Stoichiometric Modeling and Nonsmooth Dynamics

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in collaboration with
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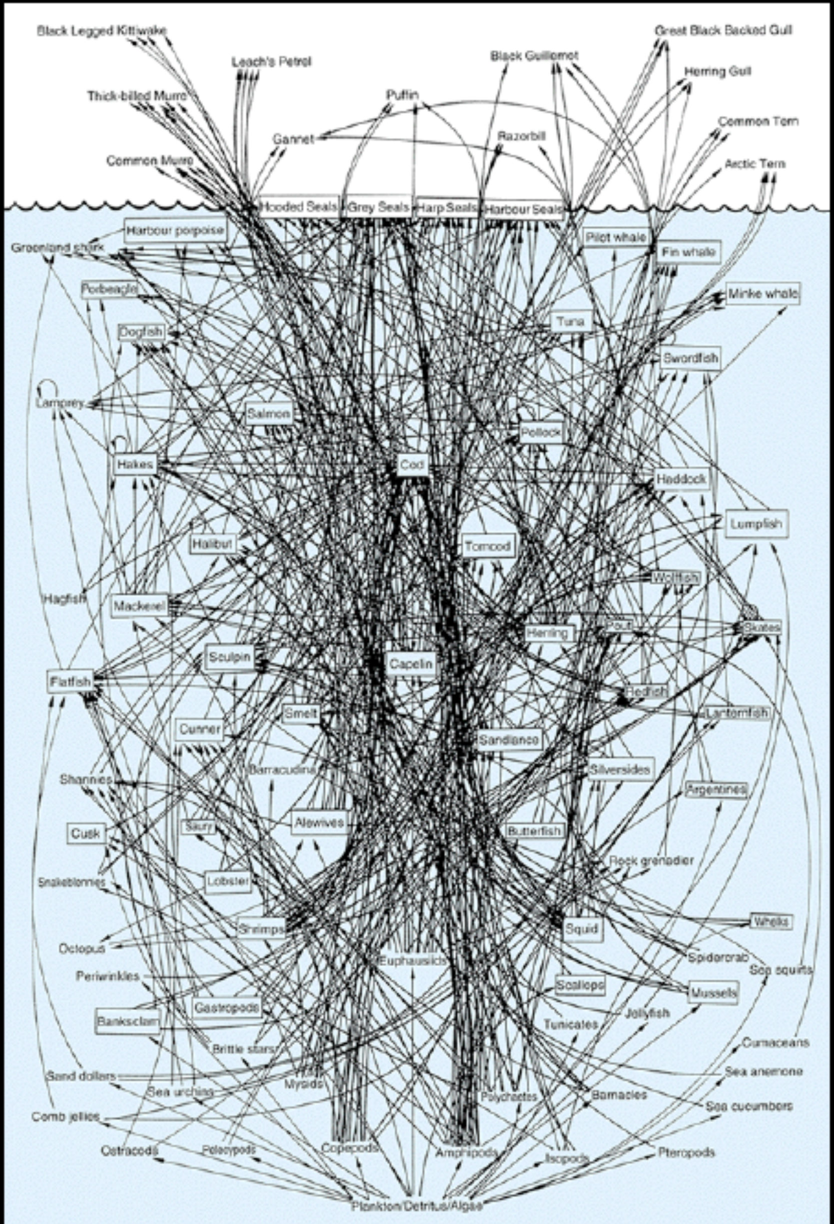
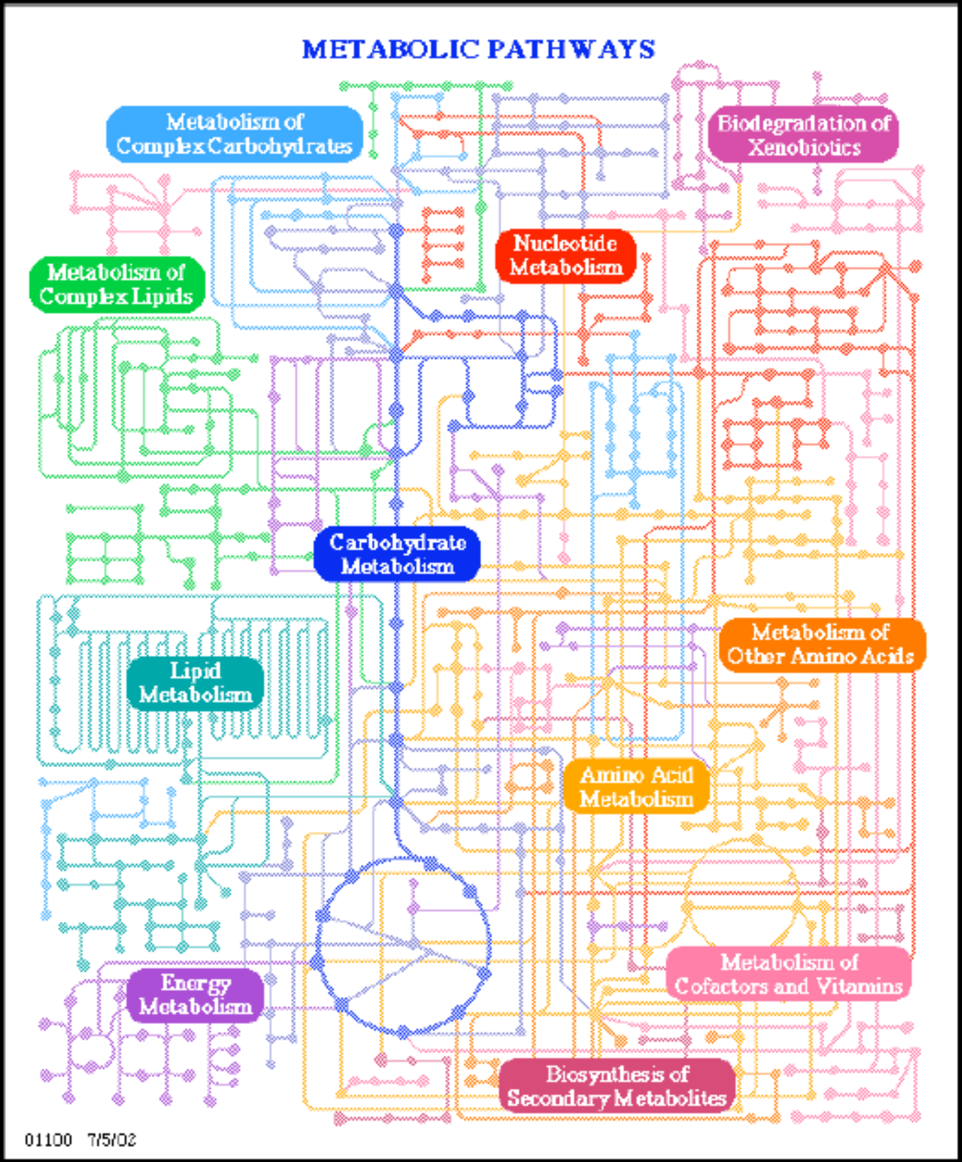
- Introduction of ecological stoichiometry
- LKE model and nonsmooth dynamics
- WKL model with nonsmooth dynamics
- Daphnia competition experiments and modeling
- The “strict homeostasis” hypothesis
- Bacteria-algae models in epilimnion
- Summary



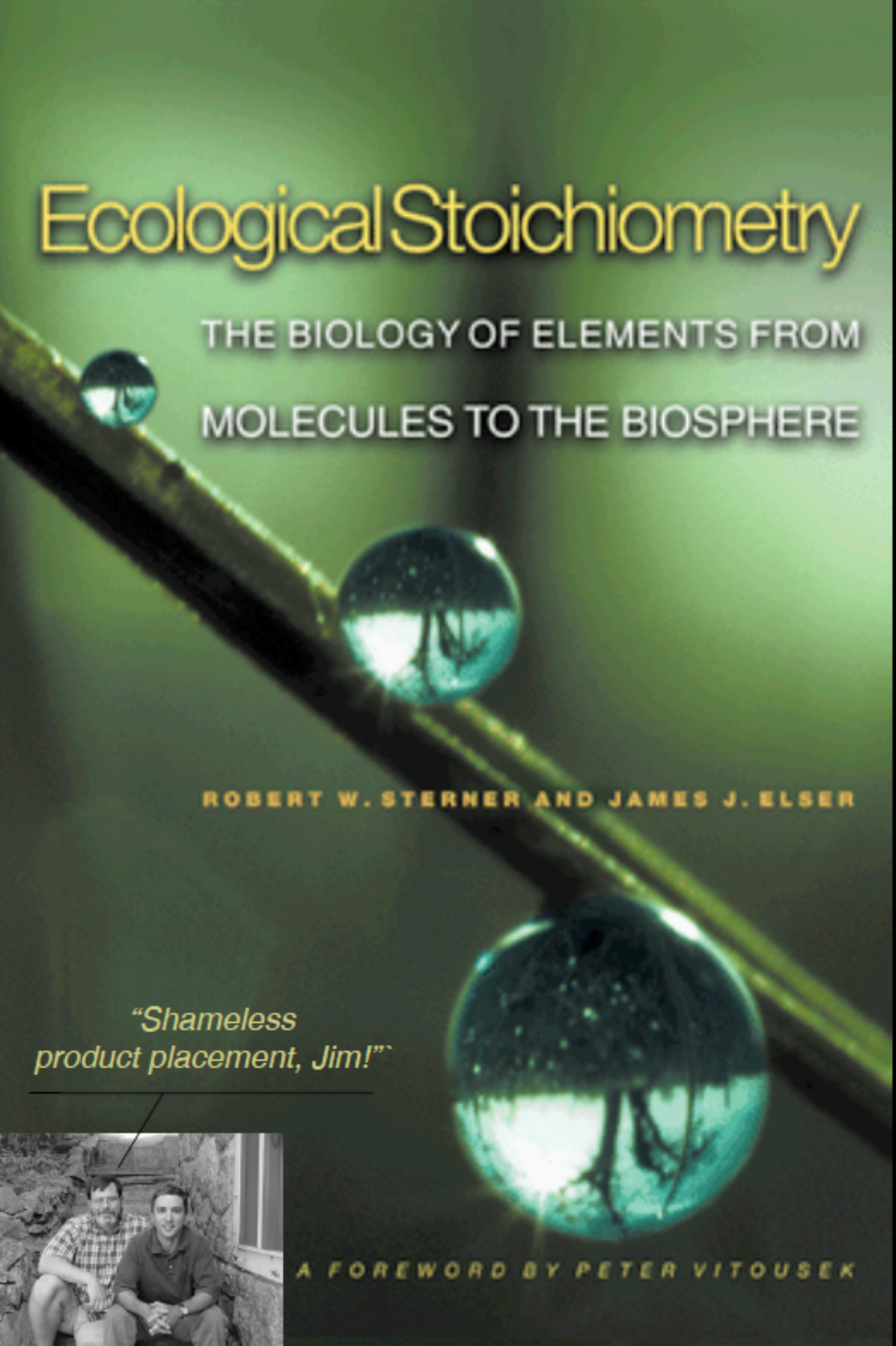
A simplified food web for the Northwest Atlantic



Biology is hard. Really hard.

In fact, it’s kind of like finding a needle...

Perhaps there's a way of making the needle bigger?



Ecological Stoichiometry

THE BIOLOGY OF ELEMENTS FROM MOLECULES TO THE BIOSPHERE

ROBERT W. STERNER AND JAMES J. ELSER

A FOREWORD BY PETER VITOUSEK

"Shameless product placement, Jim!"`

Ecological Stoichiometry

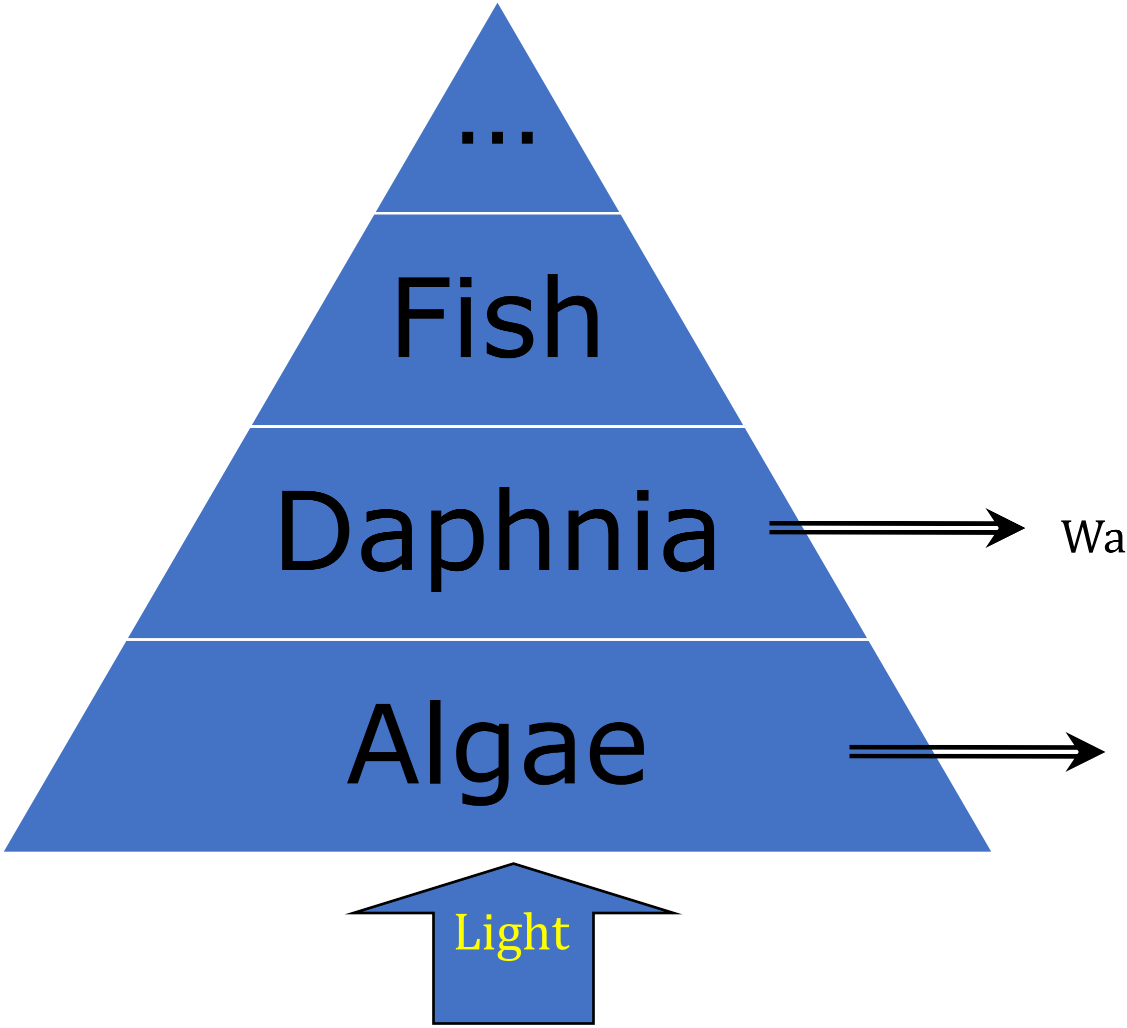
The study of the balance of energy and multiple chemical elements in ecological systems

- e.g. competition, herbivory, mutualism, food webs, biogeochemistry, etc.

Biological Stoichiometry

The study of the balance of energy and multiple chemical elements in biological systems

- e.g. cellular metabolism, growth and development, physiological homeostasis, behavior, evolutionary change, ecology, etc.



...

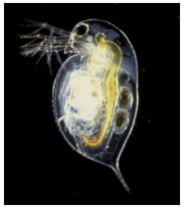
Fish

Daphnia

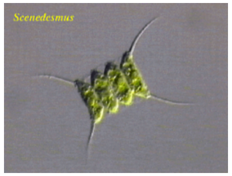
Algae

Light

Water fleas



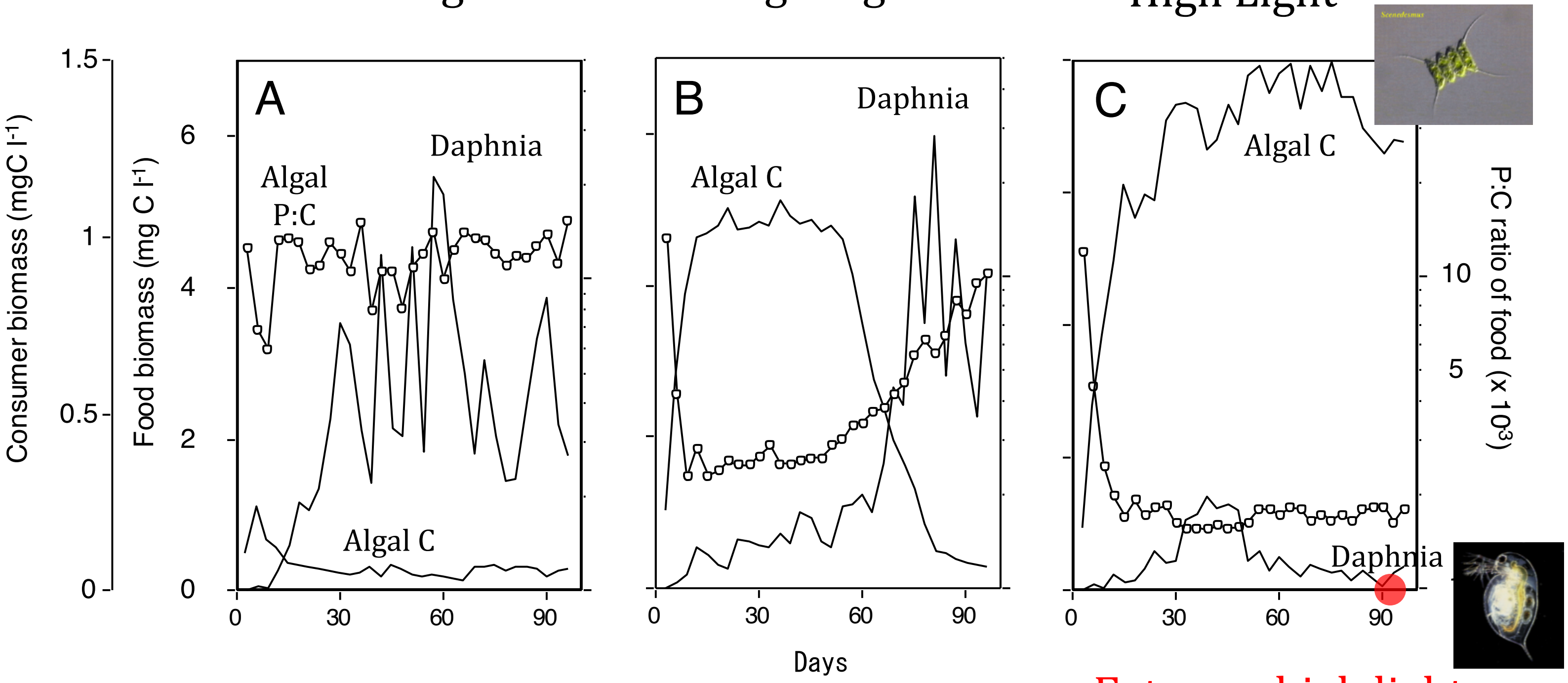
Phytoplankton



Low Light

High Light

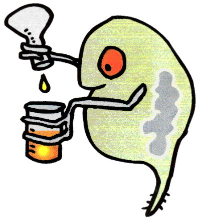
(Extra)
High Light

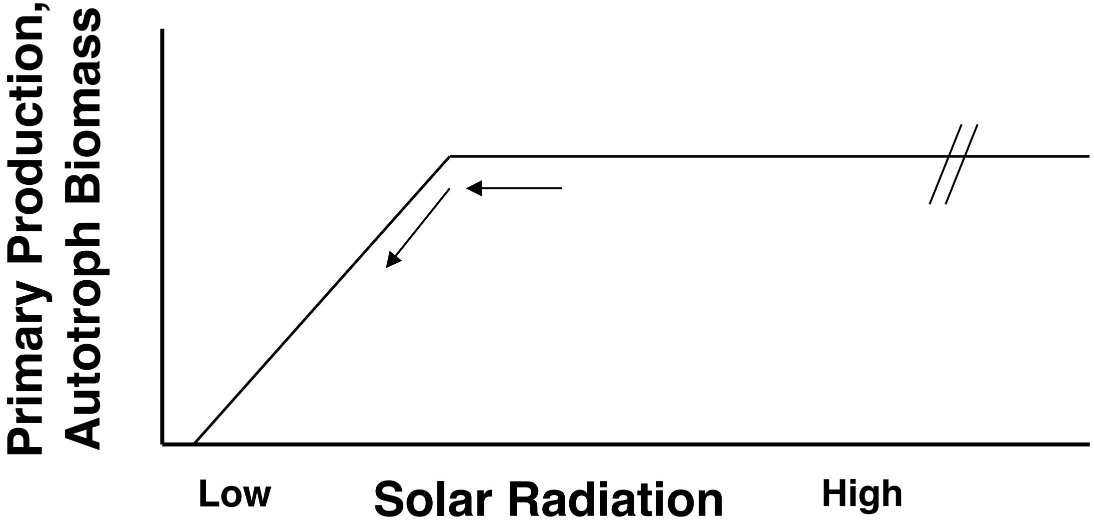


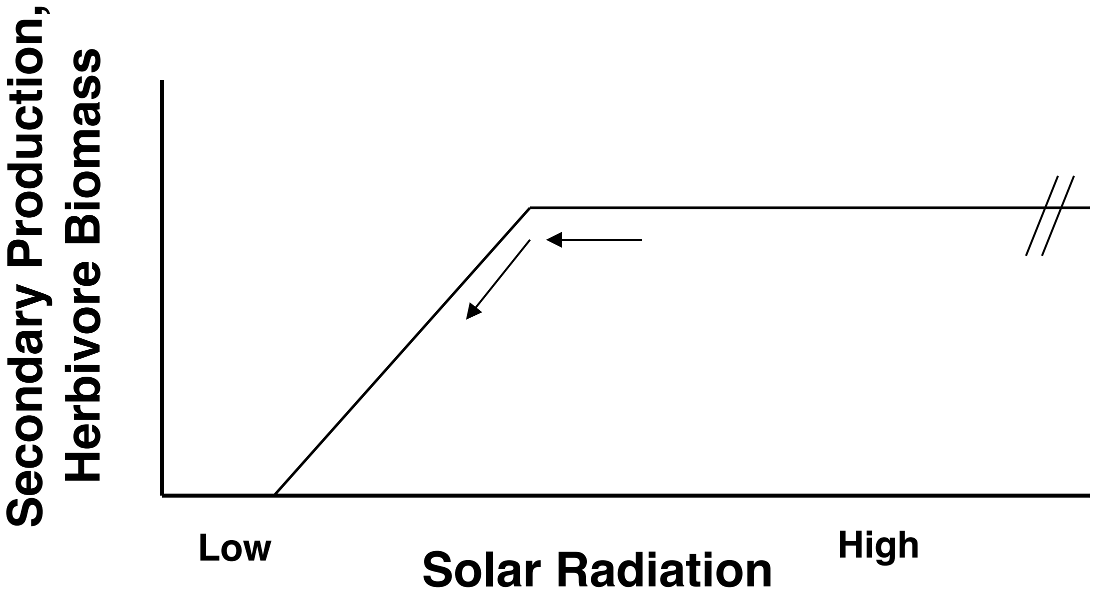
Extreme high light
→Daphnia extinction

What would happen to secondary production if solar radiation was reduced?

