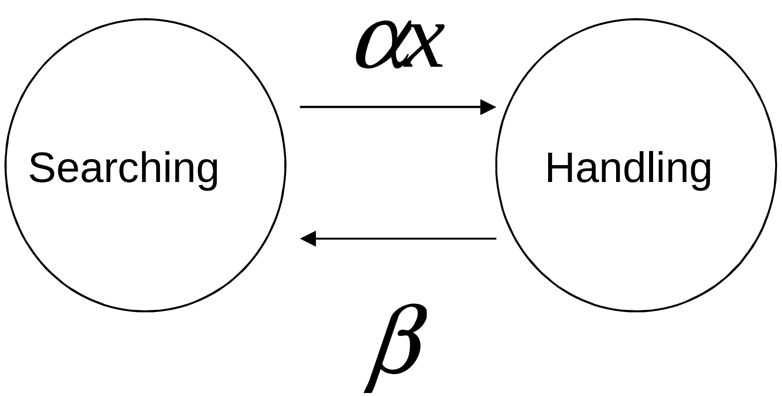
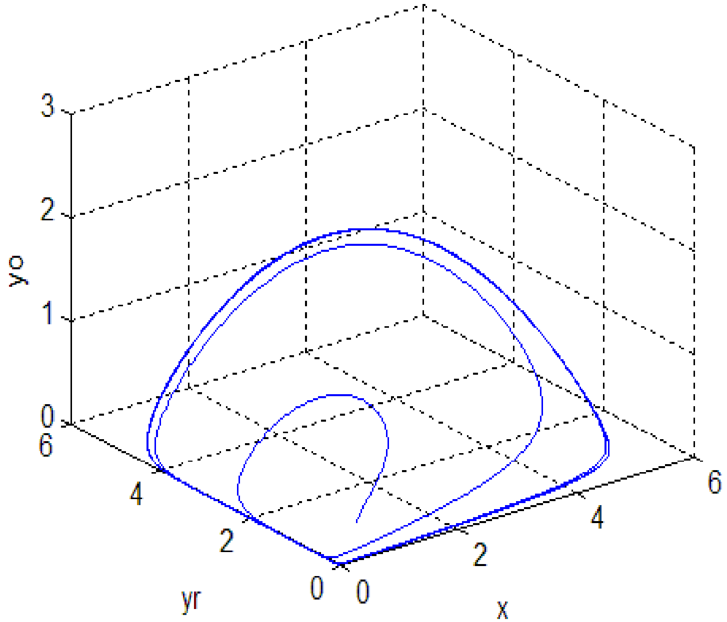


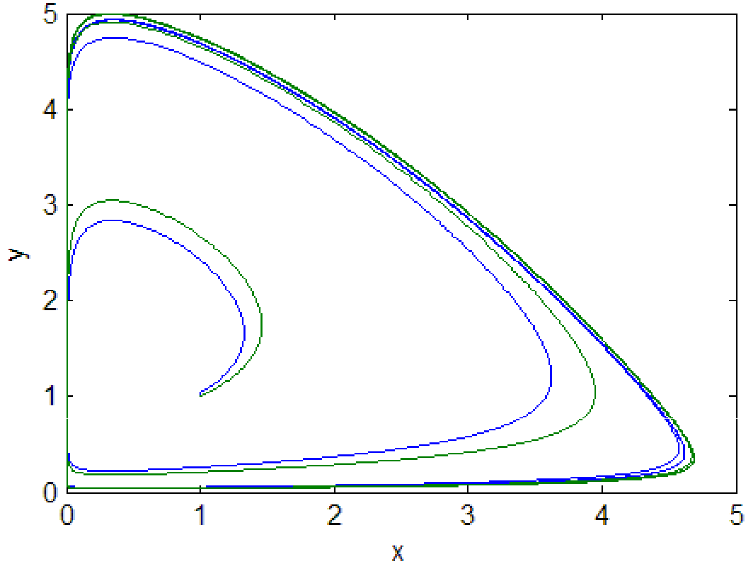
$$y = y_r + y_o$$

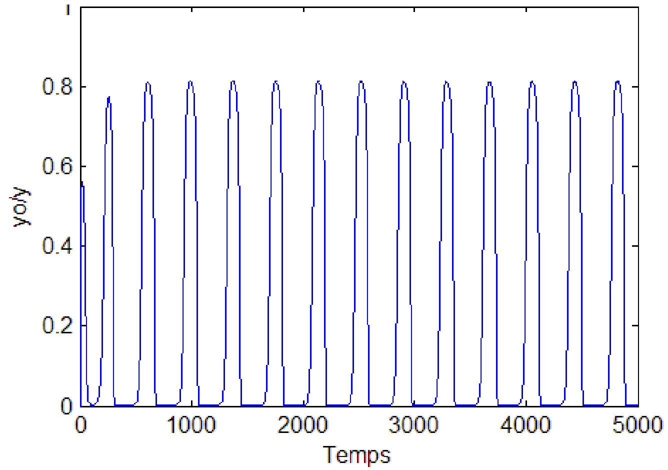
$$y_r \to \frac{\beta}{\alpha x + \beta} y$$

$$g(x) = \frac{ax}{1 + \frac{\alpha}{\beta} x}$$

Functional response



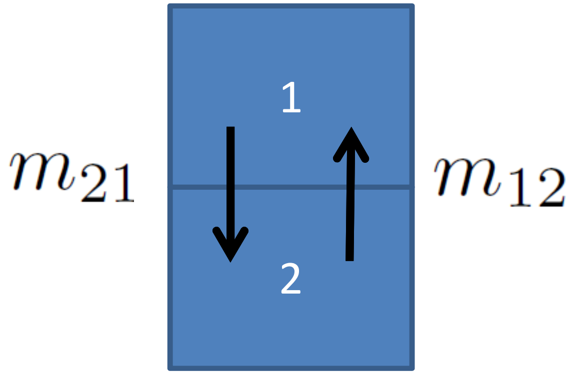




Functional response

$$\frac{dx}{d\tau} = \varepsilon\Big(rx(1-\frac{x}{K}) - g_{loc}(x)y_1\Big)$$
$$\frac{dy_1}{d\tau} = m_{12}y_2 - m_{21}y_1 + \varepsilon\Big(eg_{loc}(x)y_1 - my_1\Big)$$
$$\frac{dy_2}{d\tau} = m_{21}y_1 - m_{12}y_2 + \varepsilon\Big(r_y(y_2) - my_2\Big)$$