Expectations from single-currency ecological theory

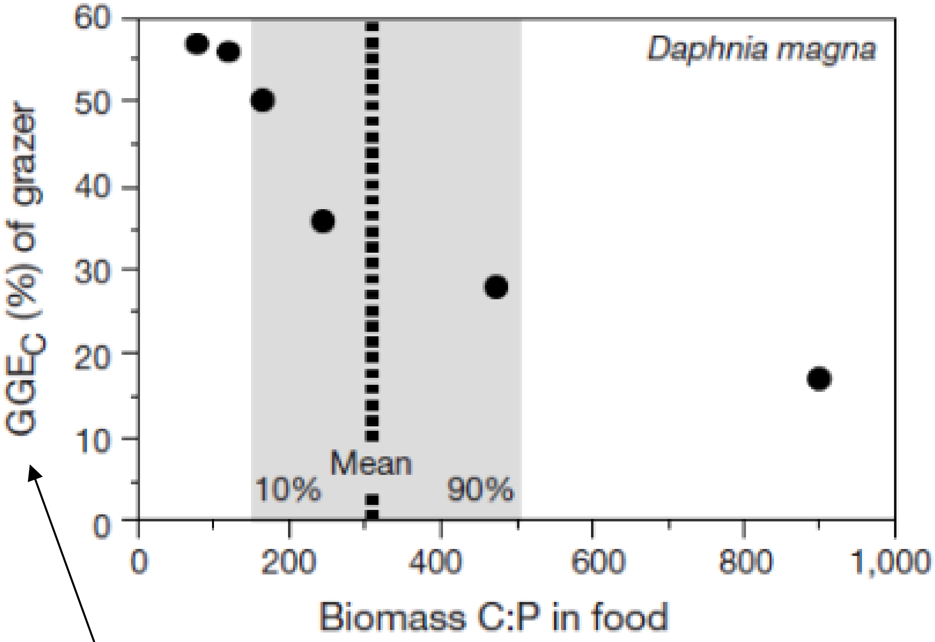




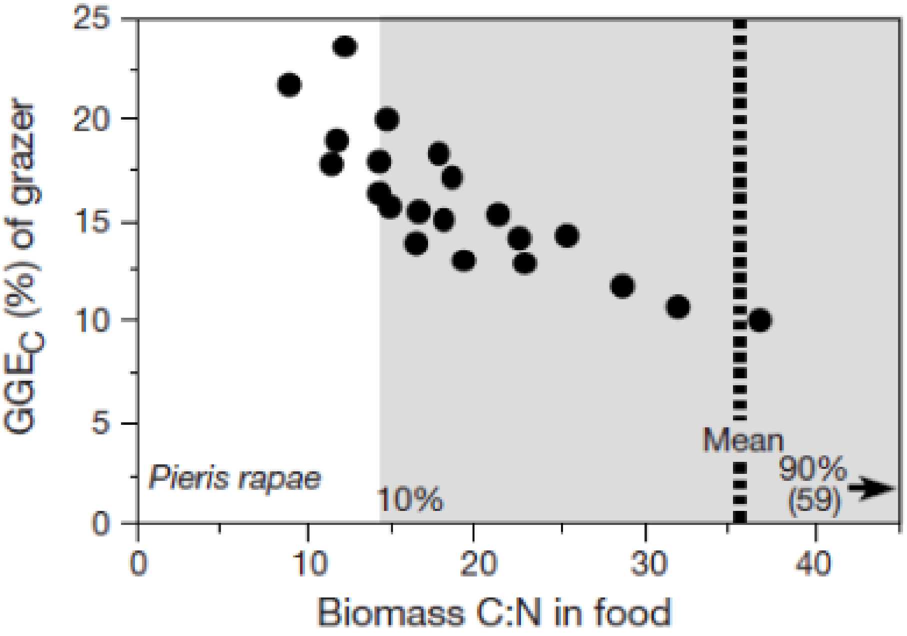


Stoichiometric Imbalance Impairs Herbivores In Freshwater and Terrestrial Ecosystems

Freshwater herbivore (*Daphnia*)

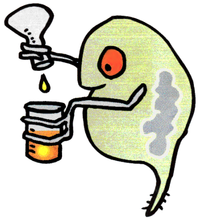


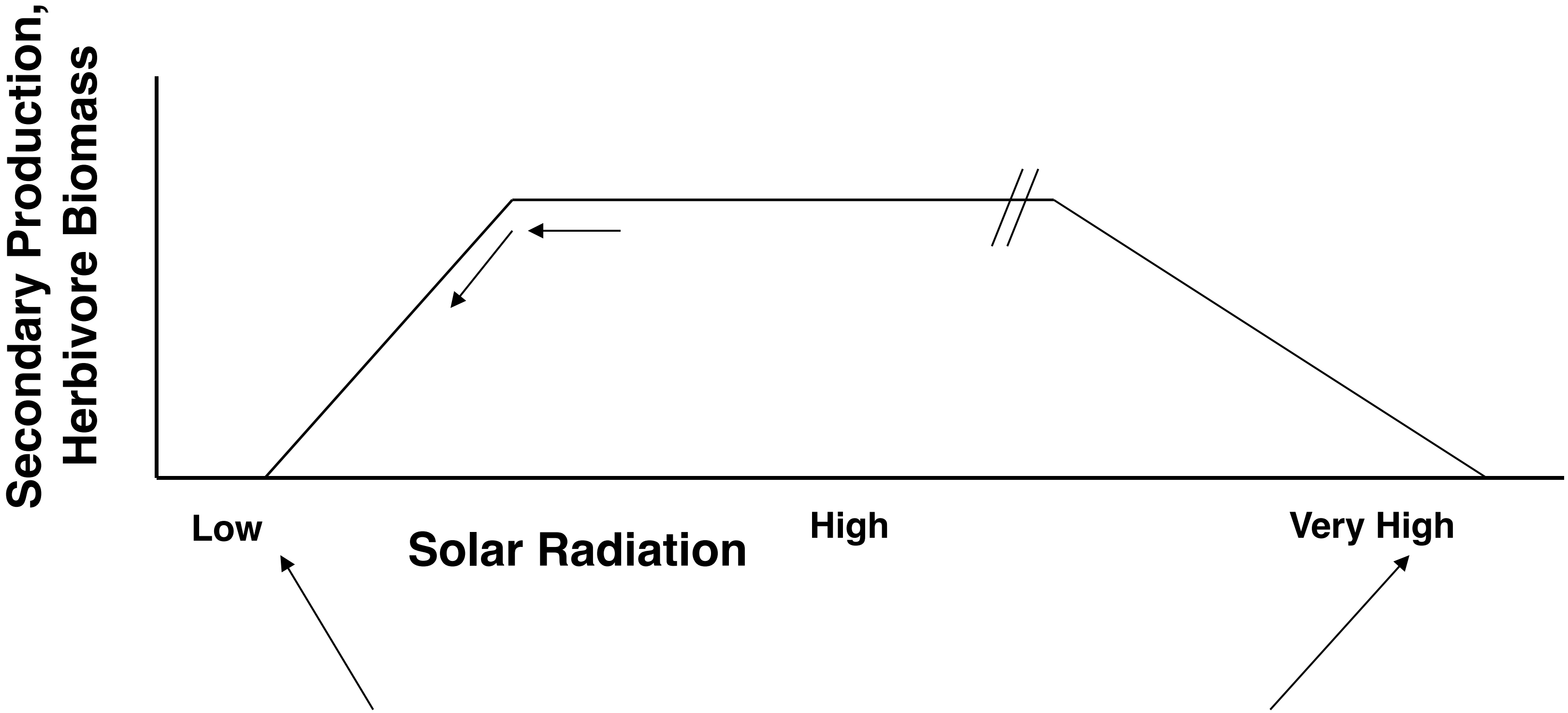
Terrestrial herbivore (*Pieris*)



$$\text{GGE(gross growth efficiency)} = \frac{\text{Mass of New Biomass Produced}}{\text{Mass Ingested}}$$

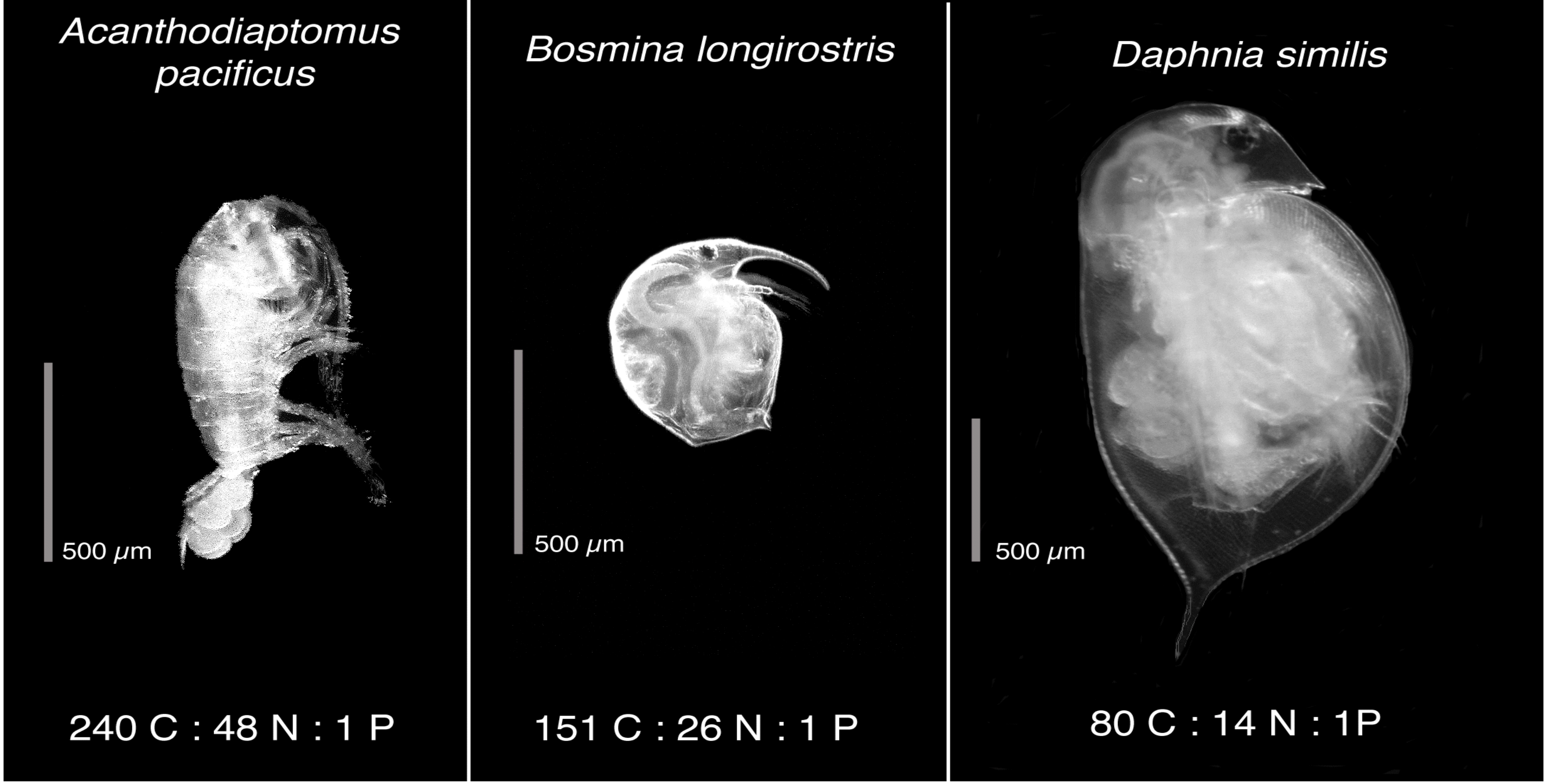
From: Elser, J.J., W.F. Fagan, R.F. Denno, D.R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S.S. Kilham, E. McCauley, K.L. Schulz, E.H. Siemann, and R.W. Sterner. 2000. Nutritional constraints in terrestrial and freshwater food webs. Nature **408**: 578-580.





Starvation

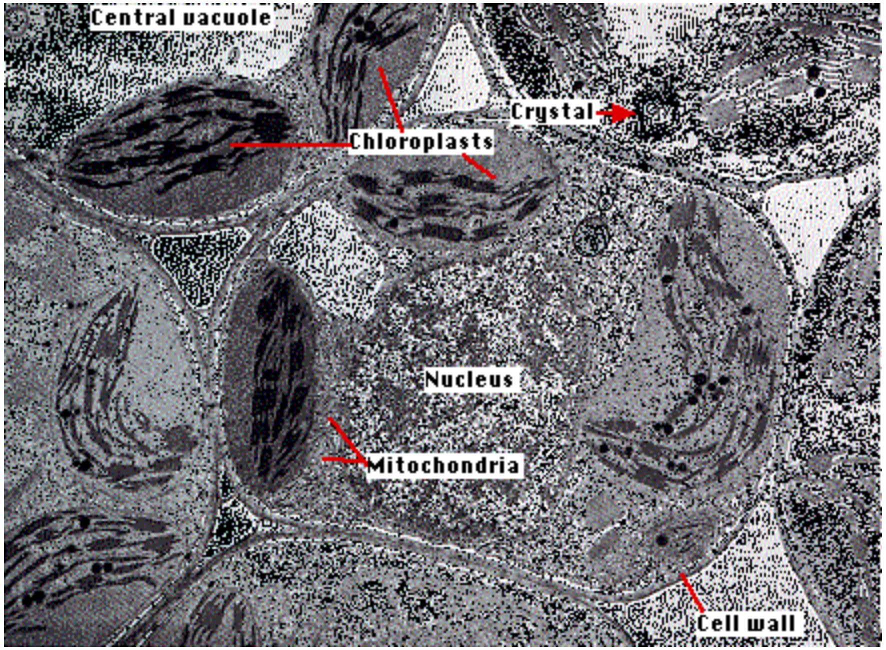
Junk food



$$(C_X N_Y P_Z)_{\text{inorganic}} + (C_X N_Y P_Z)_{\text{autotroph}} + \text{light} \rightarrow Q\,(C_X N_Y P_Z)'_{\text{autotroph}} + (C_X N_Y P_Z)'_{\text{inorganic}}$$

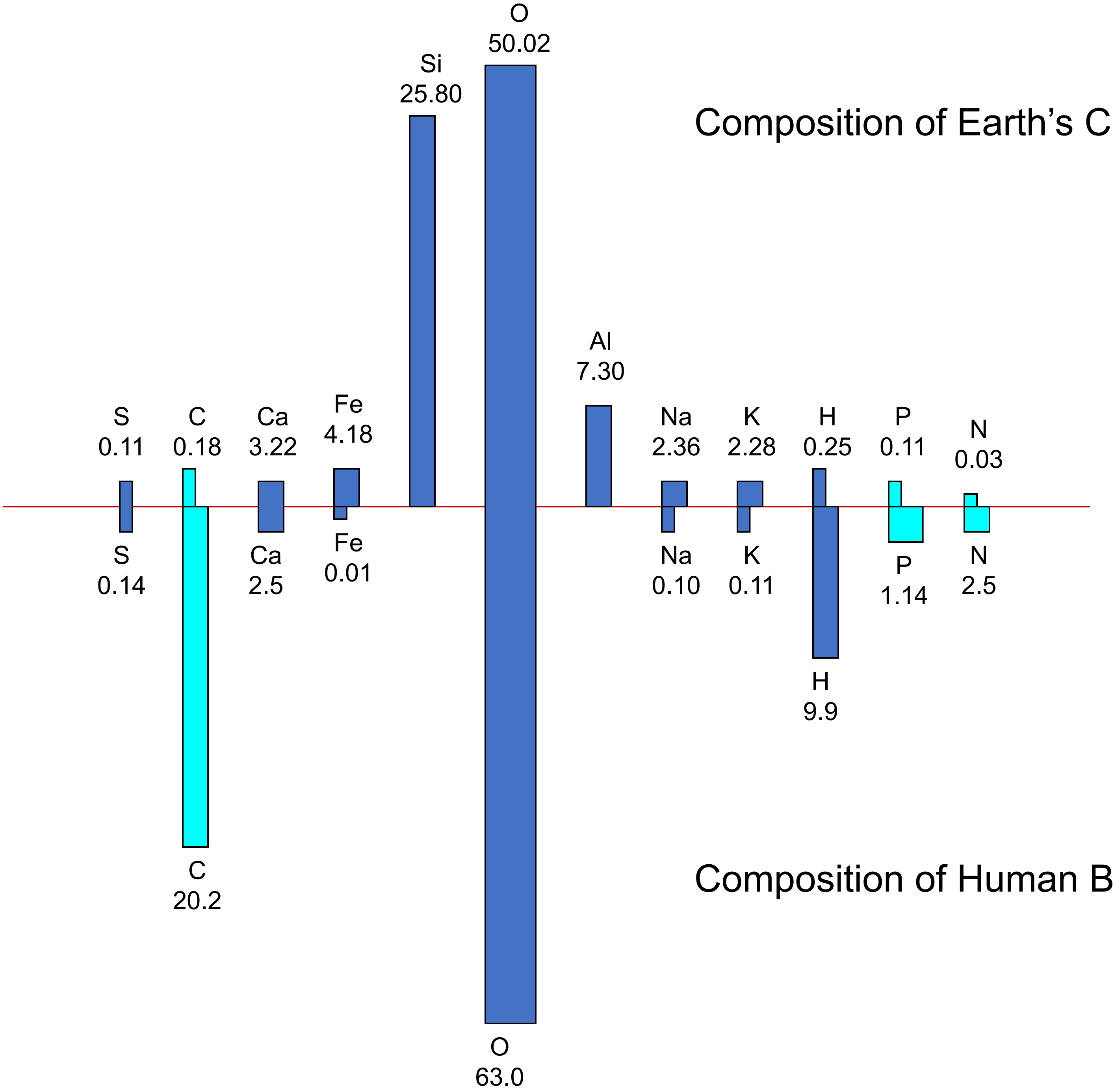
$$(C_X N_Y P_Z)_{\text{prey}} + (C_X N_Y P_Z)_{\text{predator}} \rightarrow Q\,(C_X N_Y P_Z)_{\text{predator}} + (C_X N_Y P_Z)'_{\text{waste}}$$

From: Elser, J.J., and J. Urabe. 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. Ecology **80**: 735-751.



Fundamental Reason: C supplies energy to cells, N is essential to build proteins, P is essential to build nucleic acids (DNA&RNA), … …

However, most predator-prey (=consumer-resource) models only consider the carbon flow (=biomass or population), which cannot explain this experiment.

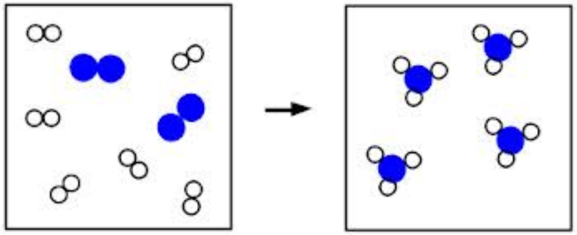


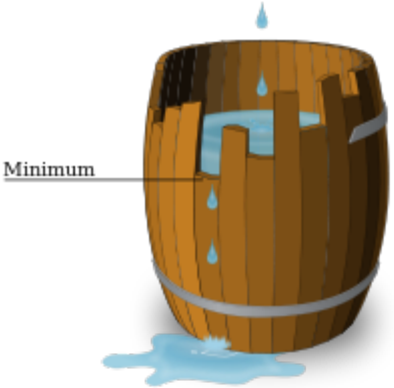
Composition of Earth’s Crust

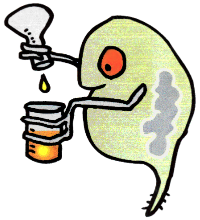
Composition of Human Body

Laws and Hypotheses

- Conservation Law of Matter
- Homeostasis
- Liebig's Minimum Law
- Growth Rate Hypothesis
- Light:Nutrient Hypothesis







Assumptions

- The total mass of phosphorus in the entire system is fixed, denoted by P. (closed P, open C)
- P:C ratio (=cell quota) in algae varies, but it never falls below a minimum q; Daphnia maintains a constant P:C ratio, denoted by θ. (Homeostasis)
- All phosphorus in the system is divided into two pools: phosphorus in daphnia and phosphorus in algae (no phosphorus in media).

LKE Model

$$bx\min\left(1-\frac{x}{K},1-\frac{q}{(P-\theta y)/x}\right)$$

growth limited by the mosting limiting element,
carbon (logistic growth) or phosphorus (Droop model)

Algal population
(measured by carbon)

$$\frac{dx}{dt}=\boxed{bx\left(1-\frac{x}{\min(K,(P-\theta y)/q)}\right)}-f(x)y \tag{1}$$

Daphnia population
(measured by carbon)

$$\frac{dy}{dt}=e\min\left(1,\boxed{\frac{(P-\theta y)/x}{\theta}}\right)f(x)y-dy \tag{2}$$

compare P:C ratio in algae
with P:C ratio in daphnia

Loladze et al. “Stoichiometry in Producer-Grazer Systems: Linking Energy Flow with Element Cycling”, BMB, Vol. 62, pp 1137-1162 (2000).

Li, X., Wang, H. and Kuang, Y., 2011. Global analysis of a stoichiometric producer–grazer model with holling type functional responses. *Journal of mathematical biology*, *63*(5), pp.901-932.

Holling Type I

Basic assumptions for mathematical analysis :

(i) $f(x) = \alpha x$ (Holling type I functional response);

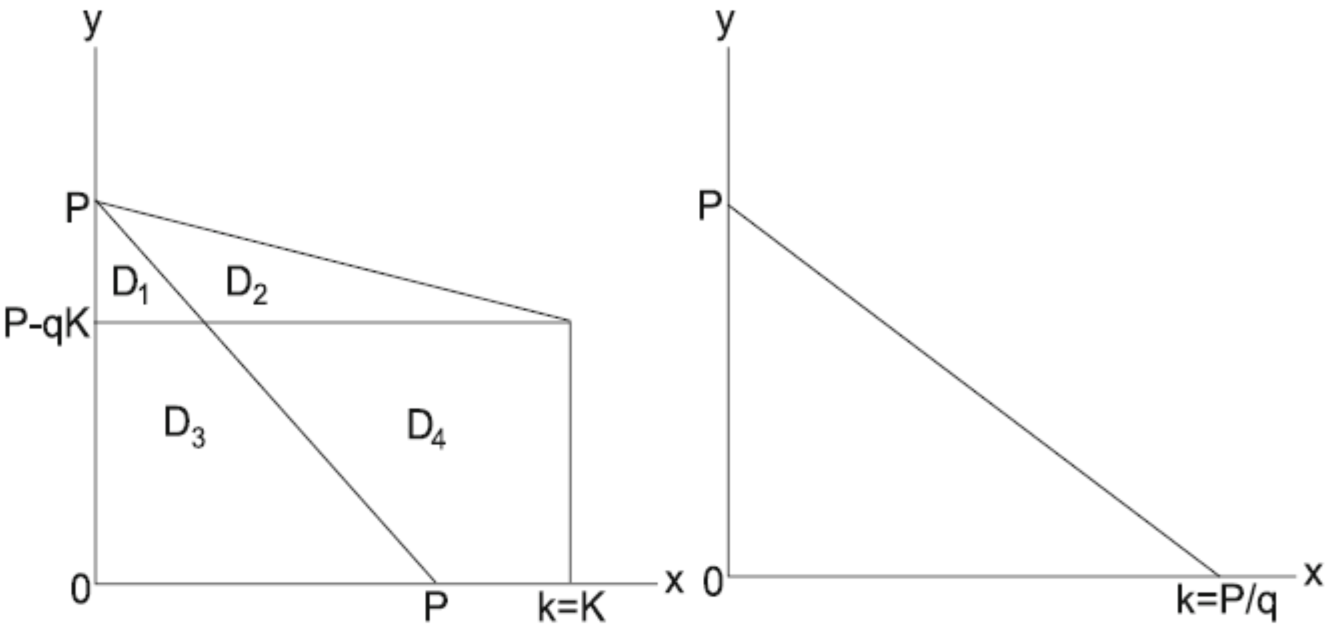
(ii) $q < \theta$ (biologically reasonable for most plants and their corresponding herbivores);

(iii) $e < 1$ (due to thermodynamic limitations).

$$P/\theta \to P, \quad q/\theta \to q, \quad \alpha dt \to dt, \quad b/\alpha \to b, \quad d/\alpha \to d$$

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{\min\{K, (P-y)/q\}}\right) - xy \triangleq xF(x, y), \tag{3}$$

$$\frac{dy}{dt} = e\min\{x, P-y\}\,y - dy \triangleq yG(x, y). \tag{4}$$



(a) The phase space Ω for $k = K$. **(b)** The phase space Ω for $k = P/q$.

Fig. 1 When $k = K$, Ω is an *open trapezoid*, while when $k = P/q$, Ω is an *open triangle*

$$k = \min\{K, P/q\} = \begin{cases} K, & K < P/q; \\ P/q, & K \geq P/q, \end{cases}$$

$$\Omega = \{(x, y) : 0 < x < k, 0 < y < P, qx + y < P\}.$$

$$D_1 = \{(x, y) \in \Omega : y > P - qK, x + y < P\},$$

$$D_2 = \{(x, y) \in \Omega : y > P - qK, x + y > P\},$$

$$D_3 = \{(x, y) \in \Omega : y < P - qK, x + y < P\},$$

$$D_4 = \{(x, y) \in \Omega : y < P - qK, x + y > P\}.$$

Theorem 1 (Dissipativity) Ω *is positively invariant for the semiflow generated by system* (3)–(4).

Theorem 2 *System* (3)–(4) *has no nontrivial periodic solutions in* Ω.

x**-nullcline**: $x = 0$ and $F(x, y) = 0$, where $F(x, y) = 0$ implies

$$y = (1/2)\left[b + P - \sqrt{(b - P)^2 + 4bqx}\right] \triangleq g(x).$$

y**-nullcline**: $y = 0$ and $G(x, y) = 0$.

$$J(x, y) = \begin{pmatrix} F(x, y) + xF_x(x, y) & xF_y(x, y) \\ yG_x(x, y) & G(x, y) + yG_y(x, y) \end{pmatrix}.$$

Fig. 2 The nullclines and equilibria for $K \geq P/q$ and $b < P$

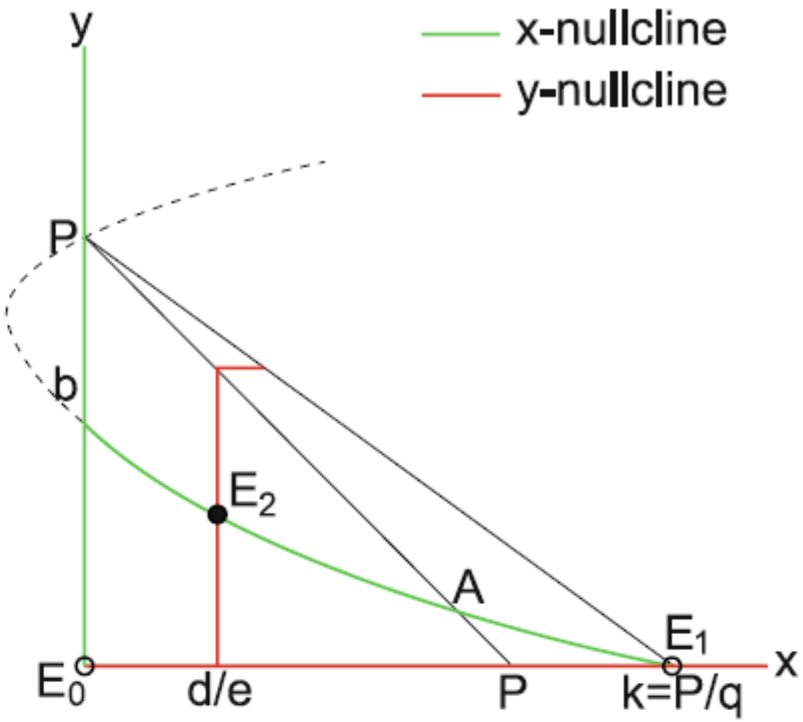


Fig. 3 The nullclines and equilibria for $K \geq P/q$ and $P \leq b < P/(1-q)$

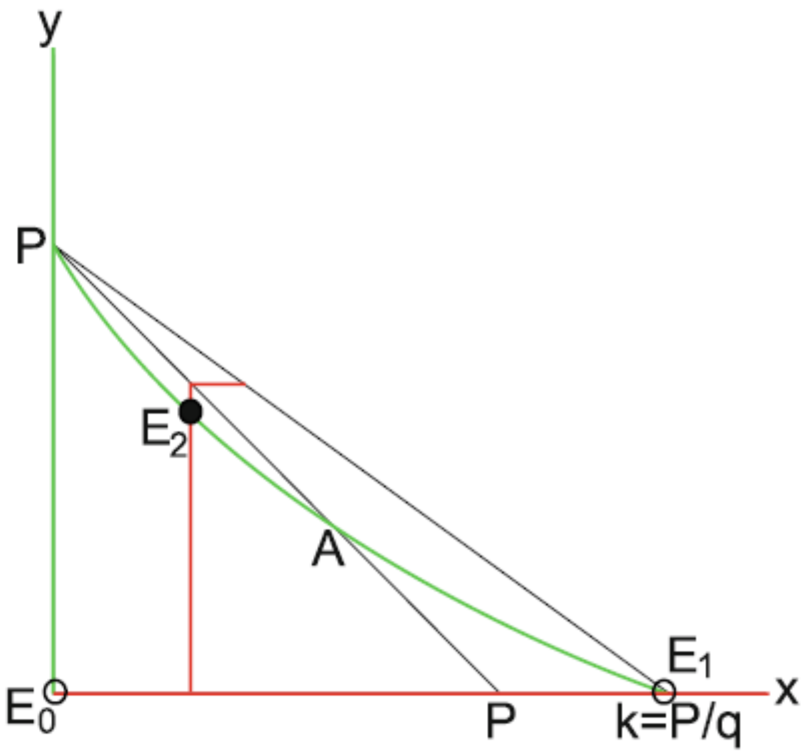


Fig. 4 The nullclines and equilibria for $K \geq P/q$ and $b \geq P/(1-q)$

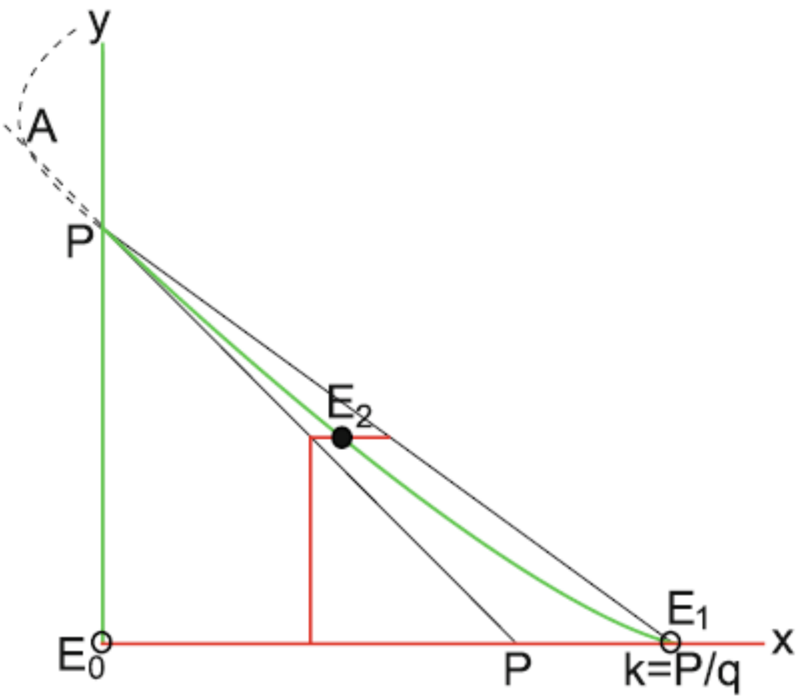


Fig. 5 The nullclines and equilibria for $P \le K < P/q$ and $P - qK < b < (P - qK)/(1 - q)$

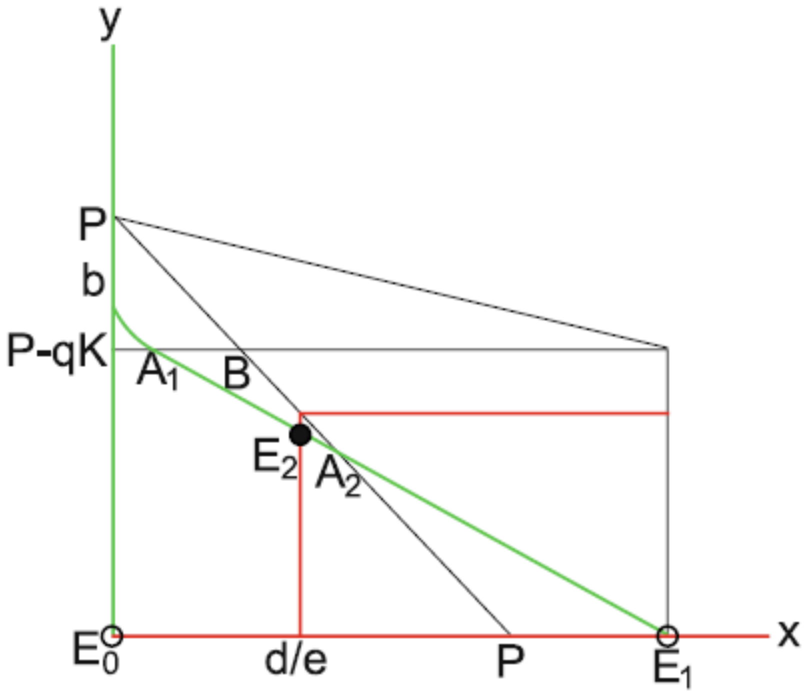


Fig. 6 The nullclines and equilibria for $P \leq K < P/q$ and $0 < b \leq P - qK$

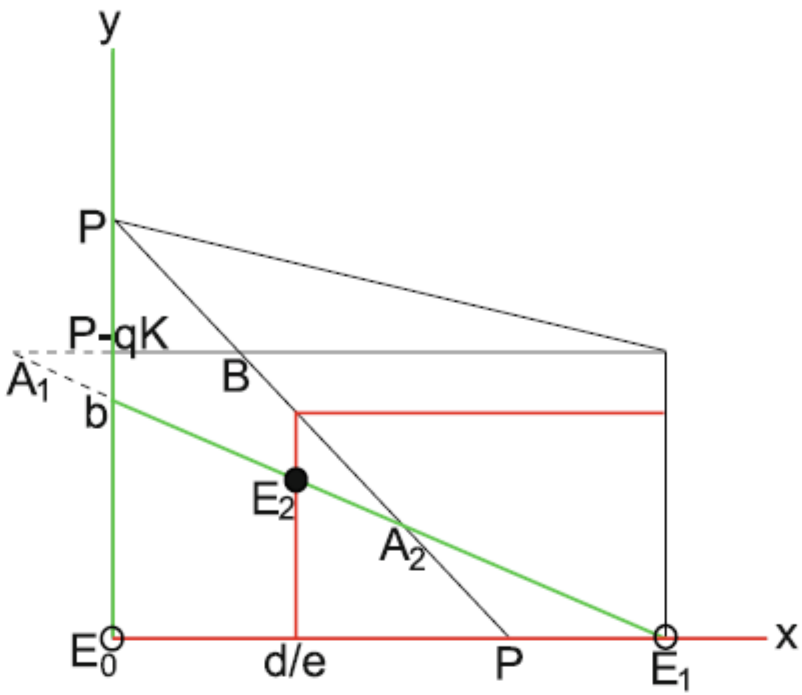


Fig. 7 The nullclines and equilibria for $P \leq K < P/q$ and $(P - qK)/(1 - q) \leq b < P/(1 - q)$

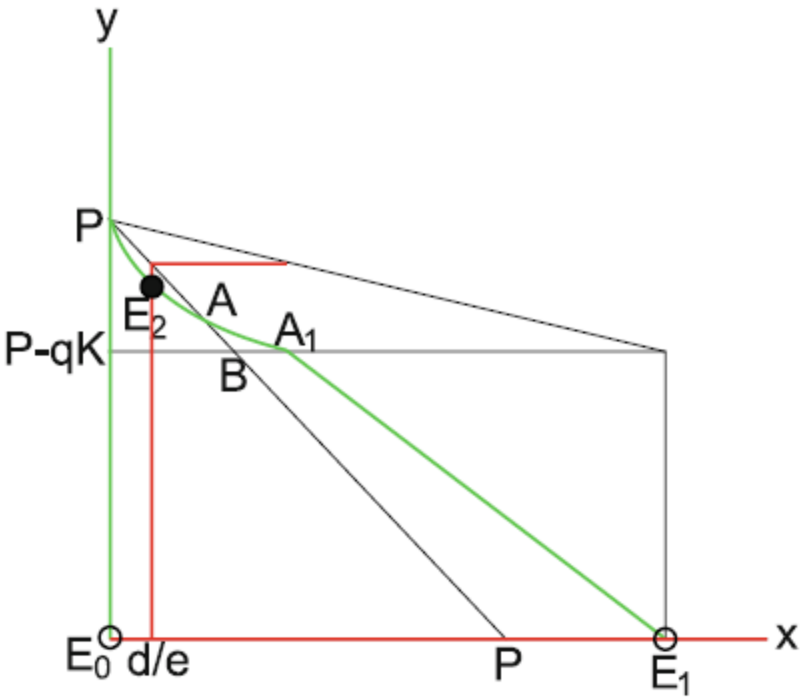
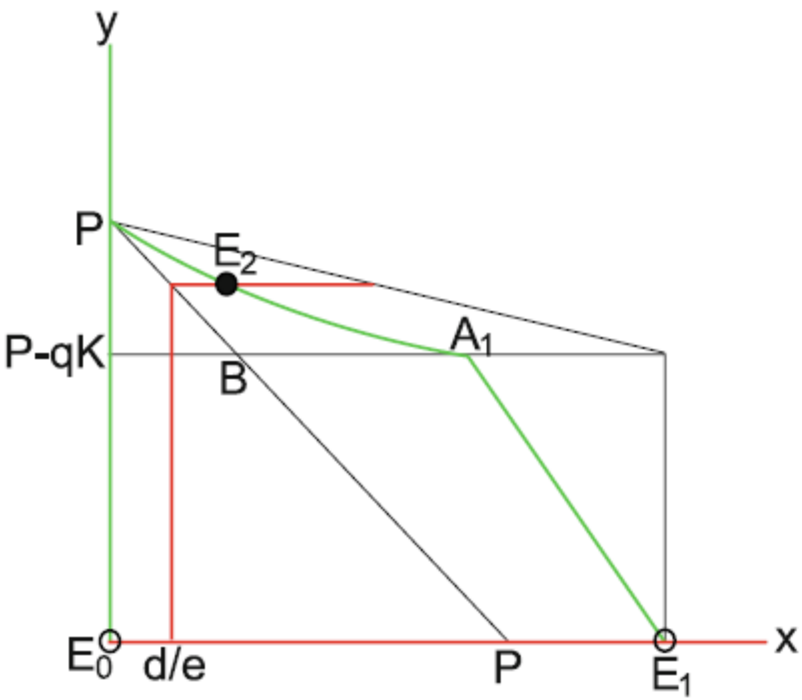
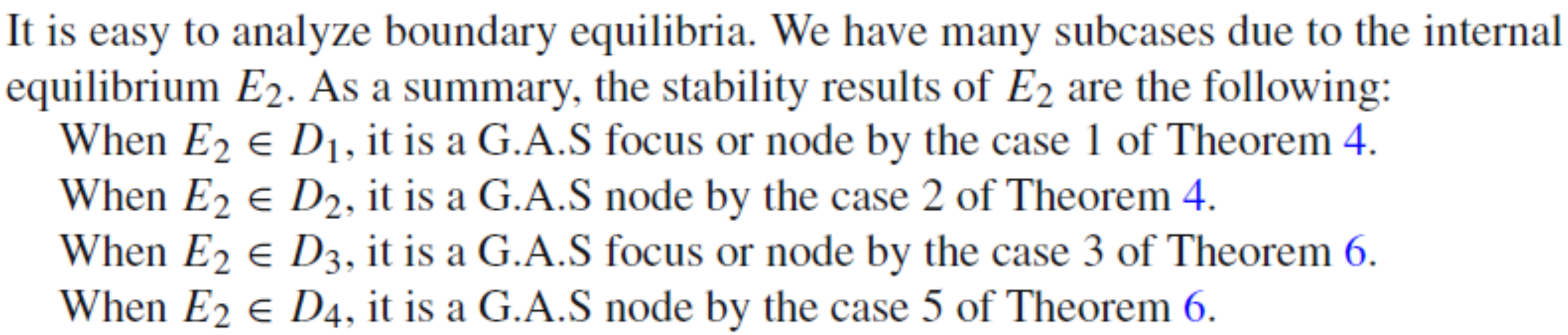


Fig. 8 The nullclines and equilibria for $P \leq K < P/q$ and $b \geq P/(1-q)$



The case $K<P$ is similar, skip figures.

Theorem 3-Theorem 13 present all global stability results of all equilibrium points of the system with Holling type I functional response.



It is easy to analyze boundary equilibria. We have many subcases due to the internal equilibrium E_2. As a summary, the stability results of E_2 are the following:

When $E_2 \in D_1$, it is a G.A.S focus or node by the case 1 of Theorem 4.

When $E_2 \in D_2$, it is a G.A.S node by the case 2 of Theorem 4.

When $E_2 \in D_3$, it is a G.A.S focus or node by the case 3 of Theorem 6.

When $E_2 \in D_4$, it is a G.A.S node by the case 5 of Theorem 6.

Holling Type II

$$f(x) = \frac{cx}{a+x}$$

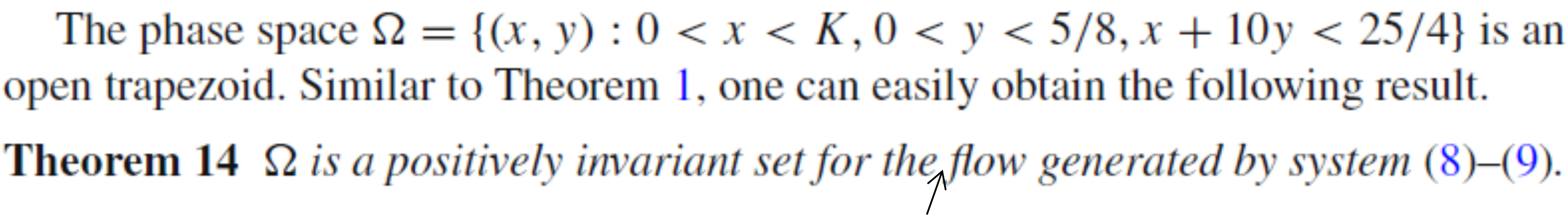
We fix all parameters (except K) with realistic values:

$P = 0.025$, $e = 0.8$, $b = 1.2$, $d = 0.25$, $\theta = 0.04$, $q = 0.004$, $c = 0.8$, $a = 0.25$;

K has the range 0 - 2.0.

$$\frac{dx}{dt} = \frac{6}{5}x\left(1 - \frac{x}{\min\{K, \frac{25}{4} - 10y\}}\right) - \frac{16xy}{5+20x}, \tag{8}$$

$$\frac{dy}{dt} = \frac{4}{5}\min\left\{x, \frac{5}{8} - y\right\}\frac{16y}{5+20x} - \frac{1}{4}y. \tag{9}$$

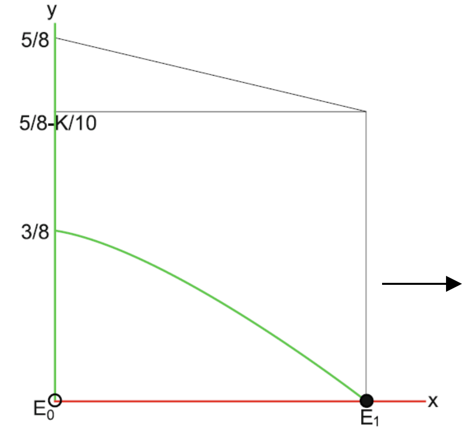


The phase space $\Omega = \{(x, y) : 0 < x < K, 0 < y < 5/8, x + 10y < 25/4\}$ is an open trapezoid. Similar to Theorem 1, one can easily obtain the following result.

Theorem 14 *Ω is a positively invariant set for the flow generated by system* (8)–(9).

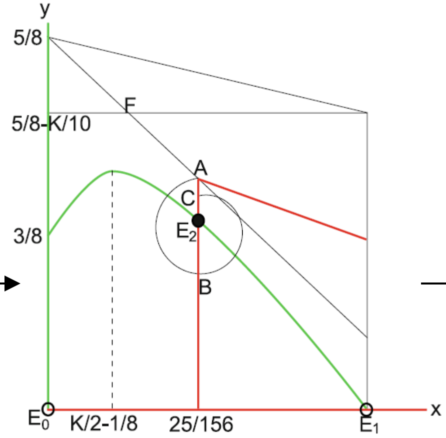
semi

Now we start to perform global and bifurcation analysis according to the varying parameter *K* (representing the light intensity).