$$g_{loc}(x) = \frac{a_1 x}{1 + b_1 x}$$



$$m_{12} = \alpha \text{ and } m_{21} = \frac{\beta}{x}$$

Functional response

$$\frac{dx}{d\tau} = \varepsilon\Big(rx(1-\frac{x}{K}) - g_{loc}(x)y_1\Big)$$
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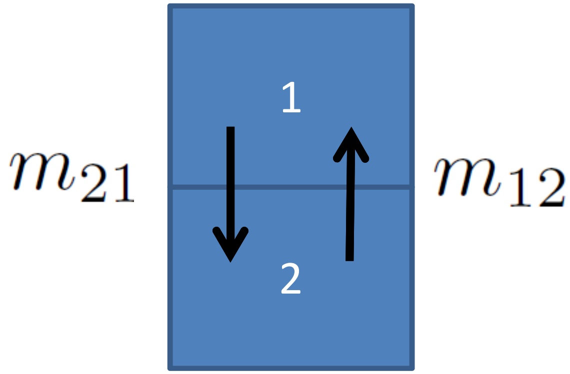


$$y = y_1 + y_2$$

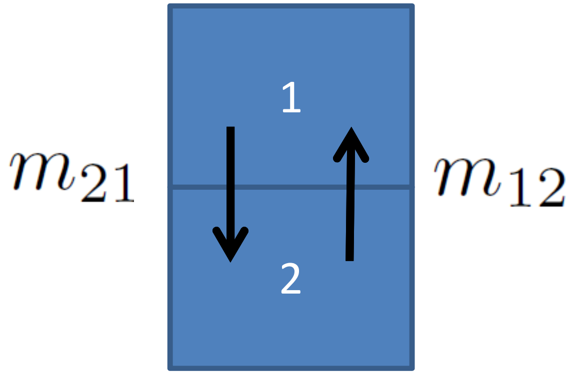
$$m_{12} = \alpha \text{ and } m_{21} = \frac{\beta}{x}$$

$$y_1 = \frac{m_{12}}{m_{12}+m_{21}}y + O(\varepsilon) = \frac{\alpha x}{\alpha x + \beta}y + O(\varepsilon)$$

Functional response

$$\begin{aligned}\frac{dx}{d\tau} &= \varepsilon\Big(rx(1-\frac{x}{K}) - g_{loc}(x)y_1\Big)\\ \frac{dy_1}{d\tau} &= m_{12}y_2 - m_{21}y_1 + \varepsilon\Big(e g_{loc}(x)y_1 - my_1\Big)\\ \frac{dy_2}{d\tau} &= m_{21}y_1 - m_{12}y_2 + \varepsilon\Big(r_y(y_2) - my_2\Big)\end{aligned}$$

$$g_{loc}(x) = \frac{a_1 x}{1 + b_1 x}$$



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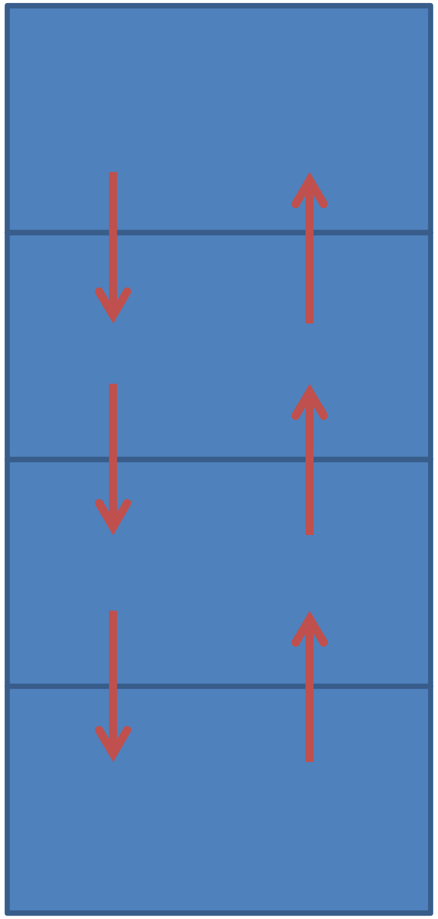
$$y_1 = \frac{m_{12}}{m_{12}+m_{21}}y + O(\varepsilon) = \frac{\alpha x}{\alpha x + \beta}y + O(\varepsilon)$$

$$\begin{aligned}\frac{dx}{dt} &= rx(1-\frac{x}{K}) - G_{global}(x)y + O(\varepsilon)\\ \frac{dy}{dt} &= R(y)y - my + O(\varepsilon)\end{aligned}$$

$$G_{global}(x) = \frac{\alpha x}{\alpha x + \beta}\frac{a_1 x}{1 + b_1 x}$$

Functional response



$$\frac{dx_i}{dt} = M_{x,i}\mathbf{x} + \varepsilon\Big(r_i x_i (1 - \frac{x_i}{K_i}) - \frac{a_i x_i}{b_i + x_i} y_i\Big)$$

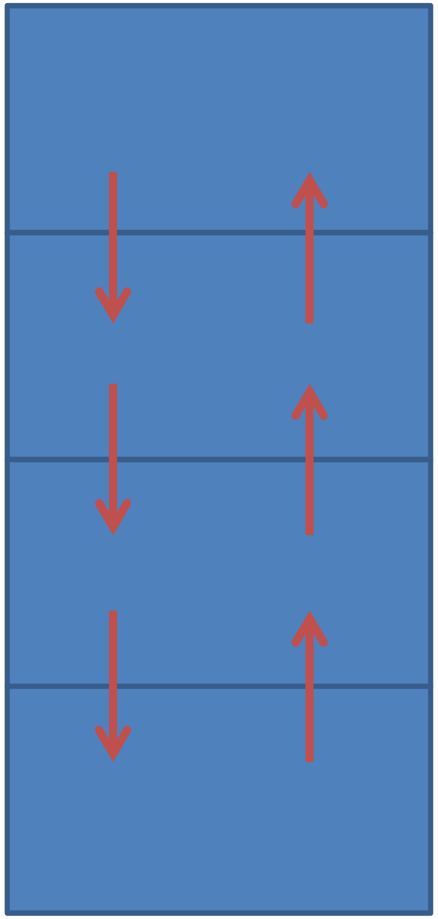
$$\frac{dy_i}{dt} = M_{y,i}(\mathbf{x})\mathbf{y} + \varepsilon\Big(e\frac{a_i x_i}{b_i + x_i} y_i - m_i y_i\Big)$$