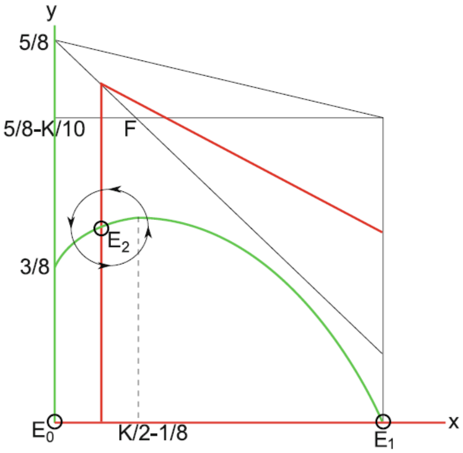
The nullclines and equilibria for $0 < K \le 25/156$

light



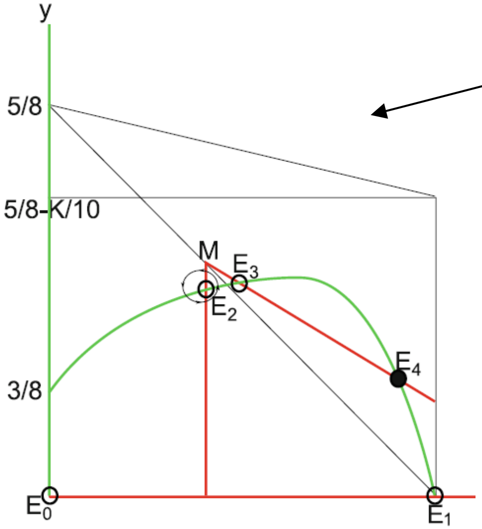
The nullclines and equilibria for $25/156 < K < 89/156$

light

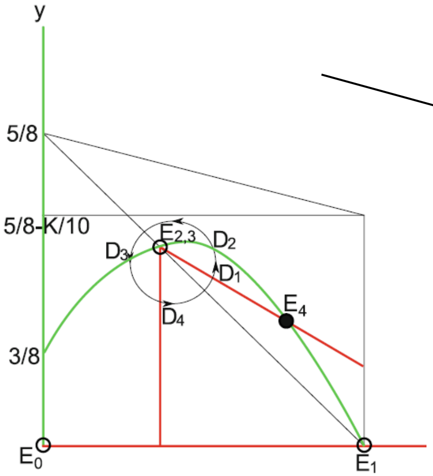


The nullclines and equilibria for $89/156 < K < 0.585185$

light



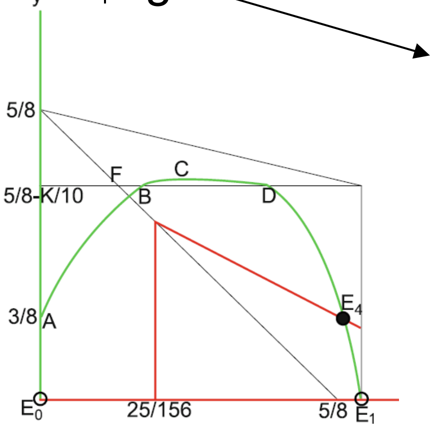
The nullclines and equilibria for $0.585185 < K < 0.654664$



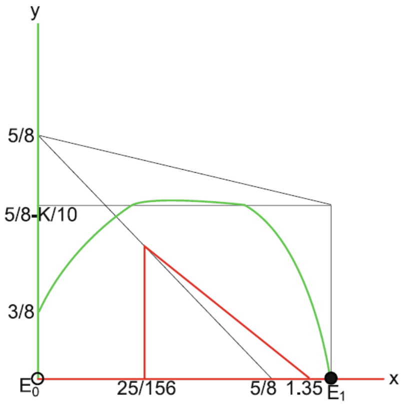
The nullclines and equilibria for $K = 0.654664$

(no limit cycle, the one plotted is only for proof)

light



The nullclines and equilibria for $0.654664 < K < 1.35$



The nullclines and equilibria for $1.35 < K < 2$

Case 1. $0 < K \leq 25/156$

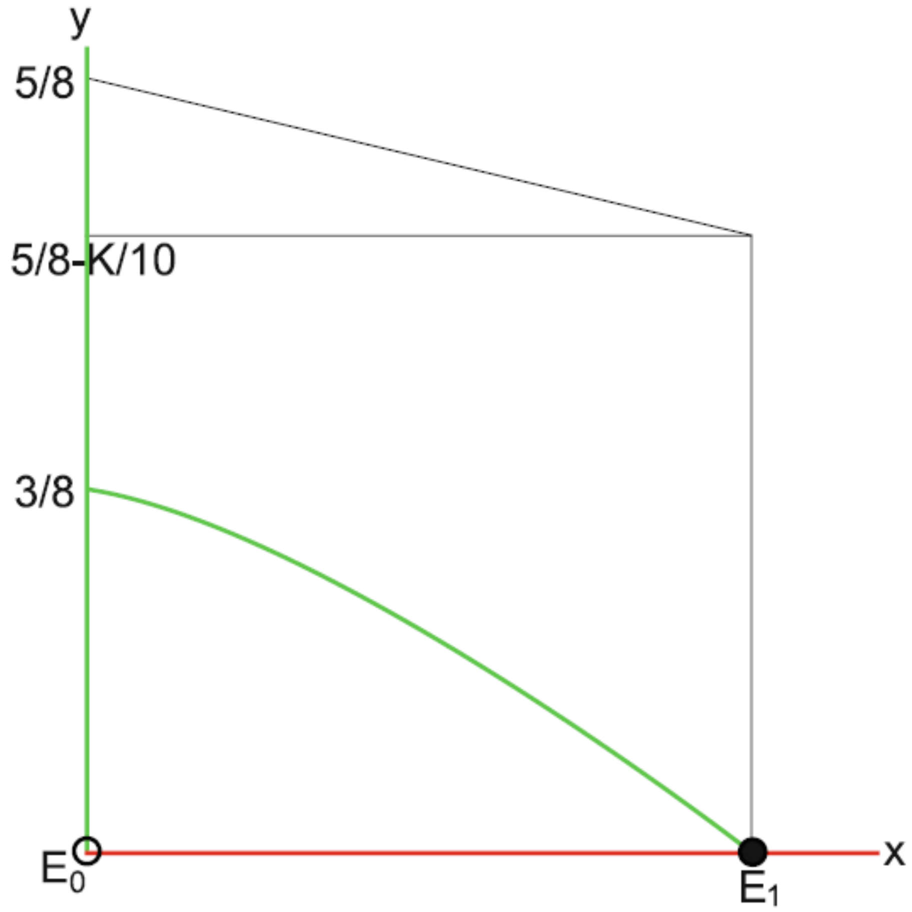


Fig. 9 The nullclines and equilibria for $0 < K \leq 25/156$

The system has only the boundary equilibria $E_0 = (0, 0)$, $E_1 = (K, 0)$. No internal equilibria exist in this case (see Fig. 9). E_0 is a saddle, E_1 is G.A.S. If $0 < K < 25/156$, E_1 is a G.A.S. node; if $K = 25/156$, E_1 is a saddle-node, transcritical bifurcation appears, and all orbits in Ω tend to E_1.

Case 2. $25/156 < K \leq 89/156$

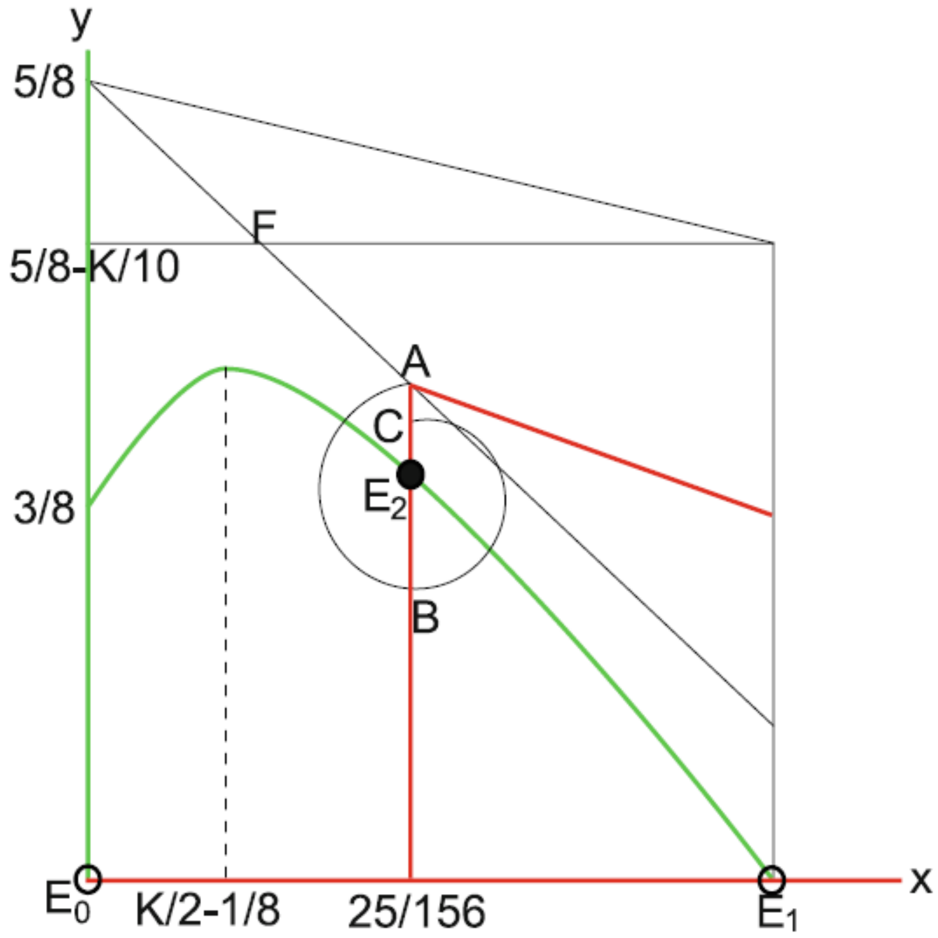


Fig. 10 The nullclines and equilibria for $25/156 < K < 89/156$

Theorem 15 *When* $25/156 < K \leq 89/156$, *the system has two boundary equilibria* E_0, E_1, *which are unstable saddles, and one internal equilibrium* E_2, *which is G.A.S. When* $K = 89/156$, *Hopf bifurcation occurs.*

Case 3. $89/156 < K < 0.585185$

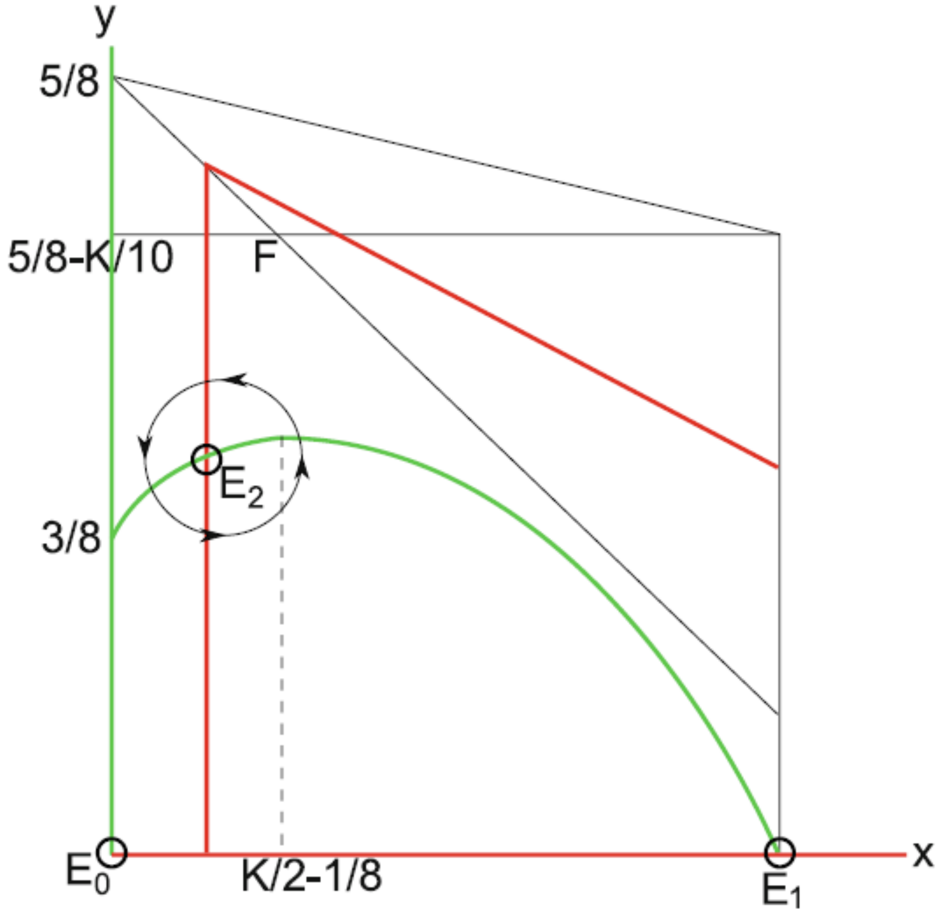


Fig. 11 The nullclines and equilibria for $89/156 < K < 0.585185$

Theorem 16 *When* $89/156 < K < 0.585185$, *the system has two boundary equilibria* E_0, E_1, *which are unstable saddles, and one internal equilibrium* E_2, *which is unstable, and has at least one limit cycle* (*see* Fig. 11).

Case 4. $0.585185 \leq K \leq 0.654664$

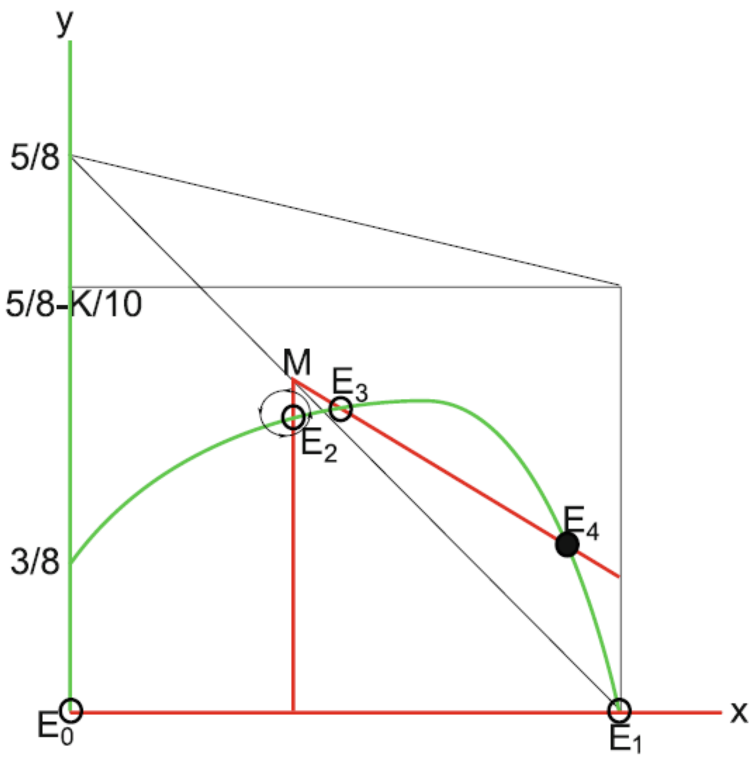


Fig. 12 The nullclines and equilibria for $0.585185 < K < 0.654664$

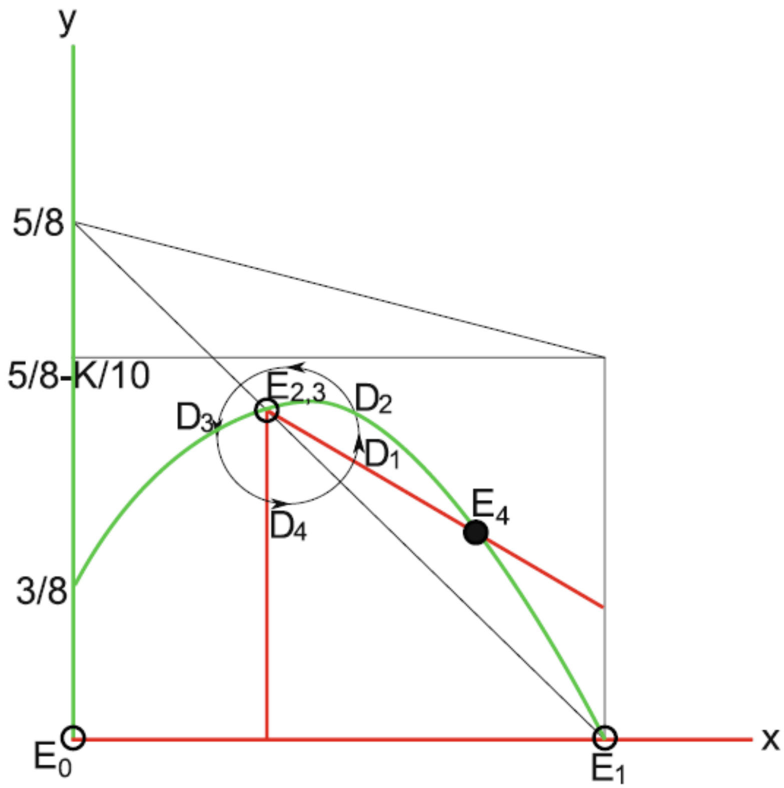


Fig. 13 The nullclines and equilibria for $K = 0.654664$

(no limit cycle, the one
plotted is only for proof)

Theorem 17 *When* $0.585185 \leq K \leq 0.654664$, *the system has two boundary equilibria* E_0, E_1, *which are unstable saddles.*

When $0.585185 < K < 0.654664$, *the system has three internal equilibria* E_2, E_3, E_4. E_2 *lying in the domain* $\{(x, y) \in \Omega : x + y < 5/8\}$ *is unstable.* E_3, E_4 *lying in the domain* $\{(x, y)\Omega : x + y > 5/8\}$ *are an unstable saddle and a stable node, respectively. Moreover, the system has at least one limit cycle surrounding the equilibrium* E_2.

When $K = 0.585185$, *the system has two internal equilibria* E_2, $E_{3,4}$. E_2 *lying in the domain* $\{(x, y) \in \Omega : x+y < 5/8\}$ *is unstable.* $E_{3,4}$ *lying on the line* $x+y = 5/8$ *is an unstable saddle-node. Moreover, the system has at least one limit cycle surrounding the equilibrium* E_2.

When $K = 0.654664$, *the system has two internal equilibria* $E_{2,3}$, E_4. $E_{2,3}$ *lying on the line* $x + y = 5/8$ *is an unstable saddle-node.* E_4 *lying in the domain* $\{(x, y) \in \Omega : x + y > 5/8\}$ *is a G.A.S. node. Moreover, the system has no limit cycles.*

Case 5. $0.65466 < K < 2$

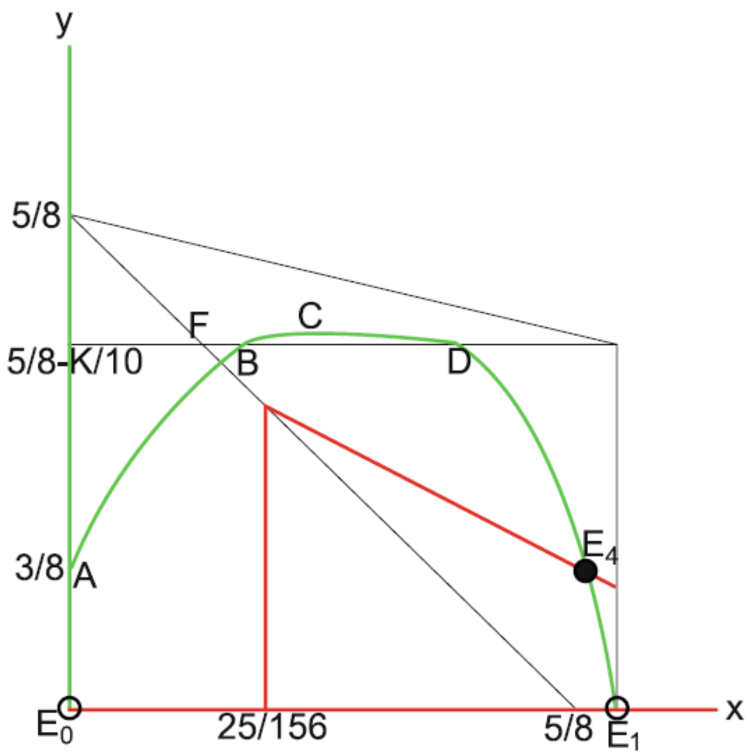


Fig. 14 The nullclines and equilibria for $0.654664 < K < 1.35$

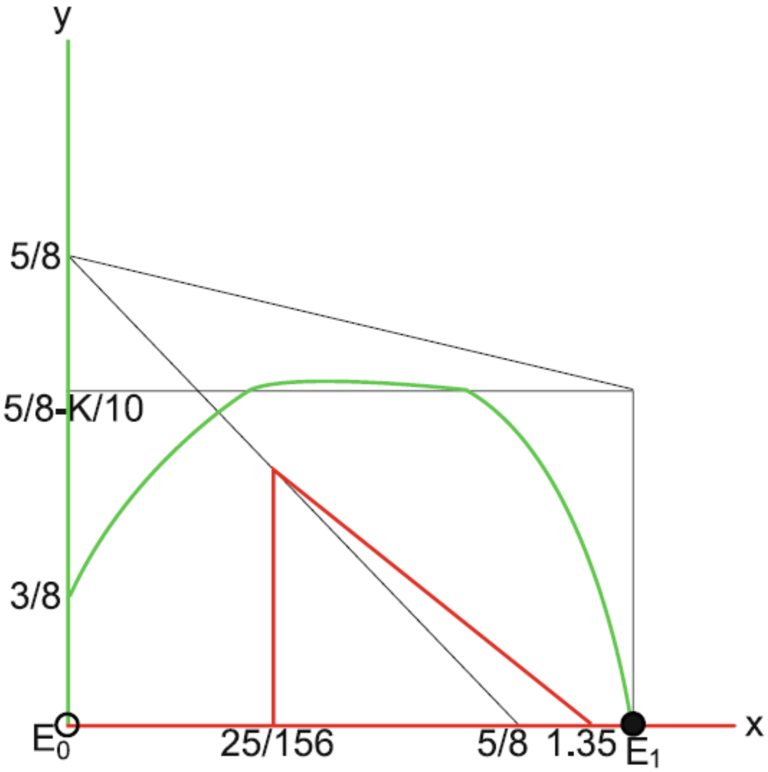


Fig. 15 The nullclines and equilibria for $1.35 < K < 2$

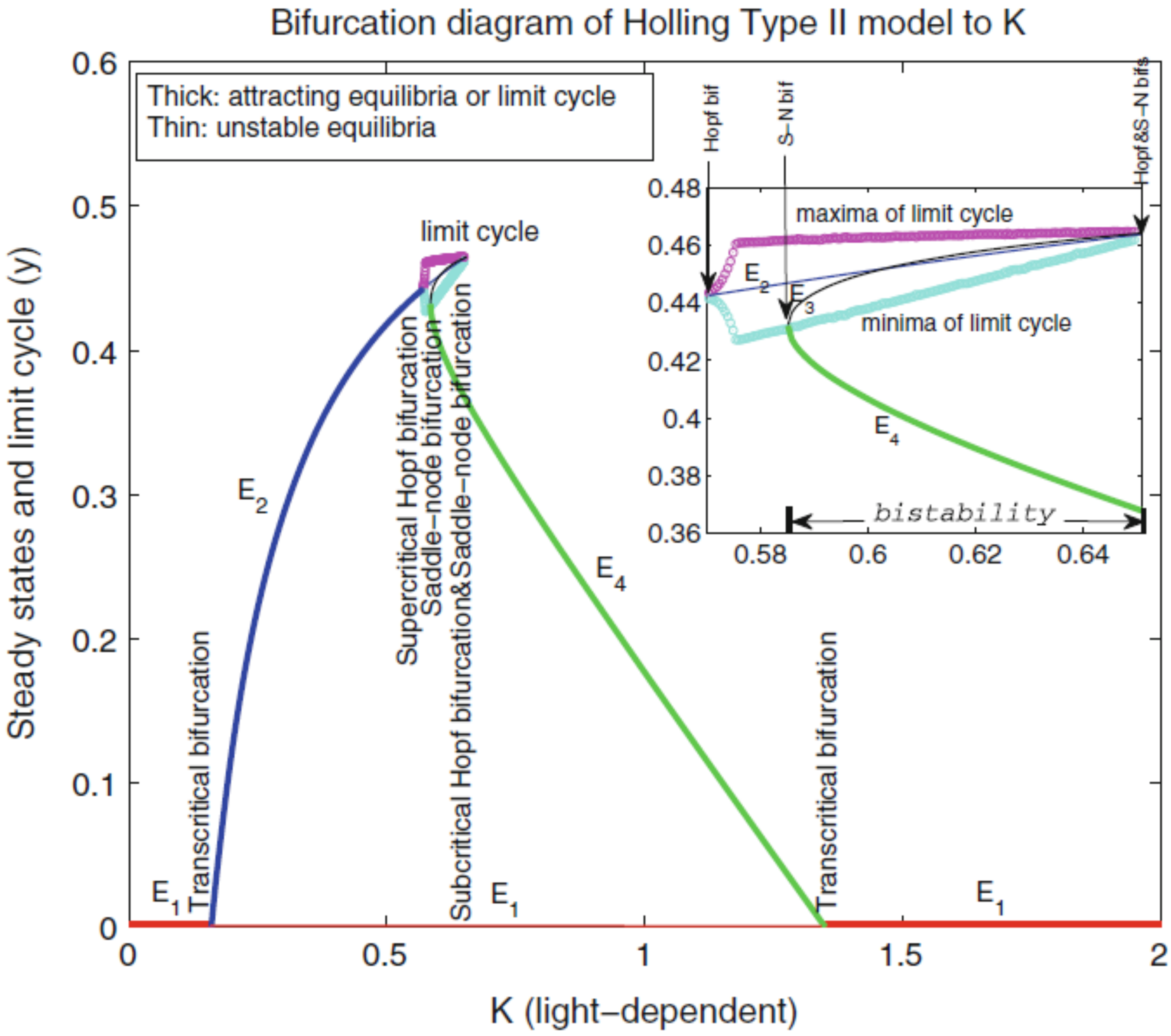
Theorem 18 *When* $0.654664 < K < 1.35$, *the system has two boundary equilibria* E_0, E_1 *which are unstable saddles and one internal equilibrium* E_4 *which is a G.A.S. node, and the system has no limit cycles. Moreover, there exists a heteroclinic orbit connecting* E_1 *and* E_4.

When $K = 1.35$, E_0 *is an unstable saddle,* E_4 *and* E_1 *collide and become a G.A.S. saddle-node* E_1 *(for the studied trapping region), and all orbits of the system in* Ω *tend to* E_1.

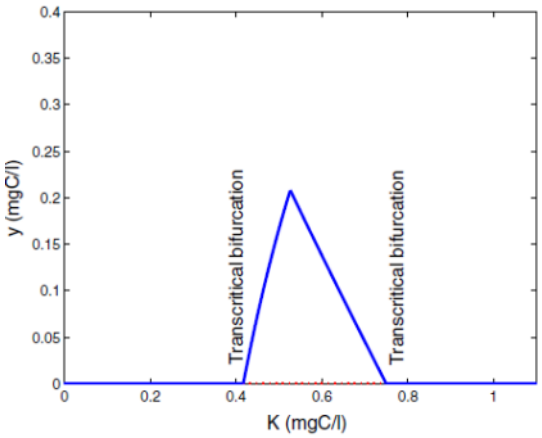
When $K > 1.35$, *the system has only the boundary equilibria* E_0, E_1 *but no internal equilibria.* E_0 *is an unstable saddle, and* E_1 *is a G.A.S. node.*

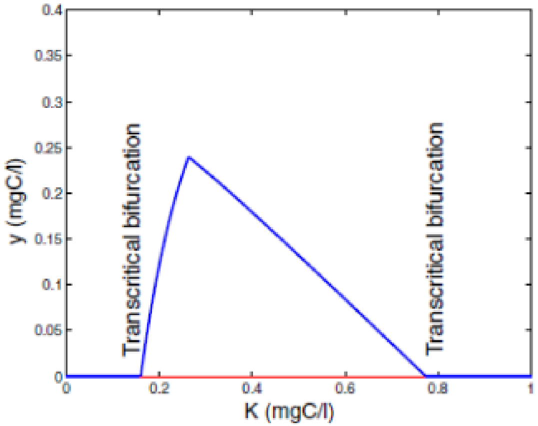
Summary

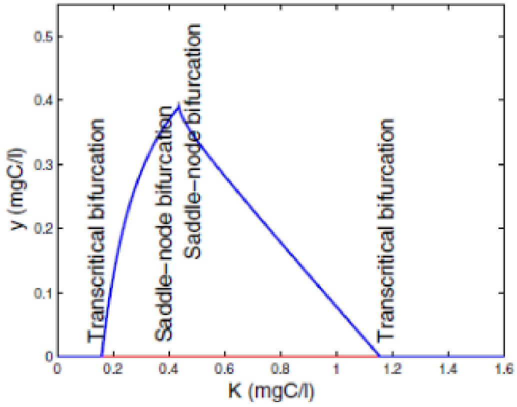
- When $0 < K \leq 25/156$, there exist no internal equilibria, and the boundary equilibrium E_1 is G.A.S.
- When $25/156 < K \leq 89/156$, there exists a unique internal equilibrium E_2 which is G.A.S, and all boundary equilibria are unstable.
- When $89/156 < K < 0.585185$, there exists a unique internal equilibrium E_2 which is unstable, all boundary equilibria are also unstable, and there exists at least one limit cycle.
- When $K = 0.585185$, there exist two internal equilibria: E_2 and $E_{3,4}$ are unstable, and there exists at least one limit cycle.
- When $0.585185 < K < 0.654664$, there exist three internal equilibria: E_2 and E_3 are unstable, E_4 stable; there exists at least one limit cycle; all solutions either tend to the limit cycle or tend to E_4 (bistability).
- When $K = 0.645664$, there exist two internal equilibria: $E_{2,3}$ is unstable, E_4 is G.A.S.
- When $0.654664 < K < 1.35$, there exists a unique internal equilibrium E_4 which is G.A.S.
- When $1.35 \leq K < 2$, there exist no internal equilibria, and the boundary equilibrium E_1 is G.A.S.

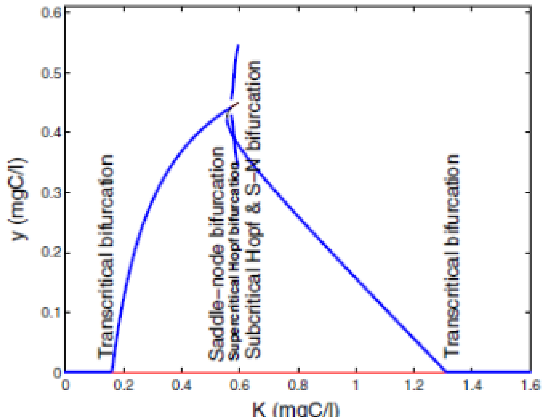

Bifurcation diagram of Holling Type II model to K
Thick: attracting equilibria or limit cycle
Thin: unstable equilibria
Steady states and limit cycle (y)
K (light−dependent)
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.5
1
1.5
2
limit cycle
E_1
E_2
E_4
E_1
E_1
Transcritical bifurcation
Supercritical Hopf bifurcation
Saddle−node bifurcation
Subcritical Hopf bifurcation&Saddle−node bifurcation
Transcritical bifurcation
Hopf bif
S−N bif
Hopf&S−N bifs
maxima of limit cycle
minima of limit cycle
E_2
E_3
E_4
bistability
0.48
0.46
0.44
0.42
0.4
0.38
0.36
0.58
0.6
0.62
0.64

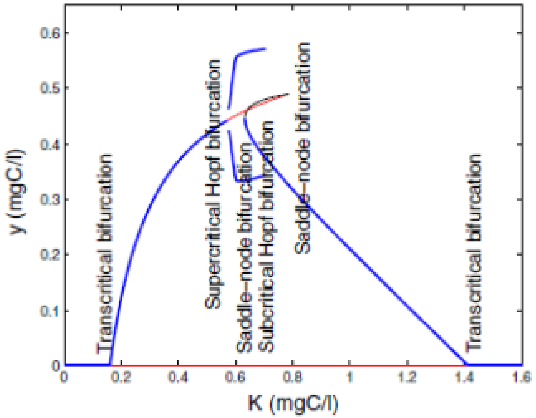
All possible bifurcation diagrams

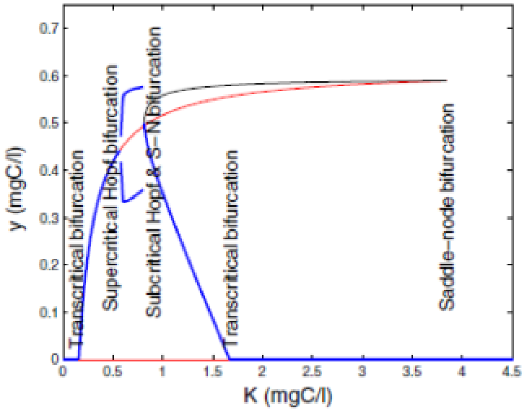






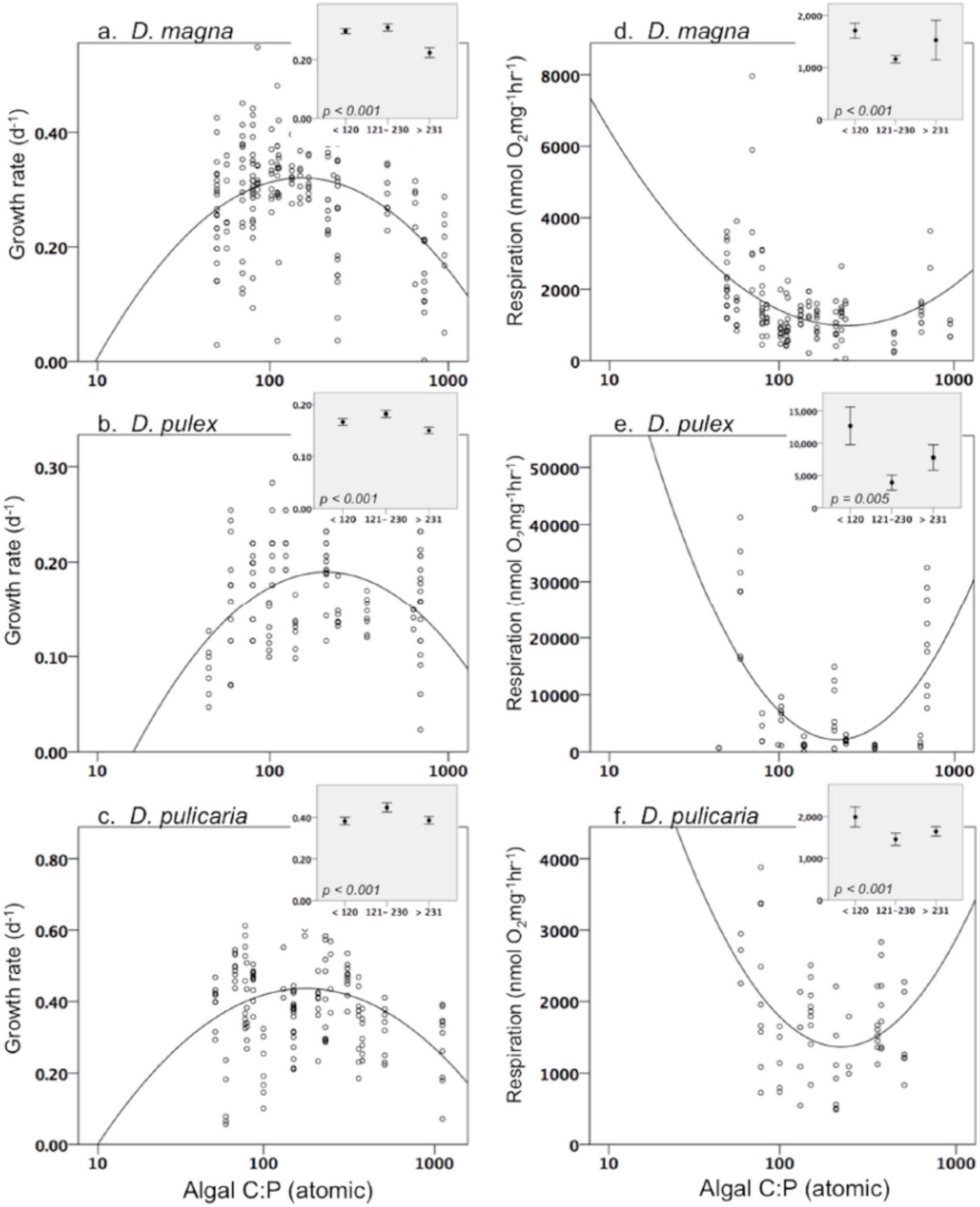






Xie, T., Yang, X., Li, X. and Wang, H., 2018. Complete Global and Bifurcation Analysis of a Stoichiometric Predator–Prey Model. *Journal of Dynamics and Differential Equations*, *30*(2), pp.447-472.

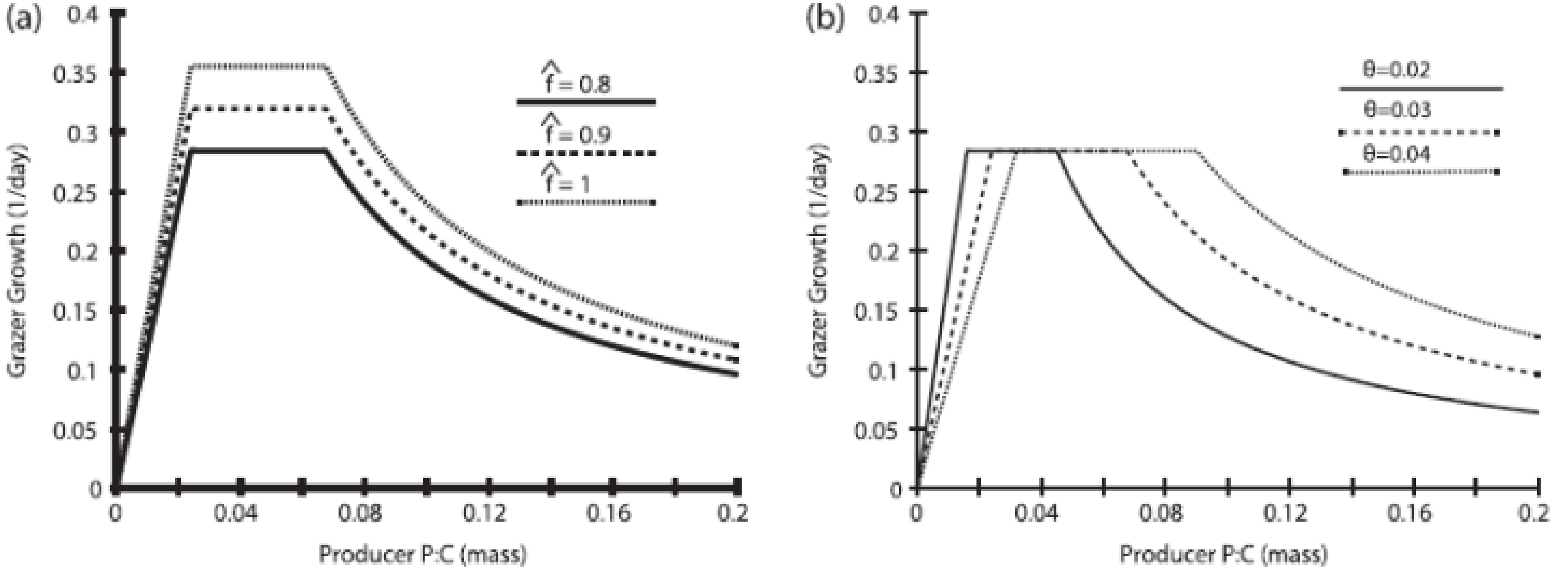
Knife-edge effect



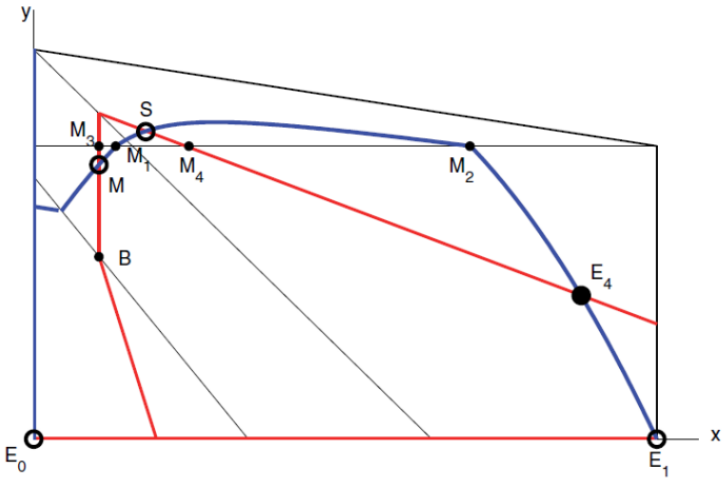
James J. Elser, Marcia Kyle, Jennifer Learned, Michelle L. McCrackin, Angela Peace & Laura Steger (2016) Life on the stoichiometric knife-edge: effects of high and low food C:P ratio on growth, feeding, and respiration in three Daphnia species, Inland Waters, 6:2, 136-146

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{\min\{K, (P-\theta y)/q\}}\right) - \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\} y,$$

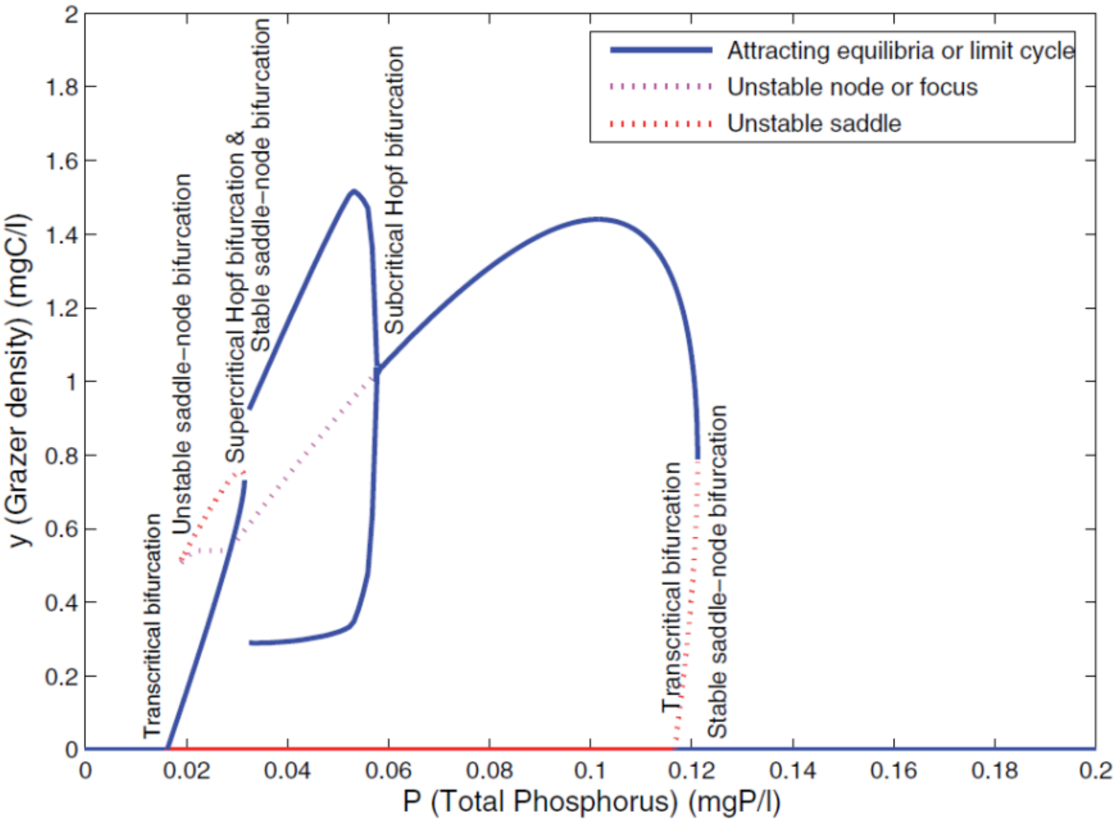
$$\frac{dy}{dt} = \min\left\{ef(x), \frac{Q}{\theta}f(x), e\hat{f}\frac{\theta}{Q}\right\} y - dy,$$



Peace, A., Zhao, Y., Loladze, I., Elser, J.J. and Kuang, Y., 2013. A stoichiometric producer-grazer model incorporating the effects of excess food-nutrient content on consumer dynamics. *Mathematical biosciences*, *244*(2), pp.107-115.



Bifurcation diagram for the knife-edge model



Yang, X., Li, X., Wang, H. and Kuang, Y., 2016. Stability and bifurcation in a stoichiometric producer-grazer model with knife edge. *SIAM Journal on Applied Dynamical Systems*, *15*(4), pp.2051-2077.