$$\frac{dx}{d\tau} = rx(1 - \frac{x}{K}) - g(x)y$$

$$\frac{dy}{d\tau} = eg(x)y - my$$

$$g(x) = \sum_{i=1}^{N} \frac{a_i u_i}{b_i + u_i x} x v_i(x)$$

Functional response



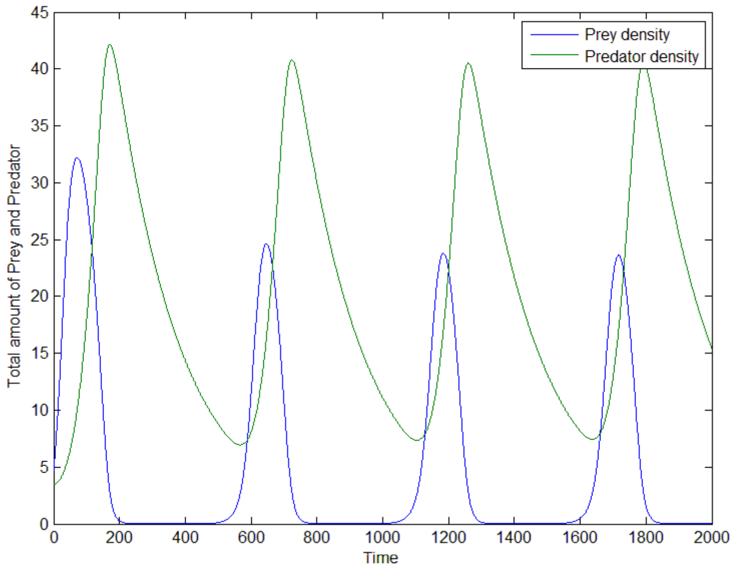
$$g_i''(0) < 0$$ Local Holling type II functional responses

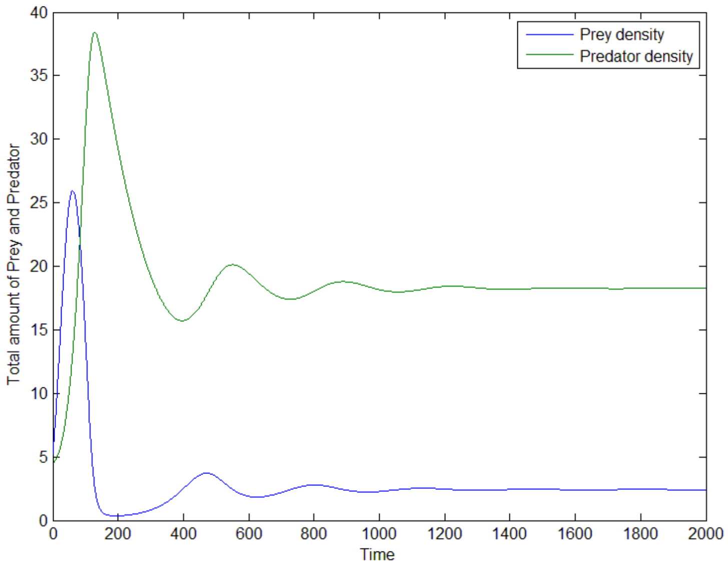
$$g''(0) > 0$$ Global Holling type III functional response

$$g''(0) = \underbrace{\sum_{i=1}^{N} g_i''(0) v_i(0)}_{<0} + 2 \sum_{i=1}^{N} \underbrace{g_i'(0)}_{>0} v_i'(0)$$

=> Conditions can be found to get the criterion for Holling Type III functional responses

Dynamical consequences

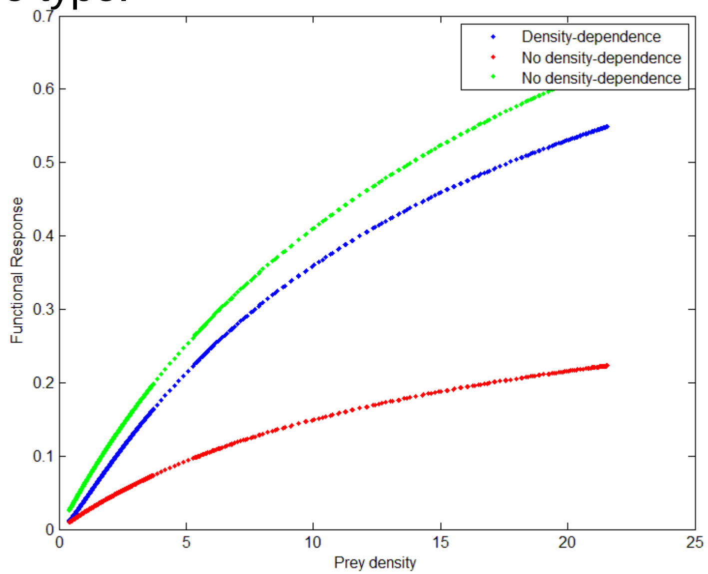




1 – On each patch separately, the parameter values are such that periodic solutions occur.

2 – With density-dependent migration rates of the predator satisfying the above mentioned criterion for Holling Type III functional response, the system is stabilized

3 – With constant migration rates, taking extreme values observed in the situation described in 2, the system exhibits periodic fluctuations : the stabilization results from the change of functional response type.



Dynamical consequences

• Global type III FR can emerge from local type II functional responses associated to density-dependent displacements

• The Holling Type III functional response leads to stabilization

• The stability actually results from the type (type II functional responses lead to periodic fluctuations even if they are quantitatively close to the type III FR)

• The Type III results from density-dependence : the effect of density-dependent migration rates on the global functional response can be understood explicitely.

Dynamical consequences

Functional response in the field : a set of functions instead of one function?

- We use functions to represent FR at a global scale even if we know that it is a bad representation, because it is simpler : is there a simple alternative?

- Shifts between models

- Multi-stability of the fast dynamics

- Changes of fast attractors : bifurcation in the fast part of the system induced by the slow dynamics

SHIFTS BETWEEN MODELS : LOSS OF NORMAL HYPERBOLICITY

Slow-Fast vector fields

$$\frac{dx}{d\tau} = f(x,y)$$

$$\frac{dy}{d\tau} = \varepsilon g(x,y)$$

$$\dot{x} = f(x,y,0)$$
$$\dot{y} = 0$$

$$x \rightarrow x^{*}(y)$$

Top – down

$$\dot{x} = f(x,y,\varepsilon)$$
$$\dot{y} = \varepsilon g(x,y,\varepsilon)$$

$$\longrightarrow$$

$$x = x^{*}(y,\varepsilon)$$
$$\dot{y} = \varepsilon g\left(x^{*}(y,\varepsilon),y,\varepsilon\right) = G(y,\varepsilon)$$

Bottom – up

Fenichel theorem (Geometrical Singular Perturbation Theory)

$$\begin{aligned}\frac{dx}{d\tau} &= f(x,y,\varepsilon)\\ \frac{dy}{d\tau} &= g(x,y,\varepsilon)\\ \frac{d\varepsilon}{d\tau} &= 0\end{aligned}$$

$x \in \mathbb{R}^{k_1}$

$y \in \mathbb{R}^{k_2}$

Definition 1 *The invariant manifold* M_0 *(set of equilibria with* $\varepsilon = 0$*) is normally hyperbolic if the linearized system at each point of* M_0 *admits exactly* $k_2 + 1$ *eigenvalues on the imaginary axis.*

Fenichel theorem (Geometrical Singular Perturbation Theory)

$$\frac{dx}{d\tau} = f(x, y, \varepsilon)$$
$$\frac{dy}{d\tau} = g(x, y, \varepsilon)$$
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$x \in \mathbb{R}^{k_1}$

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Theorem 2 *(Fenichel, 1971) : if ε is small enough, there exists an invariant manifold M_1 close and diffeomorph to M_0. Moreover, it is locally invariant by the flow.*

Fenichel theorem (Geometrical Singular Perturbation Theory)

$$\frac{dx}{d\tau} = f(x, y, \varepsilon)$$

$$\frac{dy}{d\tau} = g(x, y, \varepsilon) \qquad x \in \mathbb{R}^{k_1}$$

$$\frac{d\varepsilon}{d\tau} = 0 \qquad y \in \mathbb{R}^{k_2}$$

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Theorem 3 *(Fenichel, 1971) : The dynamics in the vicinity of the invariant manifold is close to the restriction onto the manifold.*

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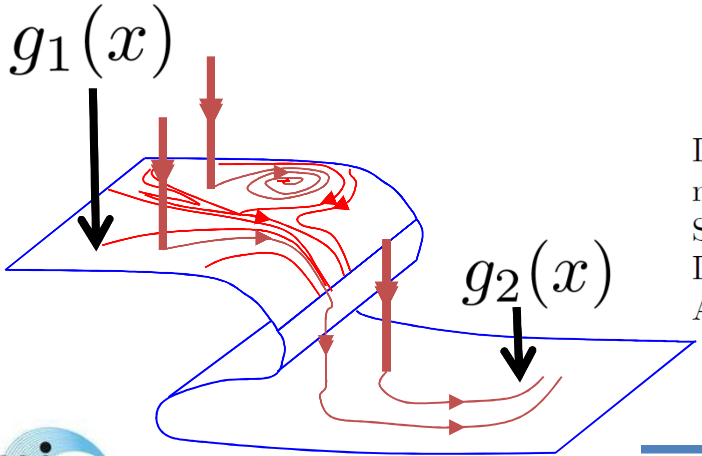

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An example of loss of normal hyperbolicity

Pseudoalteromonas sp.
hbmmd.hboi.edu/ jpegs2/L261.jpg

MICROBIAL ECOLOGY

Microb Ecol (2000) 40:114–124
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Bacterial Growth Rate and Marine Virus–Host Dynamics

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Received: 12 November 1999; Accepted: 2 May 2000; Online Publication: 11 August 2000

Three experiments in a chemostat environment
A realistic simple model (explicit substrate, resistant bacteria)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY A MATHEMATICAL, PHYSICAL & ENGINEERING SCIENCES

Study of a virus–bacteria interaction model in a chemostat: application of geometrical singular perturbation theory

J.-C. Poggiale, P. Auger, F. Cordoleani and T. Nguyen-Huu

Phil. Trans. R. Soc. A 2009 **367**, 4685-4697
doi: 10.1098/rsta.2009.0132

$$\frac{\mathrm{d}s}{\mathrm{d}t} = D(s_0 - s) - \frac{as}{b+s}x,$$

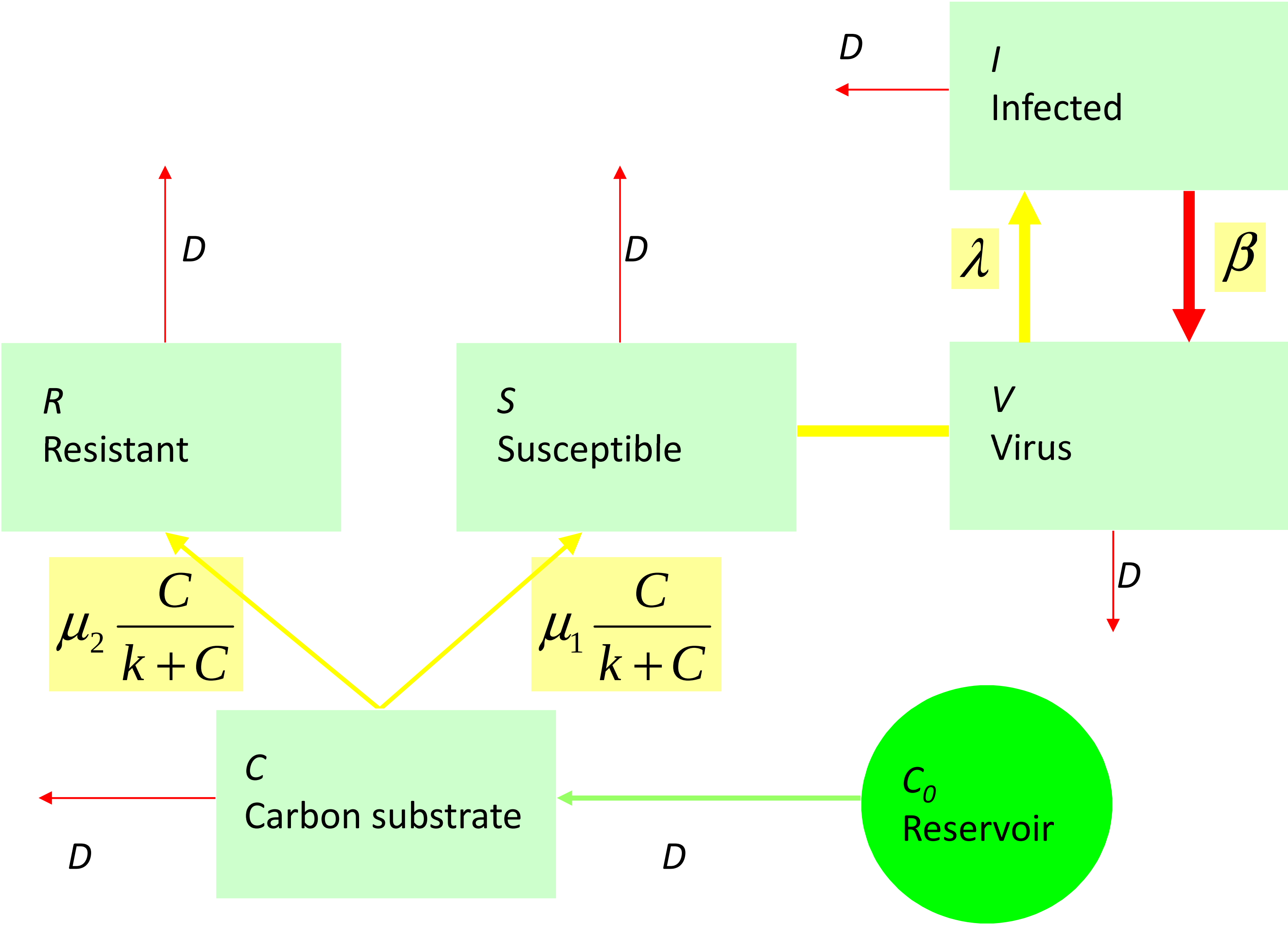
$$\frac{\mathrm{d}x}{\mathrm{d}t} = e\frac{as}{b+s}x - Dx - kxz,$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = kxz - \lambda y - Dy$$