Take home messages

The increase of light increases plant’s quantity but decreases its quality

It is important to incorporate nutrients as a new dimension into the models of food webs

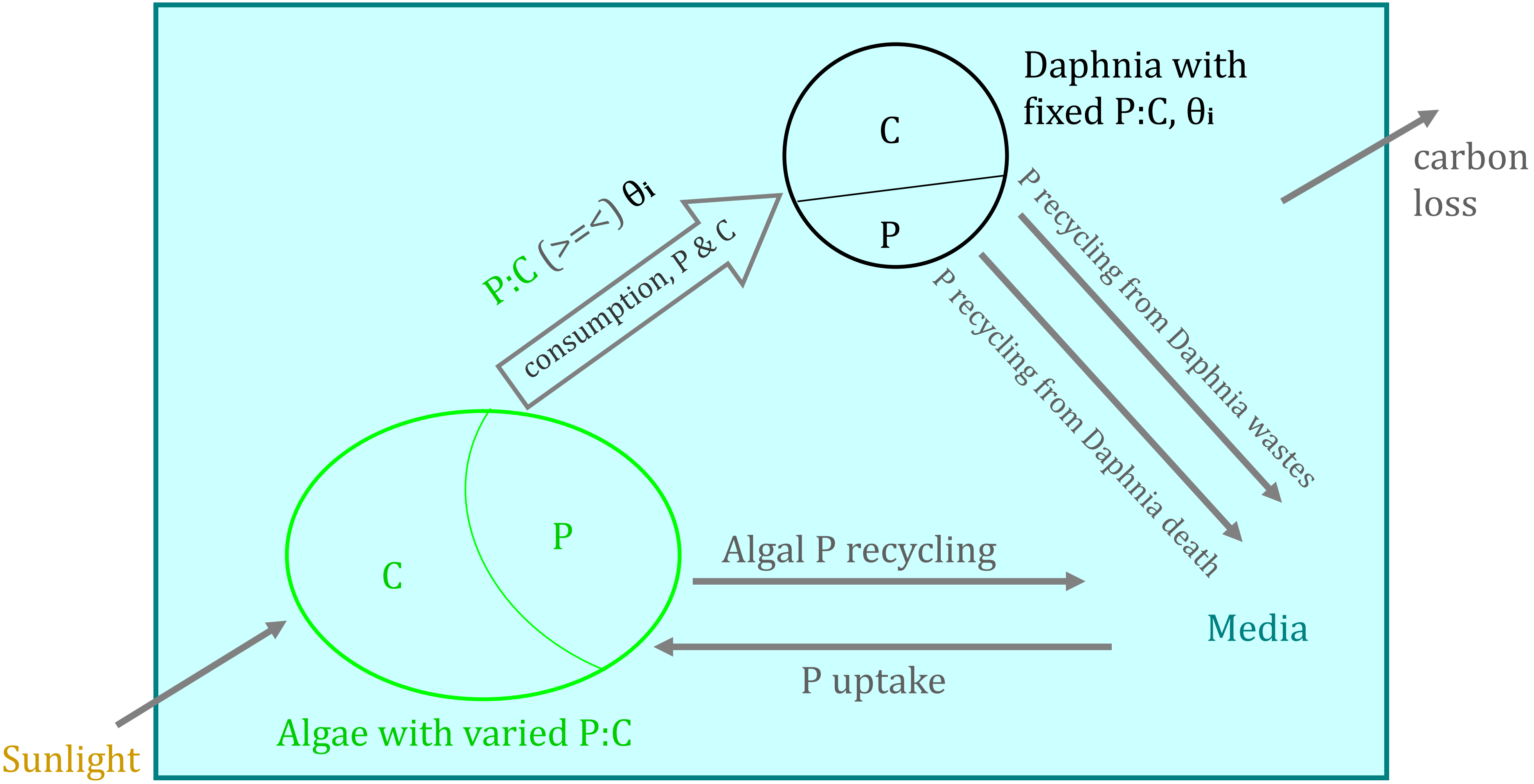
A stoichiometric predator-prey model has much more complex dynamics than a historic predator-prey model.

The conjecture for the uniqueness of limit cycle needs a rigorous proof. The nonsmoothness makes this proof much more challenging.

Assumptions

- The total mass of phosphorus in the entire system is fixed, denoted by T. (closed P, open C)
- P:C ratio (=cell quota) in algae varies, but it never falls below a minimum q; Both Daphnia species maintain constant P:C ratios, denoted by θ_1, θ_2. (Homeostasis)

Schematic Model



Daphnia with fixed P:C, θ_i

C

P

P:C (>=<) θ_i

consumption, P & C

P recycling from Daphnia wastes

P recycling from Daphnia death

carbon loss

P

C

Algal P recycling

P uptake

Media

Algae with varied P:C

Sunlight

WKL Model

$= rx\min\left\{1-\frac{x}{K}, 1-\frac{q}{p/x}\right\}$, logistic growth (light/carbon limitation) combined with Droop model (nutrient limitation)

$$\frac{dx}{dt} = \underbrace{rx\left(1-\frac{x}{\min\{K, p/q\}}\right)}_{\text{producer growth limited by nutrient and light}} - \underbrace{f(x)y}_{\text{uptake by grazers}},$$

$$\frac{dy}{dt} = \underbrace{\hat{e}\min\left\{1, \frac{p/x}{\theta}\right\}f(x)y}_{\text{grazer growth limited by food quality and quantity}} - \underbrace{\hat{d}y}_{\text{grazer death and respiration loss}},$$

$$\frac{dp}{dt} = \underbrace{g(P)x}_{\text{P uptake by producer}} - \underbrace{\frac{p}{x}f(x)y}_{\text{P loss due to grazing}} - \underbrace{dp}_{\text{P loss due to producer recycling}},$$

$$\frac{dP}{dt} = \underbrace{-g(P)x}_{\text{P uptake by producer}} + \underbrace{dp}_{\text{P recycling from producer}} + \underbrace{\theta\hat{d}y}_{\text{P recycling from dead grazer}}$$

$$+ \underbrace{\left(\frac{p}{x} - \hat{e}\min\left\{\theta, \frac{p}{x}\right\}\right)f(x)y.}_{\text{P recycling from grazer feces}}$$

WKL Model Reduction

The total phosphorus of the system,
T=p+P+**θ**y, satisfies dT/dt=0; Hence, we can
reduce the system to

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{\min\{K, p/q\}}\right) - f(x)y$$

$$\frac{dy}{dt} = \hat{e}\min\left\{1, \frac{p/x}{\theta}\right\} f(x)y - \hat{d}y$$

$$\frac{dp}{dt} = g(T - p - \theta y)x - \frac{p}{x} f(x)y - dp$$

Model Results

Theorem. Solutions with initial conditions in the set

$$\Omega = \{(x, y, P) : 0 < x < \min\{K, T/q\}, 0 < y, 0 < p, p + \theta y < T\}$$

remain there for all forward times.

Steady States: the extinction equilibrium $\mathrm{E}_0 = (0, 0, 0)$,

the grazer extinction equilibrium $\mathrm{E}_1 =$

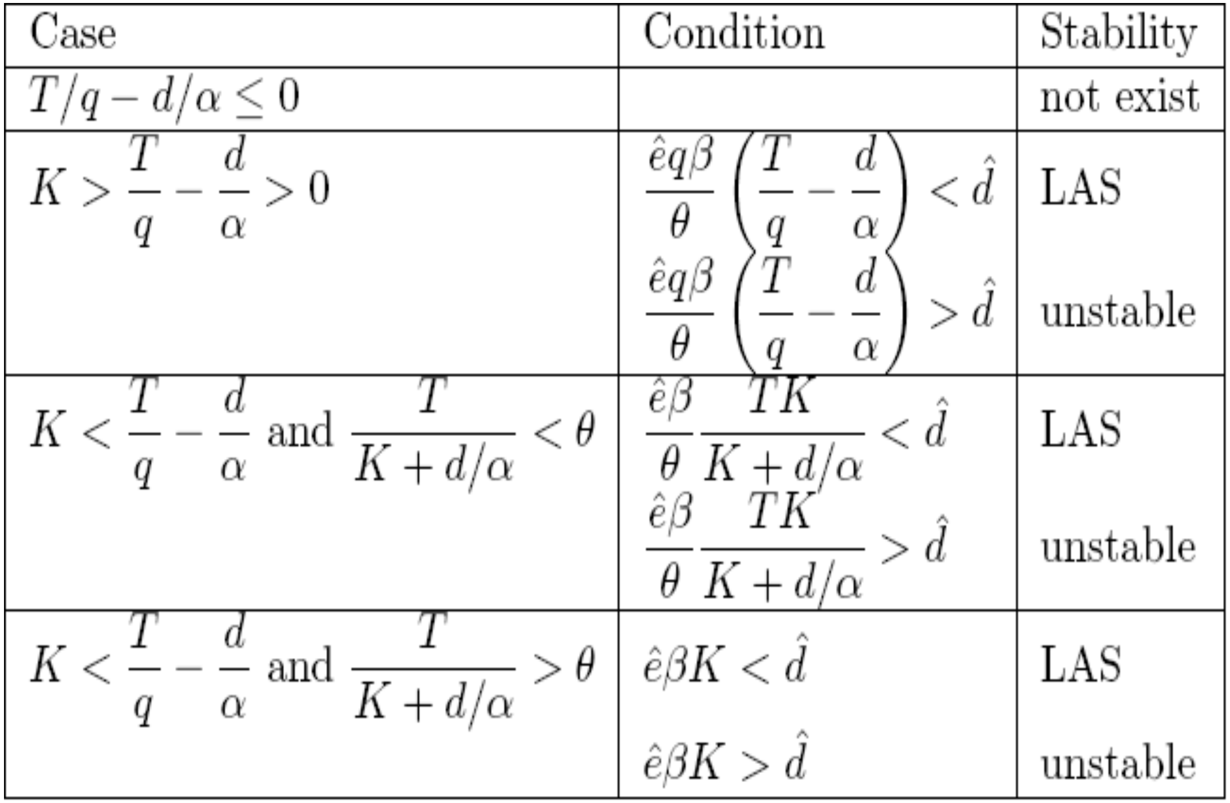
$$\begin{cases} \left(\mathrm{K}, 0, \dfrac{\mathrm{TK}}{\mathrm{K} + \mathrm{d}/\alpha}\right), & \text{if} \quad K < \dfrac{T}{q} - \dfrac{d}{\alpha} \\ \left(\dfrac{T}{q} - \dfrac{d}{\alpha}, 0, q\left(\dfrac{T}{q} - \dfrac{d}{\alpha}\right)\right), & \text{if} \quad K > \dfrac{T}{q} - \dfrac{d}{\alpha} \end{cases}$$

and a coexistence equilibrium E^*. (Here $g(P) = \alpha P, f(x) = \beta x$)

Theorem. The extinction steady state $\mathrm{E}_0 = (0,0,0)$ is globally asymptotically stable if $d > mg(T)$, where

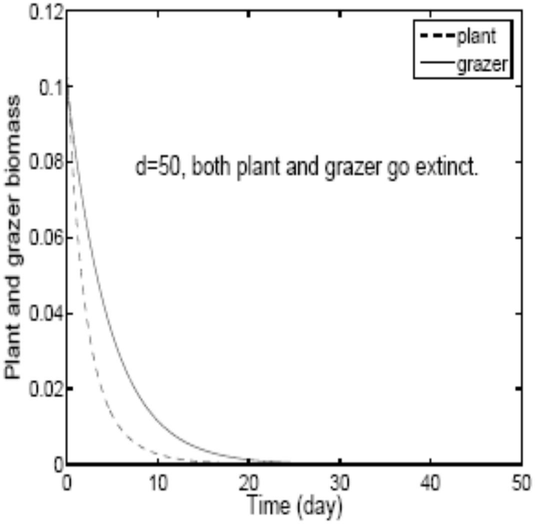
$$m = \min\left\{ \frac{x(0)}{p(0)}, \frac{1 + (d + f'(0)T/\theta)/r}{q} \right\}$$

Stability of E1

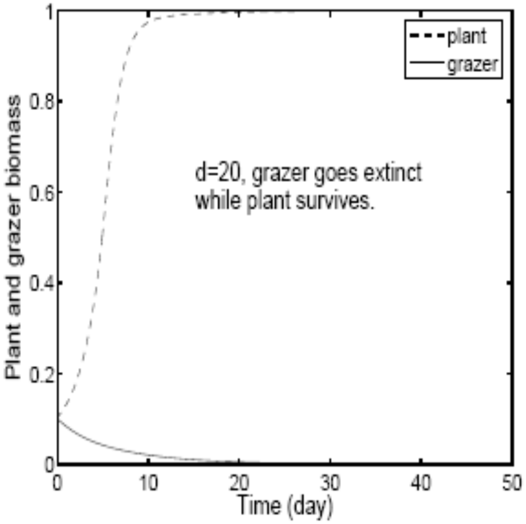


Case	Condition	Stability
$T/q - d/\alpha \le 0$		not exist
$K > \frac{T}{q} - \frac{d}{\alpha} > 0$	$\frac{\hat{e}q\beta}{\theta}\left(\frac{T}{q} - \frac{d}{\alpha}\right) < \hat{d}$ $\frac{\hat{e}q\beta}{\theta}\left(\frac{T}{q} - \frac{d}{\alpha}\right) > \hat{d}$	LAS unstable
$K < \frac{T}{q} - \frac{d}{\alpha}$ and $\frac{T}{K + d/\alpha} < \theta$	$\frac{\hat{e}\beta}{\theta}\frac{TK}{K + d/\alpha} < \hat{d}$ $\frac{\hat{e}\beta}{\theta}\frac{TK}{K + d/\alpha} > \hat{d}$	LAS unstable
$K < \frac{T}{q} - \frac{d}{\alpha}$ and $\frac{T}{K + d/\alpha} > \theta$	$\hat{e}\beta K < \hat{d}$ $\hat{e}\beta K > \hat{d}$	LAS unstable

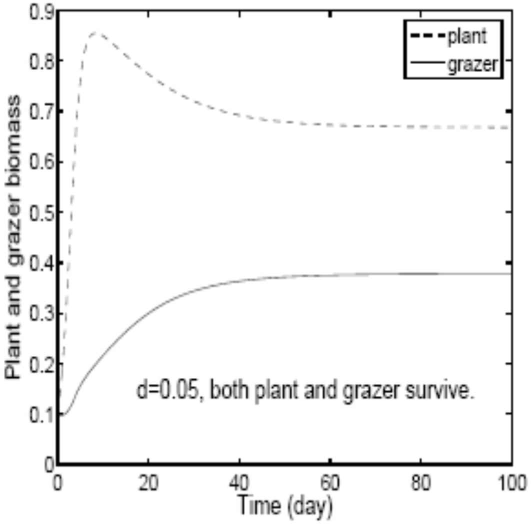
Simulations



(a) The extinction steady state E_0 is asymptotically stable.



(b) The grazer extinction steady state E_1 is asymptotically stable.



(c) The coexistence steady state E^* is asymptotically stable.

LKE model derivation

Observe that the nutrient p has a dynamics that is much faster than growth dynamics of producer and consumer. By quasi-steady state argument on the nutrient equation, we obtain

$$p = \frac{\alpha x(T-\theta y)}{\alpha x + \beta y + d} \qquad \text{if} \quad g(P) = \alpha P, f(x) = \beta x$$

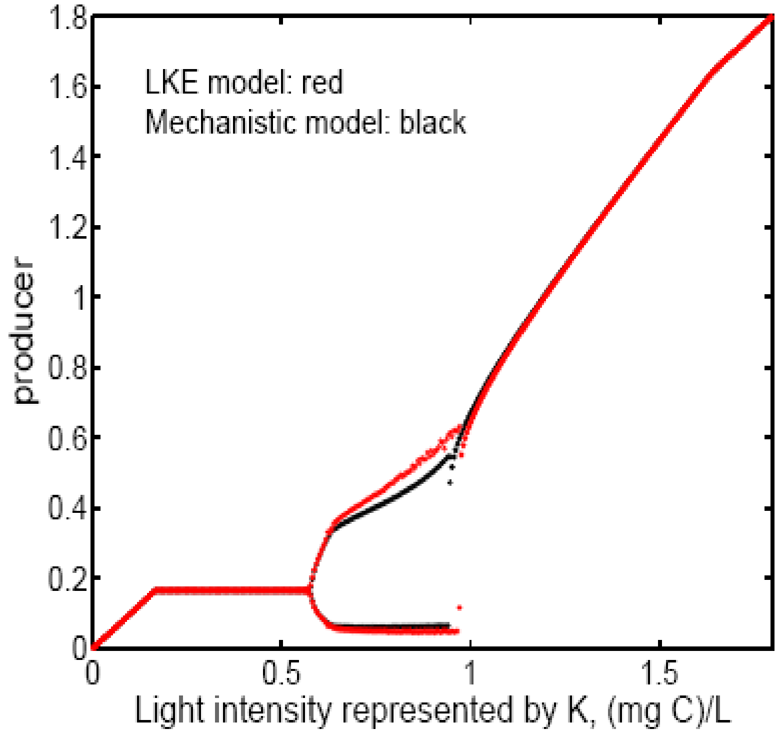
For sufficiently large α $\quad p \approx T - \theta y.$

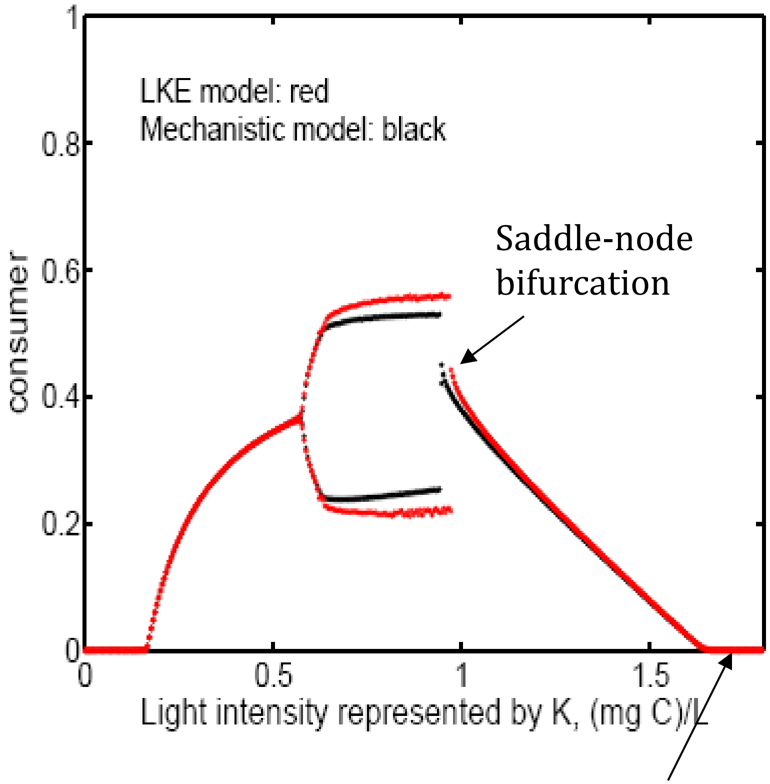
Then, the WKL model is degenerated to be the LKE model

$$\frac{dx}{dt} \approx rx\left(1 - \frac{x}{\min\{K, (T-\theta y)/q\}}\right) - f(x)y$$

$$\frac{dy}{dt} \approx \hat{e}\min\left\{1, \frac{(T-\theta y)/x}{\theta}\right\} f(x)y - \hat{d}y$$

Comparison of Bifurcations



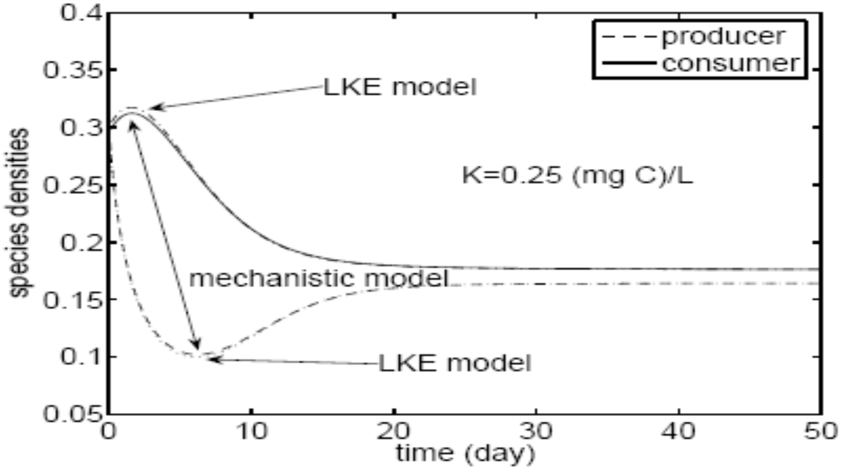


Saddle-node bifurcation

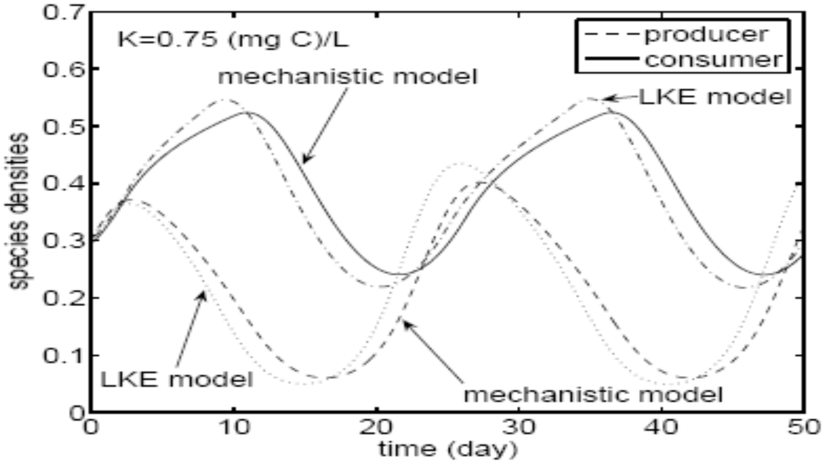
Consumer extinction: too much light will reduce food quality

We observe new mathematical and biological features from these stoichiometric models.