$$\frac{\mathrm{d}z}{\mathrm{d}t} = \delta\lambda y - Dz,$$

An example of loss of normal hyperbolicity

Model description



An example of loss of normal hyperbolicity

Model description

$$\frac{dS}{d\tau} = \left(\mu_1 \frac{C}{K+C} - kV - D\right) S$$
$$\frac{dI}{d\tau} = kSV - \lambda I - DI$$
$$\frac{dV}{d\tau} = \beta\lambda I - DV$$
$$\frac{dC}{d\tau} = D(C_0 - C) - (\mu_1 S + \mu_2 R)\frac{C}{K+C}$$
$$\frac{dR}{d\tau} = \left(\mu_2 \frac{C}{K+C} - D\right) R$$

S = susceptible

I = infected

R = resistant

V = virus

C = carbon substrat

mio Institut Méditerranéen d'Océanologie

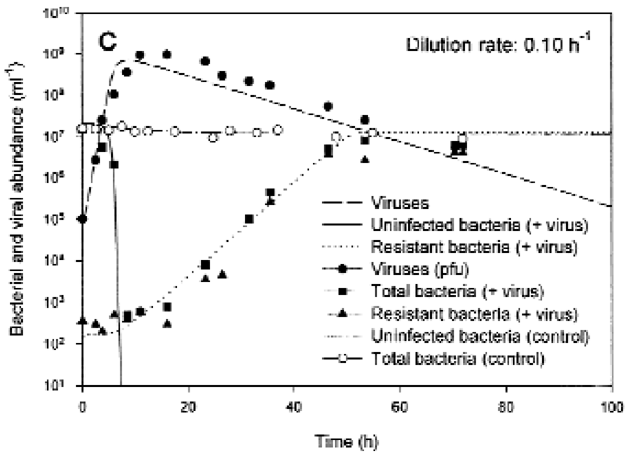
An example of loss of normal hyperbolicity

Model description

$$
\begin{aligned}
\frac{dS}{d\tau} &= \Big(\mu_1 \frac{C}{K+C} - kV - D\Big) S \\
\frac{dI}{d\tau} &= kSV - \lambda I - DI \\
\frac{dV}{d\tau} &= \beta\lambda I - DV \\
\frac{dC}{d\tau} &= D(C_0 - C) - (\mu_1 S + \mu_2 R)\frac{C}{K+C} \\
\frac{dR}{d\tau} &= \Big(\mu_2 \frac{C}{K+C} - D)R
\end{aligned}
$$

S = susceptible
I = infected
R = resistant
V = virus
C = carbon substrat

Variables	Unit
S	10^6 cell/ml
V	10^6 cell/ml
I	10^6 cell/ml
C	10^6 cell/ml
R	10^6 cell/ml



From Middelboe, 2000

Parameters	Units	Values
K	10^6 cells/ml	0.3
C_0	10^6 cells/ml	3
μ_1	1/time	2.5
μ_2	1/time	1 – 4
k	ml/time	0.1
β	virus/lysis	10 – 60
D	1/time	0.2 – 1
λ	1/time	5

Time unit : 10 h

An example of loss of normal hyperbolicity

Model and time scales

$$\frac{dS}{d\tau} = -kVS + \varepsilon\left(\mu_1 \frac{C}{K+C} - D\right)S$$

$$\frac{dV}{d\tau} = \alpha\lambda I - \varepsilon DV$$

$$\frac{dI}{d\tau} = kSV - \gamma I - \varepsilon DI$$

$$\frac{dC}{d\tau} = \varepsilon D(C_0 - C) - \varepsilon(\mu_1 S + \mu_2 R)\frac{C}{K+C}$$

$$\frac{dR}{d\tau} = \varepsilon\left(\mu_2 \frac{C}{K+C} - D\right)R$$

Fast

Slow

$$\varepsilon = \frac{\alpha}{\beta} = \frac{\gamma}{\lambda}$$

$$\varepsilon = 0.02 - 0.1$$

An example of loss of normal hyperbolicity

Model: fast dynamics

$$\frac{dS}{d\tau} = -kVS$$

$$\frac{dV}{d\tau} = \alpha\gamma I$$

$$\frac{dI}{d\tau} = kSV - \gamma I$$

$$H = S + I + \frac{V}{\alpha}$$

$$\frac{dH}{d\tau} = 0$$

$\Rightarrow$ Two fast variables and three slow variables

$$\begin{cases} \dfrac{dS}{d\tau} = -k\alpha(H - S - I)S \\ \dfrac{dI}{d\tau} = kS\alpha(H - S - I) - \gamma I \end{cases}$$

An example of loss of normal hyperbolicity

Model analysis : Slow – Fast formulation

FAST

$$\frac{dS}{d\tau} = -\alpha k S(H - S - I) + \varepsilon\left(\mu_1 \frac{C}{K+C} - D\right)S$$

$$\frac{dI}{d\tau} = \alpha k S(H - S - I) - \gamma I - \varepsilon D I$$

SLOW

$$\frac{dH}{d\tau} = \varepsilon\left(\mu_1 \frac{C}{K+C} S - DH\right)$$

$$\frac{dC}{d\tau} = \varepsilon D(C_0 - C) - \varepsilon(\mu_1 S + \mu_2 R)\frac{C}{K+C}$$

$$\frac{dR}{d\tau} = \varepsilon\left(\mu_2 \frac{C}{K+C} - D\right)R$$

An example of loss of normal hyperbolicity

Model analysis : Fast dynamics

$$\varepsilon = 0$$

$$\frac{dS}{d\tau} = -k\alpha(H - S - I)S$$

$$\frac{dI}{d\tau} = kS\alpha(H - S - I) - \gamma I$$

Equilibria

$$E_1 = (0;0) \quad \forall(H;C;R)$$

$$E_2 = \{(H;0) / S = H\} \quad \forall(H;C;R)$$

An example of loss of normal hyperbolicity

Model analysis : Fast dynamics

$$\varepsilon = 0$$

$$\frac{dS}{d\tau} = -k\alpha(H - S - I)S$$

$$\frac{dI}{d\tau} = kS\alpha(H - S - I) - \gamma I$$

Equilibria

$$E_1 = (0;0) \quad \forall(H;C;R)$$

$$E_2 = \{(H;0) / S = H\} \quad \forall(H;C;R)$$

$$J_{E_1} = \begin{pmatrix} -\alpha kH & 0 \\ \alpha kH & -\gamma \end{pmatrix}$$

$$\text{Eigenvalues: } -\alpha kH \text{ and } -\gamma$$

While *H*>0, E_1 is hyperbolically stable

$$J_{E_2} = \begin{pmatrix} \alpha kH & -\gamma kH \\ -\alpha kH & \gamma kH - \gamma \end{pmatrix}$$

$$Det(J_{E_2}) = -\alpha\gamma kH < 0$$

While *H*>0, E_2 is a saddle point

Model analysis : Slow dynamics (GSP Theory)

The Geometrical Singular Perturbation theory allows to conclude that the previous complete model can be reduced to the following 3D system, under the normal hyperbolicity condition :

$$\frac{dH}{dt} = -DH$$

$$\frac{dC}{dt} = D(C_0 - C) - \mu_2 \frac{C}{K+C} R$$

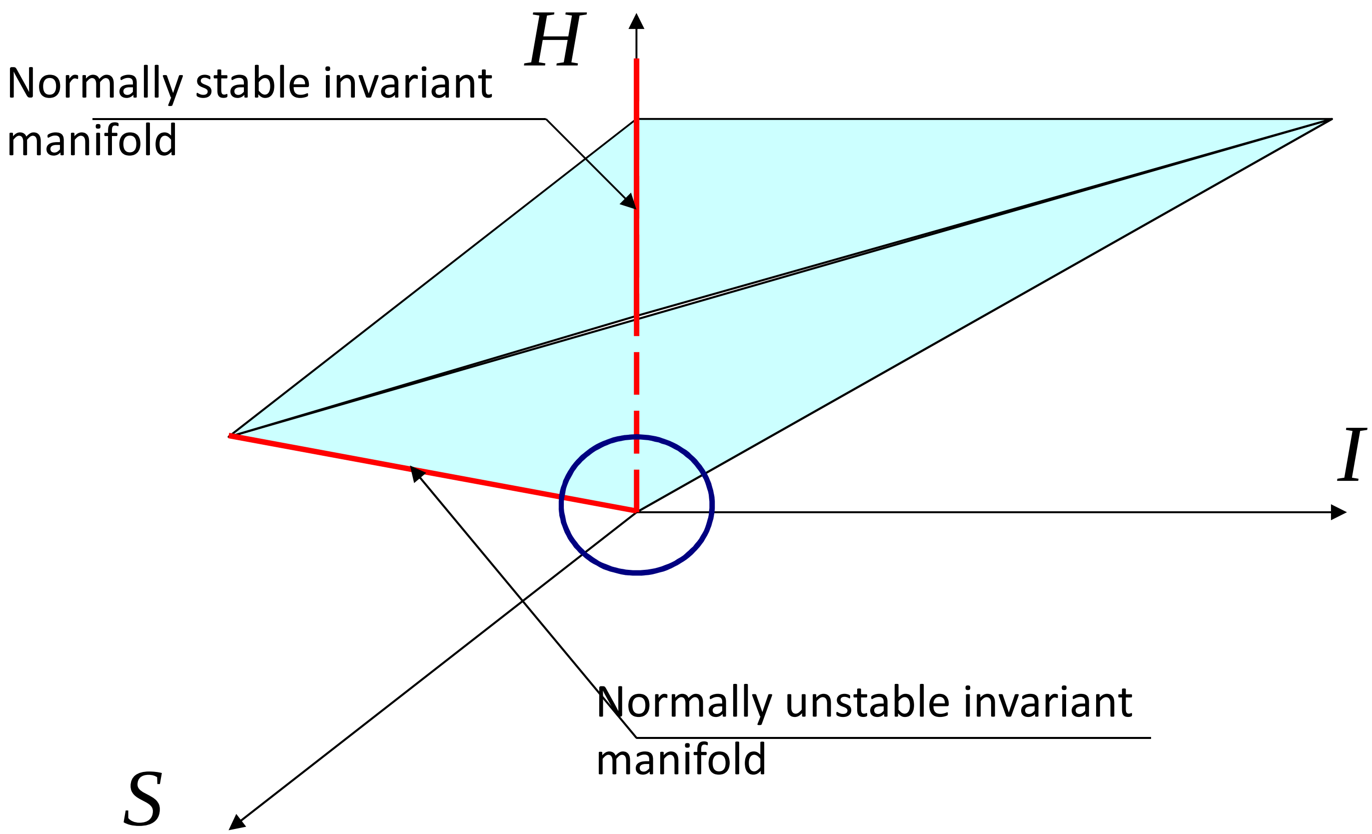
$$\frac{dR}{dt} = \left(\mu_2 \frac{C}{K+C} - D \right) R$$

$$\varepsilon \approx 0$$

$$t = \varepsilon \tau$$

Model analysis : loss of normal hyperbolicity

$$\text{in } \{S, I, H\} \times \{\bar{C}, \bar{R}\}$$



Model analysis : loss of normal hyperbolicity

Rescaling

$$H = \varepsilon h$$
$$S = \varepsilon s$$
$$I = \varepsilon i$$

Fast

$$\frac{di}{d\tau} = \varepsilon \alpha k s(h - s - i) - \gamma i - \varepsilon D i$$

Slow

$$\frac{ds}{d\tau} = -\varepsilon \alpha k s(h - s - i) + \varepsilon\left(\mu_1 \frac{C}{K+C} - D\right)s$$

$$\frac{dh}{d\tau} = \varepsilon\left(\mu_1 \frac{C}{K+C} s - Dh\right)$$

$$\frac{dC}{d\tau} = \varepsilon D(C_0 - C) - \varepsilon \mu_2 R \frac{C}{K+C} + o(\varepsilon)$$

$$\frac{dR}{d\tau} = \varepsilon\left(\mu_2 \frac{C}{K+C} - D\right)R$$

Two ODE's systems

$$C \rightarrow \overline{C} = \frac{KD}{\mu_2 - D}$$

(H. Thieme, 1992)