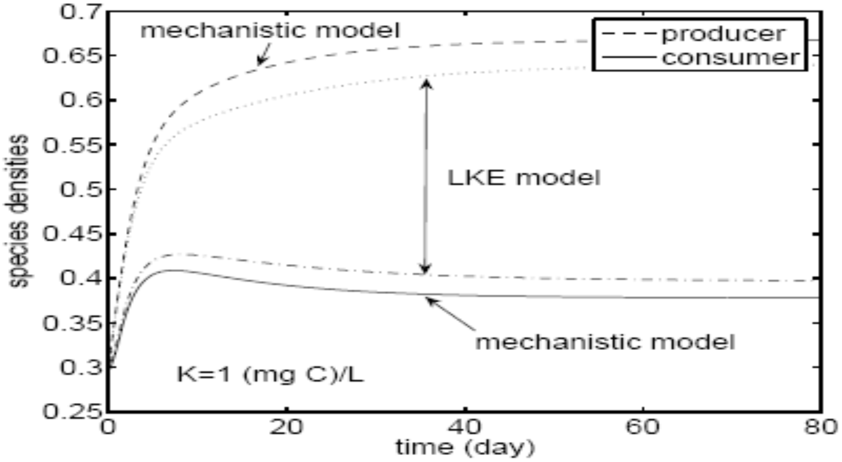
Simulations vs K



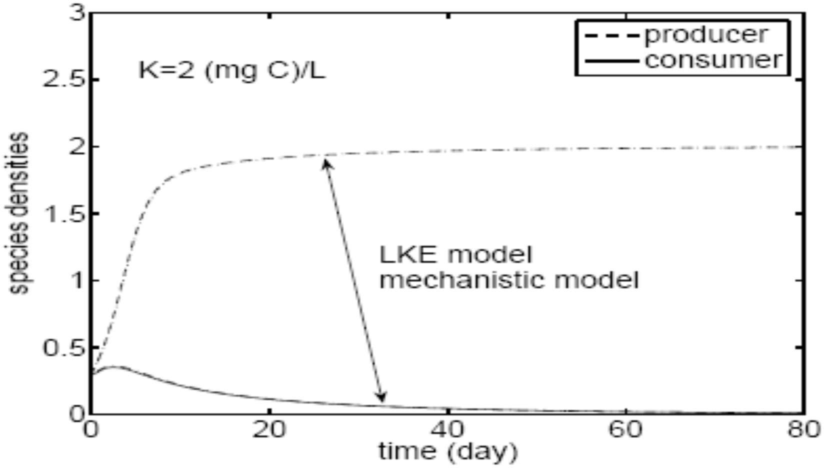
(a) coexistence at a steady state



(b) coexistence with oscillations

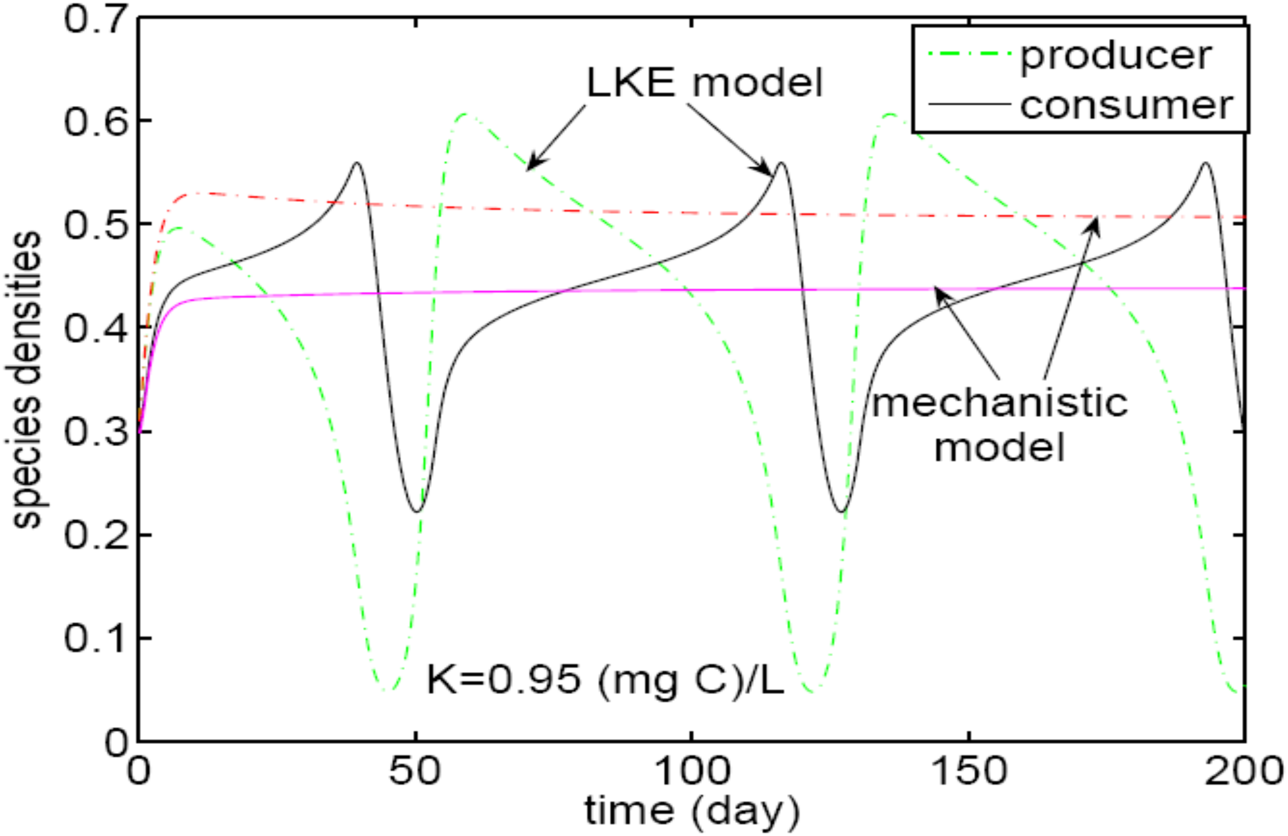


(c) coexistence at a steady state with a higher producer/grazer ratio



(d) extinction of the grazer

For the intermediate *K* values, they are slightly different quantitatively. However, when *K* is near the homoclinic bifurcation point, they are completely different. Near this point, the solution sensitivity with respect to *K* is high.

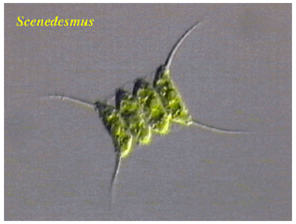


Daphnia-Algae Experiment

Study organisms

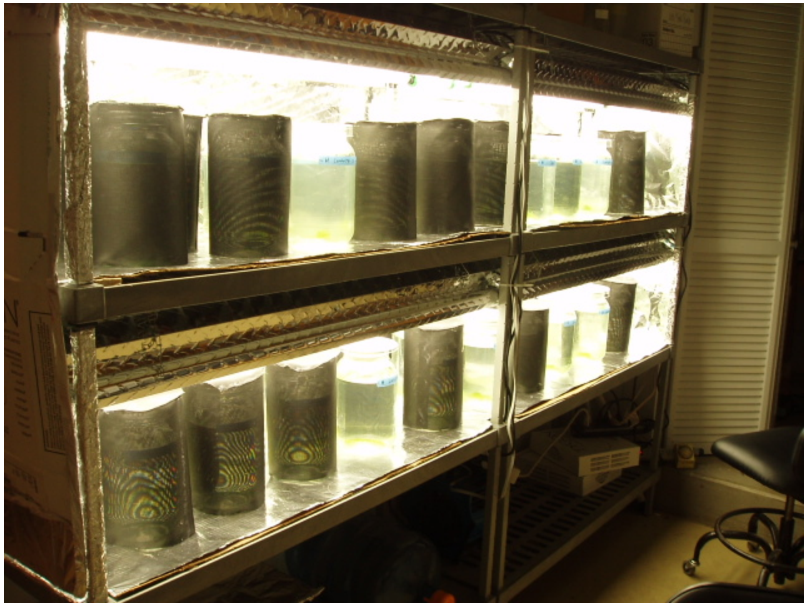
Daphnia pulex: a widespread and important planktonic herbivore in N. America

Daphnia lumholtzi: a daphnia native to Africa but now invasive in N. America.

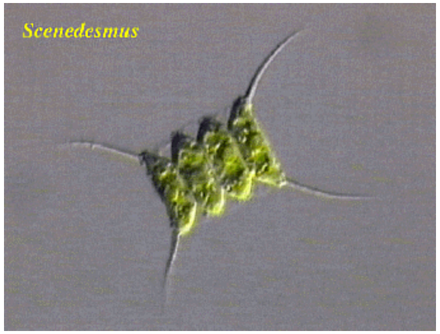


Scenedesmus obliquus: a Chlorophyte (green algae) found in many lakes and easily grown in the laboratory.

Pictures courtesy of: Paul Hebert; aslo.org; and www.biol.tsukuba.ac.jp/



© 2002 K. David Hambright

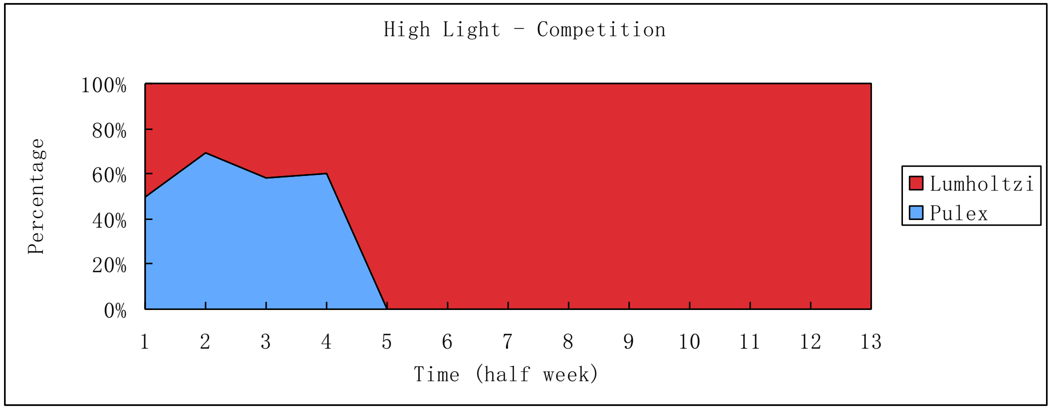


Methods

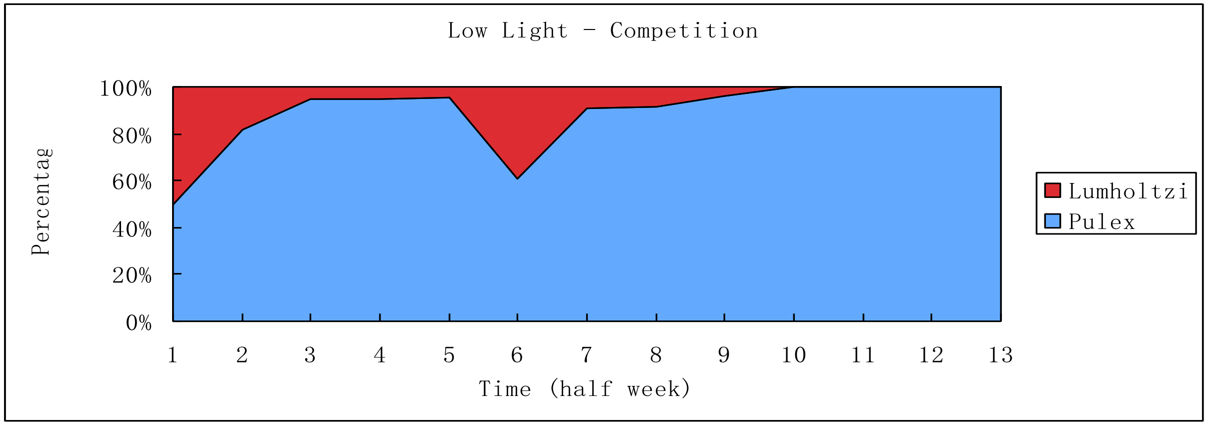
Experimental Design **3-L** Jars	High Light **218** uE/m^2/s	Low Light **21.8** uE/m^2/s
No *Daphnia*	**n = 3**	**n = 3**
Daphnia pulex alone	**n = 3**	**n = 3**
Daphnia lumholtzi alone	**n = 3**	**n = 3**
D. pulex and *D. lumholtzi* together	**n = 3**	**n = 3**

Population sizes and species composition were measured twice weekly, while algal carbon and phosphorus data and *Daphnia* body sizes and egg numbers were measured once weekly.

Main Experimental Results



Competitive Exclusion in both high light or low light!



Competition Model

Algal C $$\frac{dx}{dt} = rx\left(1 - \frac{x}{\min\{K, p/q\}}\right) - f_1(x)y_1 - f_2(x)y_2$$

Pulex C $$\frac{dy_1}{dt} = \hat{e}_1 \min\left\{1, \frac{p/x}{\theta_1}\right\} f_1(x)y_1 - \hat{d}_1 y_1$$ (D. pulex)

Lumholtzi C $$\frac{dy_2}{dt} = \hat{e}_2 \min\left\{1, \frac{p/x}{\theta_2}\right\} f_2(x)y_2 - \hat{d}_2 y_2$$ (D. lumholtzi)

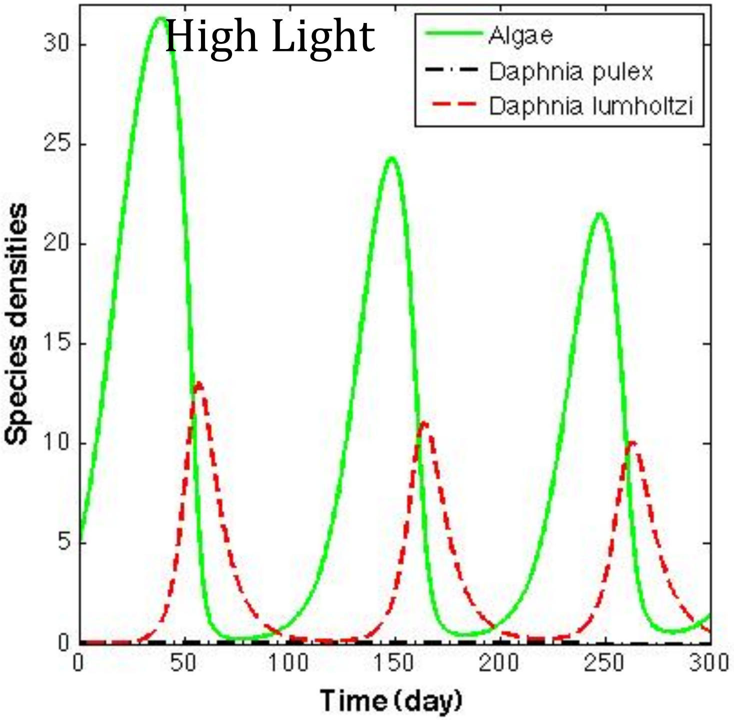
Algal P $$\frac{dp}{dt} = g(T - p - \theta_1 y_1 - \theta_2 y_2)x - \frac{p}{x} f_1(x)y_1 - \frac{p}{x} f_2(x)y_2 - dp$$

Hypothesis

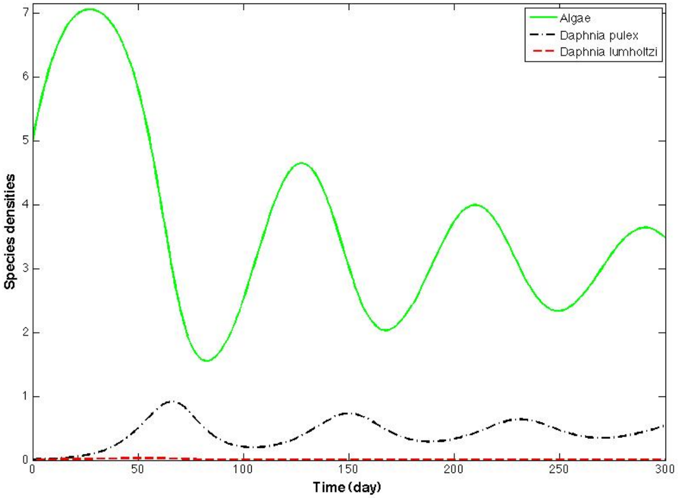
D. lumholtzi has higher requirements for C (energy) while *D. pulex* has higher requirements for P (nutrient).

measured in carbon biomass

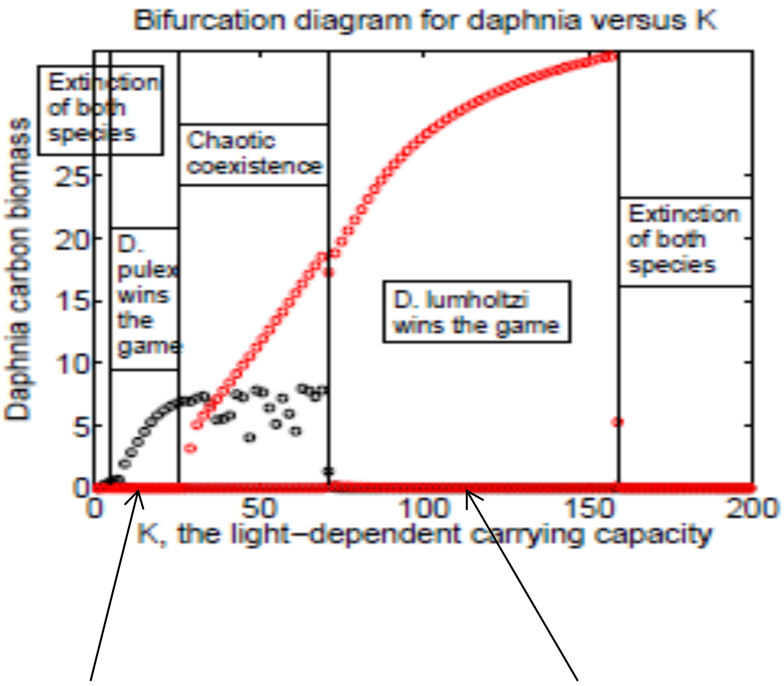
High Light



Low Light

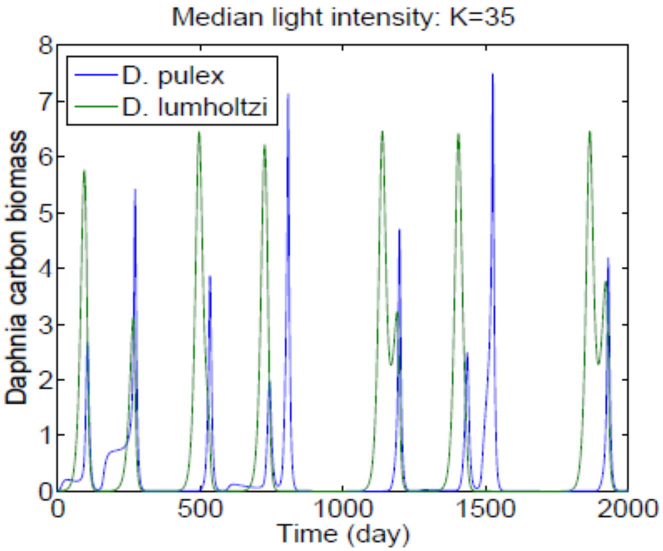


Rich Dynamics

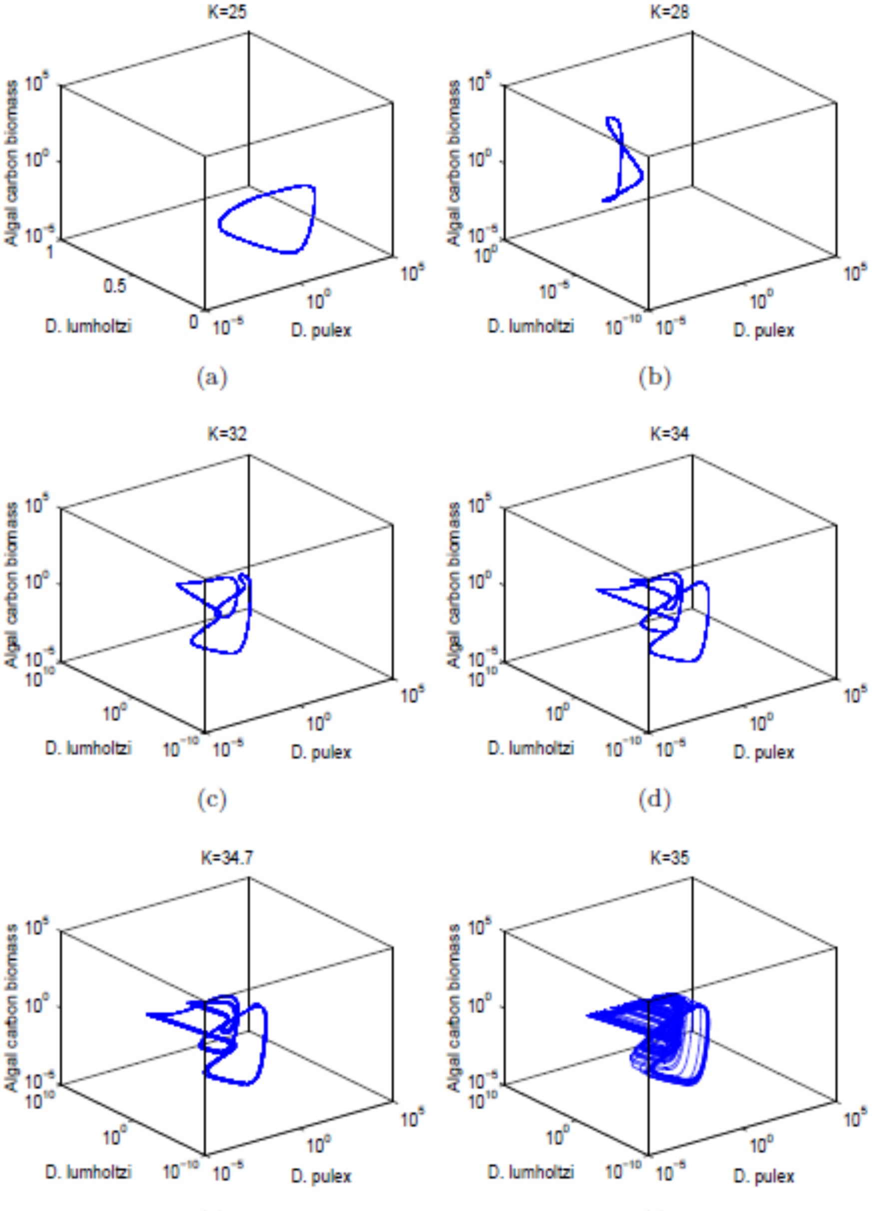


Low light intensity
in the experiment

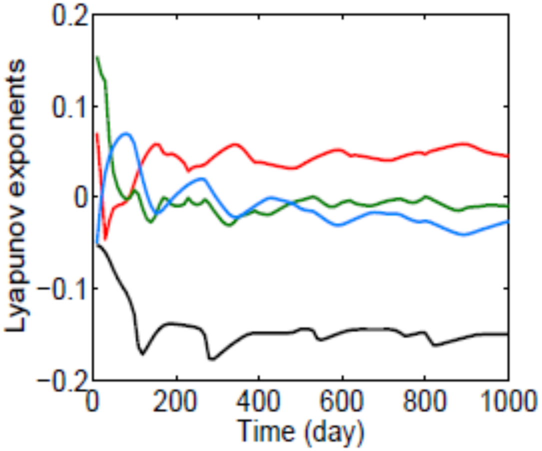
High light intensity
in the experiment



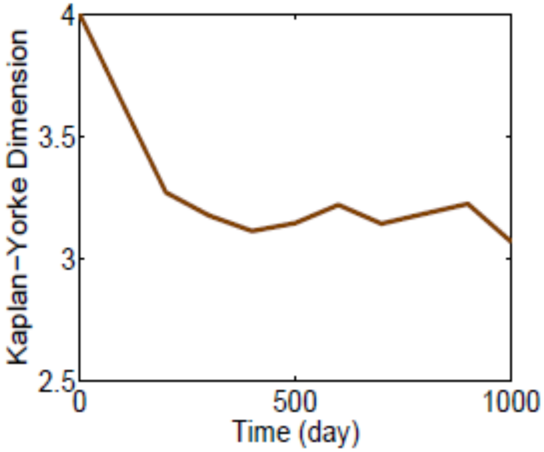
A chaotic attractor



(a) (b) (c) (d) (e) (f)