Model analysis : loss of normal hyperbolicity

$$i \to 0$$

Fast

$$\frac{ds}{dt} = -\alpha ks(h-s) + \left(\mu_1 \frac{\overline{C}}{K+\overline{C}} - D\right)s$$

$$\frac{dh}{dt} = \mu_1 \frac{\overline{C}}{K+\overline{C}} s - Dh$$

$$y = h - s$$

$$\frac{ds}{dt} = \left(\frac{\mu_1}{\mu_2} - 1\right)Ds \; - \; \alpha ksy$$

$$\frac{dy}{dt} = \alpha ksy \; - \; Dy$$

Lotka-Volterra Model

if $\mu_1 > \mu_2$

Model analysis : Invariant manifold expansion

Asymptotic expansion of the invariant manifold with respect to the small parameter :

$$i(s,y,C,R) = \varepsilon w(s,y,C,R) + o(\varepsilon)$$

$$w(s,y,C,R) = \frac{\alpha k}{\gamma} sy$$

$$\frac{ds}{dt} = \left(\frac{\mu_1}{\mu_2} - 1\right) Ds - \alpha ksy + \varepsilon \frac{(\alpha k)^2}{\gamma} s^2 y$$

$$\frac{dy}{dt} = \alpha ksy - Dy + \alpha ksy + \varepsilon \frac{(\alpha k)^2}{\gamma} s^2 y$$

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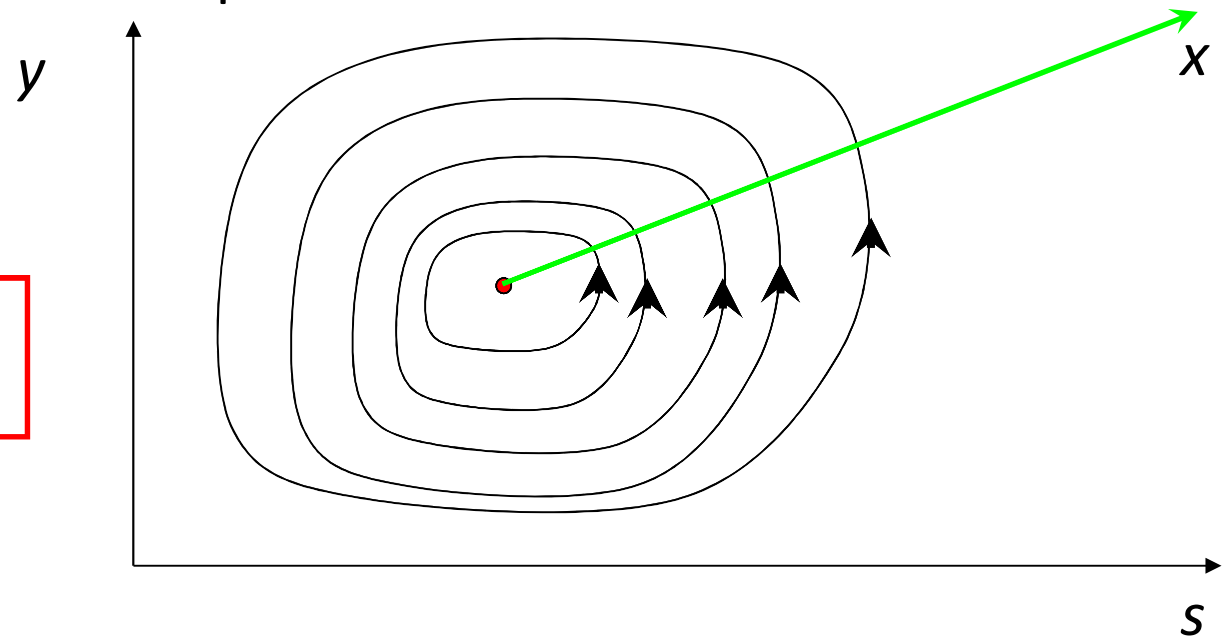
Model analysis : Centre perturbation

Let ω_ε be the duale form of the vector field defined by the previous system:

$$\omega_\varepsilon = dF(s,y) + \varepsilon\eta(s,y)$$

$P_\varepsilon(x)$ Poincaré map

$$\varepsilon = 0$$



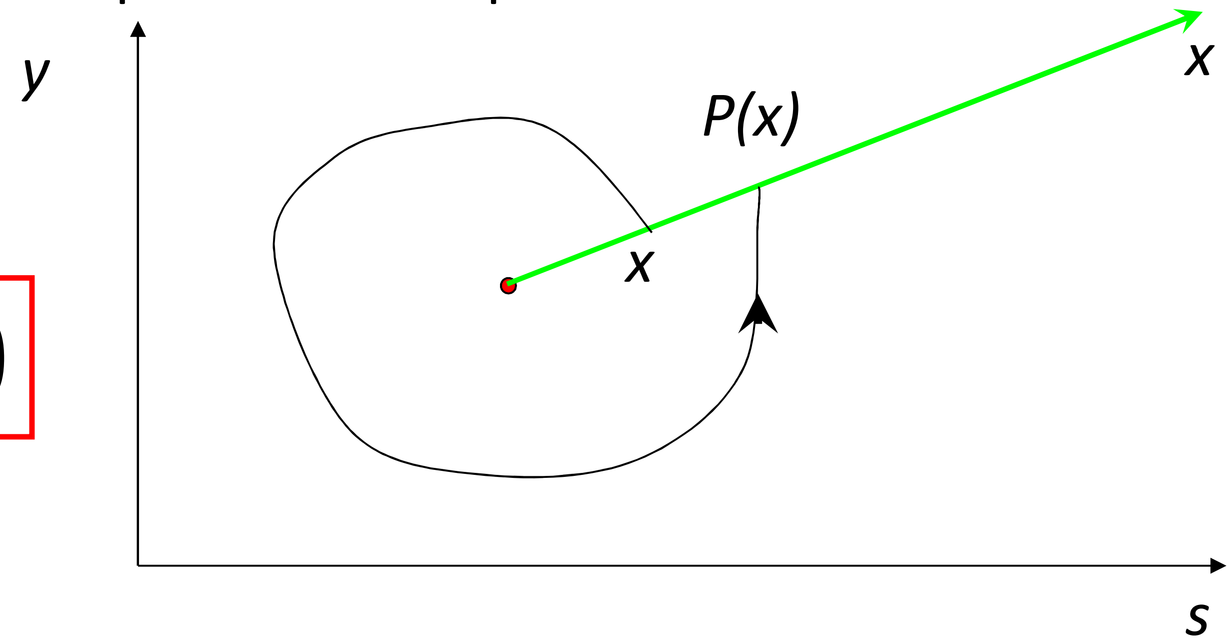
Model analysis : Centre perturbation

Let ω_ε be the duale form of the vector field defined by the previous system:

$$\omega_\varepsilon = dF(s,y) + \varepsilon\eta(s,y)$$

$\Delta_\varepsilon(x) = P_\varepsilon(x) - x$ Displacement map

$$\varepsilon \approx 0$$



An example of loss of normal hyperbolicity

Model analysis : Centre perturbation

Poincaré lemma: $$\Delta(x) = -\varepsilon \int_{\{F=x\}} \eta + o(\varepsilon)$$

Stockes theorem: $$\Delta(x) = -\varepsilon \iint_{\{F\leq x\}} d\eta + o(\varepsilon)$$

Application :

$$\Delta(x) \square\, \varepsilon \iint_{\{F\leq x\}} \left(\frac{(\alpha k)^2}{\gamma} - \frac{A(\lambda)}{y} \right) ds \wedge dy$$

$$\lambda = \left(\frac{\mu_1}{\mu_2}, D, k, \alpha, \gamma \right)$$

Model analysis : Centre perturbation

If $\frac{\mu_1}{\mu_2} < 1$, then $\Delta(x) \leq 0$

If $\frac{\mu_1}{\mu_2} > 1$, then:

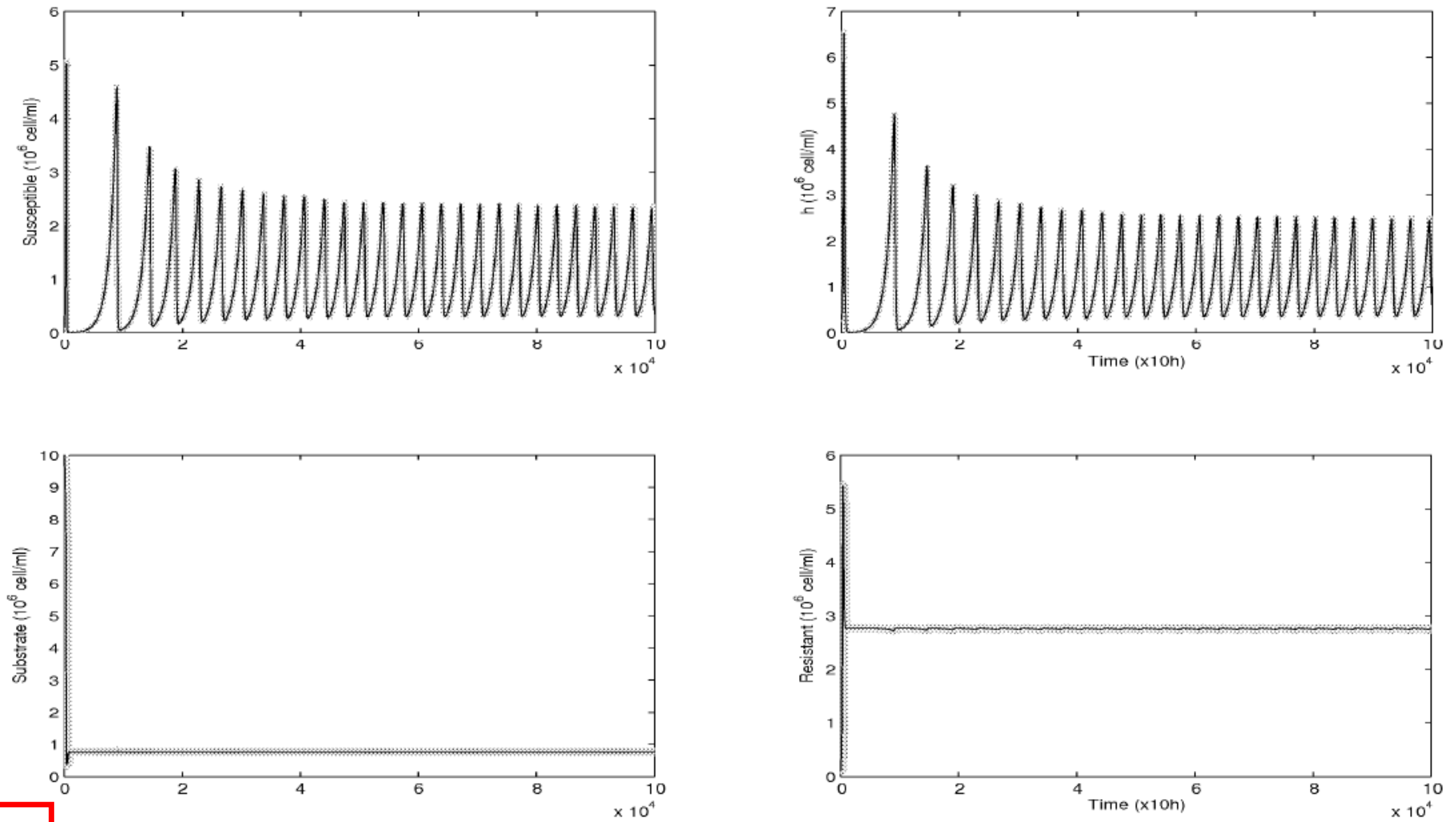
$\Delta(x) > 0$ around the equilibrium

$\Delta(x) < 0$ far from the equilibrium

There exists a limit cycle.

An example of loss of normal hyperbolicity

Numerical simulation



$$\frac{\mu_1}{\mu_2} > 1$$

$$\beta = 60$$

Conclusions (1/2)

•Structure sensitivity : process formulation can matter! In this case, data obtained at each scales are needed (data associated to explicit measures of the process and data associated to the global dynamics on which the process acts)

•Difficulty to get a formulation for a process which integrates different scales : when integrating different time scales, singular perturbations can help. Intuitive methods are based on this framework (e.g. Disc Equation of Holling)

•With this approach, the link between local and global process formulation is explicit and preserved : the global formulation is obtained by a restriction of the complete detailed system on an invariant set in the phase space.

• This allows to understand how detailed mechanisms emerge at the global scale and the feed-back of the global scale dynamics on the detailed mechanisms.

Conclusions (2/2)

•Instead of one function to formulate one process at large scale, several functions can be used.

•Multiple equilibria in the fast dynamics can provide a mechanism for this multiple representation in large scale models.

•Bifurcations of the fast dynamics induced by slow dynamics lead to shifts in the fast variables and can lead to various mathematical expression of the fast equilibrium with respect to slow variables : change of mathematical formulations at large scales

•The jump between the different formulations can be described by the Geometrical Singular Perturbation Theory : follow the trajectories of the full system around the points where normal hyperbolicity is lost («Blow up techniques »)

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