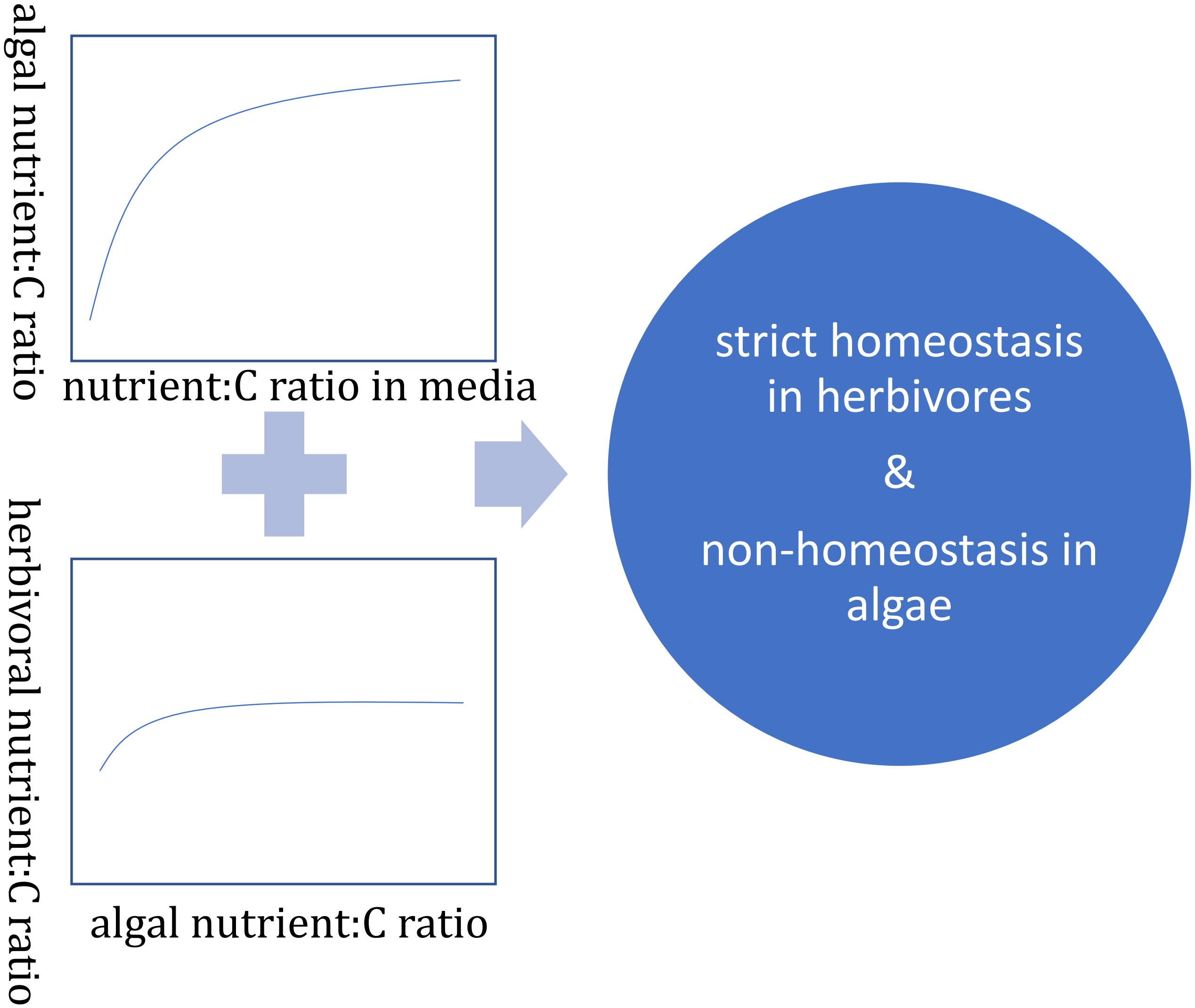
(a) Lyapunov exponents



(b) Kaplan-Yorke dimension

The “**strict homeostasis**” hypothesis is that the cellular nutrient contents (such as N:C, P:C ratios), called cell quotas, are fixed within heterotroph.

*This hypothesis has been widely used in almost all stoichiometric models including the models I presented in previous slides.

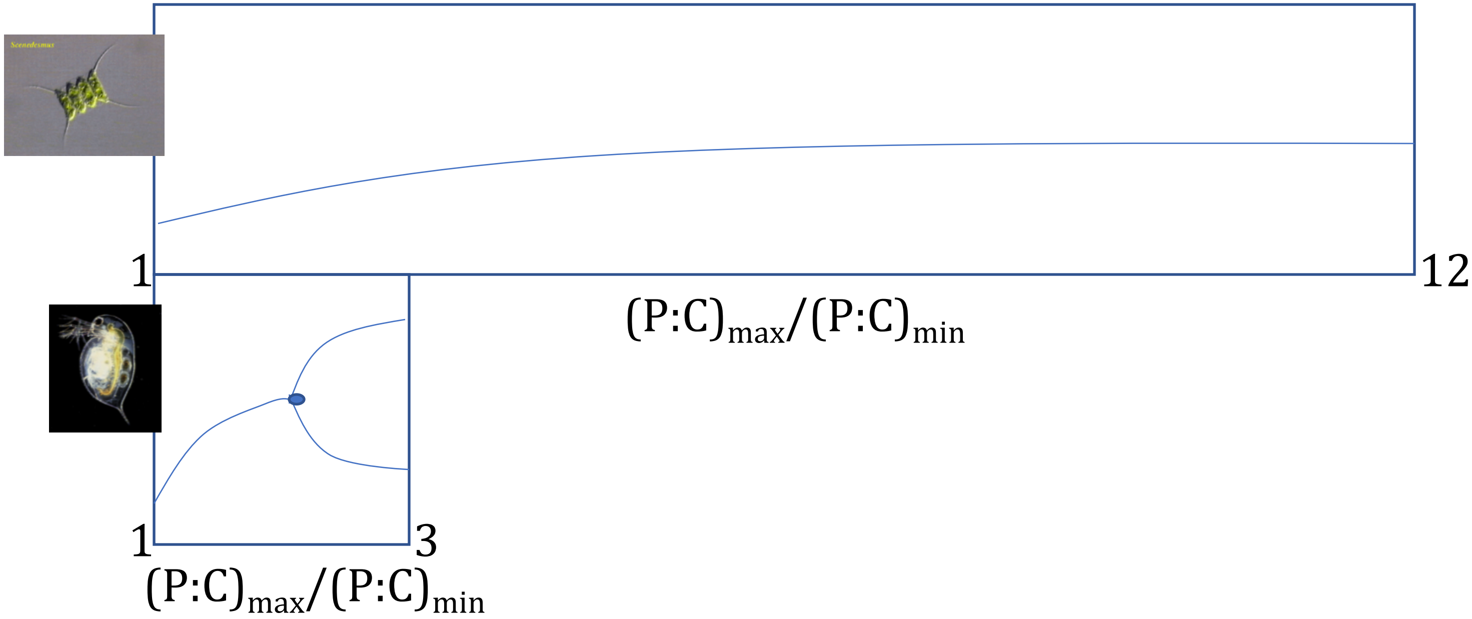


strict homeostasis in herbivores

&

non-homeostasis in algae

These results are not necessarily true, because the dynamics or studied quantities can have higher sensitivity in stoichiometric variability of herbivores than stoichiometric variability of algae.



Many stoichiometric models
(Hessen and Bjerking 1997;
Andersen 1997;
Bratbak and Thingstad 1985;
Loladze et al. 2000;
Deng and Loladze 2007;
Wang et al. 2007, 2008, 2009)
have assumed the “strict homeostasis” in heterotroph.

Quite a few experiments (DeMott et al., 1998; Acharya et al., 2004; Hood and Sterner, 2010) motivate us to relax the “strict homeostasis" assumption used in stoichiometric phytoplankton-herbivore models.

- Experiments in DeMott et al. (1998) showed that the P content of Daphnia magna was decreasing by feeding on P-defficient diets.

- Experiments in Hood and Sterner (2010) showed that the P content of Daphnia pulex in high-P treatments can be three times of that in low-P treatments.

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Diet Mixing: Do Animals Integrate Growth or Resources across Temporal Heterogeneity?

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Online enhancements: appendix table, figures.

ABSTRACT: Animals commonly experience spatial and temporal variation in resource quality, thus experiencing temporally variable diets. Methods for scaling up growth in component patches to long-term growth across heterogeneity are seldom explicitly considered. Long-term growth is sometimes considered to be a weighted average of growth rates on component diets (growth integration). However, if animals integrate resources across high- and low-quality diets, their long-term growth may be greater than predicted from diet-specific growth rates (resource integration). We measured biomass growth rates of seven *Daphnia* species exposed to different types of diel variation in algal phosphorus (P) content. Support for resource integration was found for four of the seven species, which achieved near maximal growth when high-P food was available for at least 12 h. In contrast, no support for resource integration was found for the other three species. These three species achieved only one-half maximal growth rate under the same conditions and could be considered growth integrators. The type of integration could be predicted from the degree of stoichiometric homeostasis. Species with weak homeostatic regulation exhibited a capacity for resource integration. Resource integrators should have an advantage in heterogeneous environments.

Keywords: ecological stoichiometry, homeostasis, *Daphnia*, phosphorus limitation, phosphorus storage, temporal diet mixing.

timize the intake of multiple nutrients (Behmer 2009). But biotic and abiotic factors often preclude intake of the optimal mixture (e.g., Power et al. 1989; Scrimgeour and Culp 1994; Lewis 2001; Bakker et al. 2005; Maclean et al. 2005; Hansson and Hylander 2009). When choices are restricted, strategies for integrating across heterogeneity may play key roles in ecological success and evolutionary fitness. In these situations, the long-term fitness of an individual is related to patch-specific fitness; however, the nature of integration across patches has seldom been explicitly considered.

Two approaches have been used to specify the relationships between long-term fitness and patterns of patch use. The most parsimonious approach is to experimentally identify how critical abiotic and biotic factors influence patch choice and shape long-term fitness (e.g., Power et al. 1989). This approach estimates long-term fitness within complex landscapes; however, it can be very labor intensive and case specific. It does not reliably extrapolate to novel landscapes because the relationship between patch use and fitness is not explicitly determined. The more common alternative is to identify the abiotic and biotic determinants

Some modeling efforts have been made for nonhomeostatic herbivores (Grover, 2003; Mulder and Bowden, 2007; Mulder, 2007).

The main aim of our paper is to provide the first quantitative and comprehensive understanding on how the dynamics of trophic interactions depend on stoichiometric variability of herbivores. Intuitively, when the variability is small enough, there should be same dynamics in both homeostatic and nonhomeostatic models. There should be a threshold for the switch of dynamics as the variability increases. With estimation of this threshold, we can understand when the "strict homeostasis" assumption works.

*The threshold is not unique. It depends on which bifurcation point we focus on.

Assumption: Light is sufficient, then algal growth follows the Droop's equation.

Five variables:
R - nutrient in media
A – algal carbon biomass
Q_A – algal cell quota
H – herbivore's carbon biomass
Q_H – herbivore's cell quota

Wang, H., Sterner, R.W. and Elser, J.J., 2012. On the "strict homeostasis" assumption in ecological stoichiometry. *Ecological Modelling*, *243*, pp.81-88.

Nutrient-closed model with nonhomeostatic herbivores:

dR/dt = – uptake by algae + exudation by herbivores + recycling from dead algae + recycling from dead herbivores

dA/dt = growth – death – predation

dQ_A/dt = replenishment – depletion

dH/dt = growth – death

dQ_H/dt = replenishment – depletion – exudation

$$\begin{aligned}
\frac{dR}{dt} &= -\rho_A(Q_A, R)A + \sigma_H(A, Q_A, Q_H)H + Q_A d_A A + Q_H d_H H, \\
\frac{dA}{dt} &= \mu_A \left(1 - \frac{Q_A^{min}}{Q_A}\right) A - d_A A - f(A)H, \\
\frac{dQ_A}{dt} &= \rho_A(Q_A, R) - \mu_A \left(1 - \frac{Q_A^{min}}{Q_A}\right) Q_A, \\
\frac{dH}{dt} &= \mu_H \left(1 - \frac{Q_H^{min}}{Q_H}\right) H - d_H H, \\
\frac{dQ_H}{dt} &= f(A)Q_A - \mu_H \left(1 - \frac{Q_H^{min}}{Q_H}\right) Q_H - \sigma_H(A, Q_A, Q_H),
\end{aligned}$$

where

$$\begin{aligned}
\rho_A(Q_A, R) &= V_A \left(\frac{R}{a_A + R}\right) \left(\frac{Q_A^{max} - Q_A}{Q_A^{max} - Q_A^{min}}\right), \\
\sigma_H(A, Q_A, Q_H) &= f(A)Q_A \left[1 - \frac{Q_H^{max} - Q_H}{Q_H^{max} - Q_H^{min}}\right], \\
f(A) &= \frac{c_H A}{a_H + A}, \\
Q_A^{max} &= X_A Q_A^{min}, \\
Q_H^{max} &= X_H Q_H^{min},
\end{aligned}$$

X_A	stoichiometric variability indicator of algae	no unit	5-12
X_H	stoichiometric variability indicator of herbivores	no unit	1-3
η_A	stoichiometric variability of algae	no unit	$X_A - 1$
η_H	stoichiometric variability of herbivores	no unit	$X_H - 1$
Q_A^{min}	minimal algal cell quota (structural nutrient content)	mgP/mgC	0.004
Q_A^{max}	maximal algal cell quota	mgP/mgC	varied with X_A
Q_H^{min}	minimal herbivore's cell quota (structural nutrient content)	mgP/mgC	0.025
Q_H^{max}	maximal herbivore's cell quota	mgP/mgC	varied with X_H
V_A	maximal uptake rate of nutrient by algae	$mgP/mgC/day$	0.2-1
a_A	half-saturation constant for nutrient uptake by algae	mgP/L	0.0015
c_H	maximal predation rate	$/day$	0.75
a_H	half-saturation constant for predation	mgC/L	0.25
μ_A	intrinsic growth rate of algae	$/day$	1
d_A	algal specific maintenance respiration loss rate	$/day$	0.1
μ_H	intrinsic growth rate of herbivores	$/day$	0.5
d_H	per capita mortality rate of herbivores	$/day$	0-0.2, median 0.08

Here, we use phosphorus as an example for the nutrient element.

The parameter X_A can reach up to 12 (Sterner and Elser, 2002), that is, the stoichiometric variability of algae η_A can reach up to 1100%; the parameter X_H can reach up to 3, (Daphnia pulex in Experiment 1 of Hood and Sterner, 2010), that is, the stoichiometric variability of herbivores η_H can reach up to 200%.

It is easy to see that the total nutrient in the system
$TR(t)=R(t)+A(t)Q_A(t)+H(t)Q_H(t)$
is constant, i.e., $dTR/dt=0$.
Hence, it is a nutrient-closed system.

Mathematically, we use this observation to reduce the system to be a four-dimensional system.

The hard dynamical threshold is mathematically defined as the value of stoichiometric variability for the stability switch of the herbivore's extinction equilibrium $(\bar{A}, \bar{Q}_A, 0, \bar{Q}_H)$, with

$$\begin{aligned}
\bar{Q}_A &= \frac{\mu_A Q_A^{min}}{\mu_A - d_A}, \\
\bar{A} &= \frac{(a_A + TR)\phi(\bar{Q}_A) - TR}{\bar{Q}_A(\phi(\bar{Q}_A) - 1)}, \\
\bar{Q}_H &= \frac{f(\bar{A})\bar{Q}_A Q_H^{max} + \mu_H Q_H^{min}(Q_H^{max} - Q_H^{min})}{f(\bar{A})\bar{Q}_A + \mu_H(Q_H^{max} - Q_H^{min})},
\end{aligned}$$

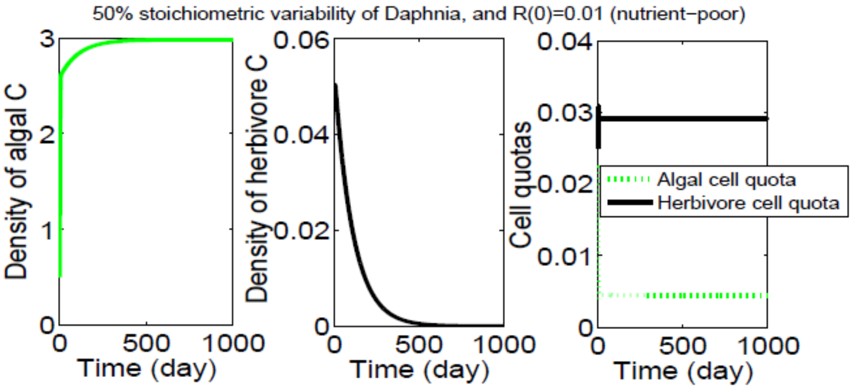
$$\text{where } \phi(\bar{Q}_A) = \frac{\mu_A(Q_A^{max} - Q_A^{min})}{V_A} \frac{\bar{Q}_A - Q_A^{min}}{Q_A^{max} - \bar{Q}_A}.$$

Other interesting dynamical thresholds can be obtained from models with more environmental conditions such as light. For example, we can discuss high grazer/low algal versus low grazer/high algal systems if we incorporate light intensity into the model. Under intermediate light intensities, herbivores always survive with or without stoichiometric variability. For this scenario, we can compute steady state level or limit cycle (Hopf Bif or Global Bif of Cycles) to compare the case “variable C:N:P ratio of herbivores” and the case “fixed C:N:P ratio of herbivores”.

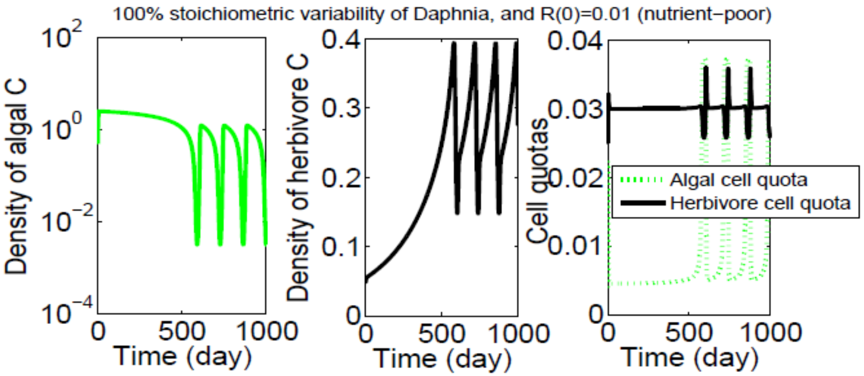
Why do we focus on the hard dynamical threshold first?

The hard dynamical threshold we obtain in this paper is most robust because it is qualitatively defined, and most interesting because the main qualitative difference between stoichiometric predator-prey models and nonstoichiometric predator-prey models occurs at sufficiently high light intensities (Loladze et al., 2000; Wang et al., 2008).

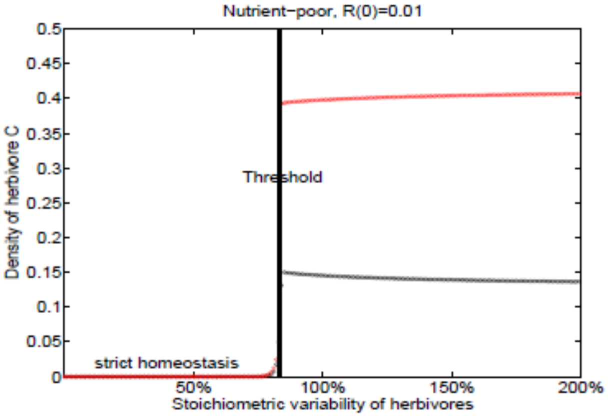
When stoichiometric variability of herbivores is greater than 83%, the dynamics will be different from the homeostatic case. Actually, stoichiometric variability of herbivores is still far less than that of algae (400%-1100%). Thus, the sensitivity of dynamics with respect to stoichiometric variability of herbivores is much higher than with respect to that of algae.



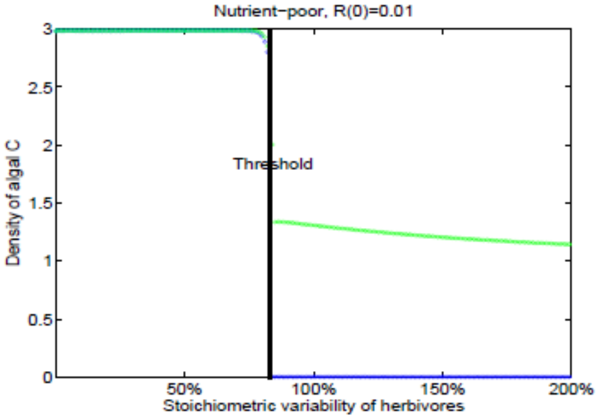
50% stoichiometric variability of Daphnia, and R(0)=0.01 (nutrient−poor)



100% stoichiometric variability of Daphnia, and R(0)=0.01 (nutrient−poor)



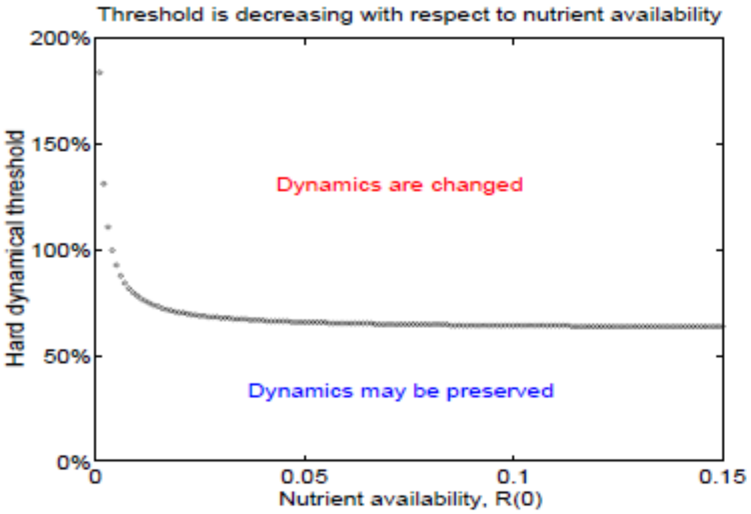
Nutrient−poor, R(0)=0.01

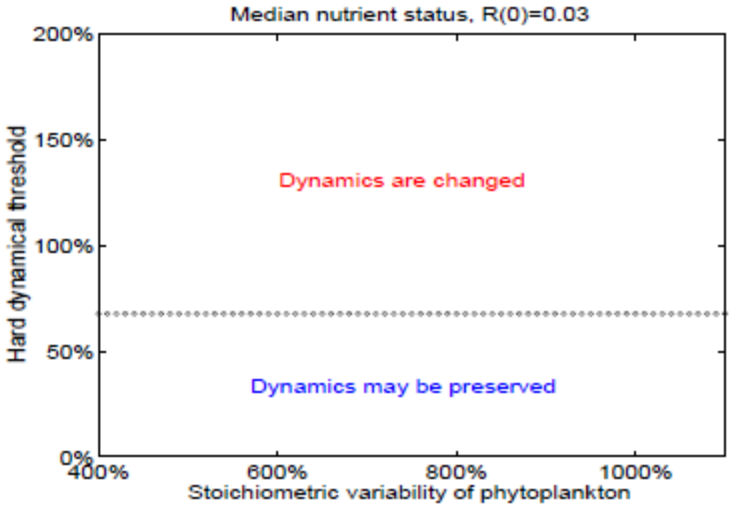


Nutrient−poor, R(0)=0.01

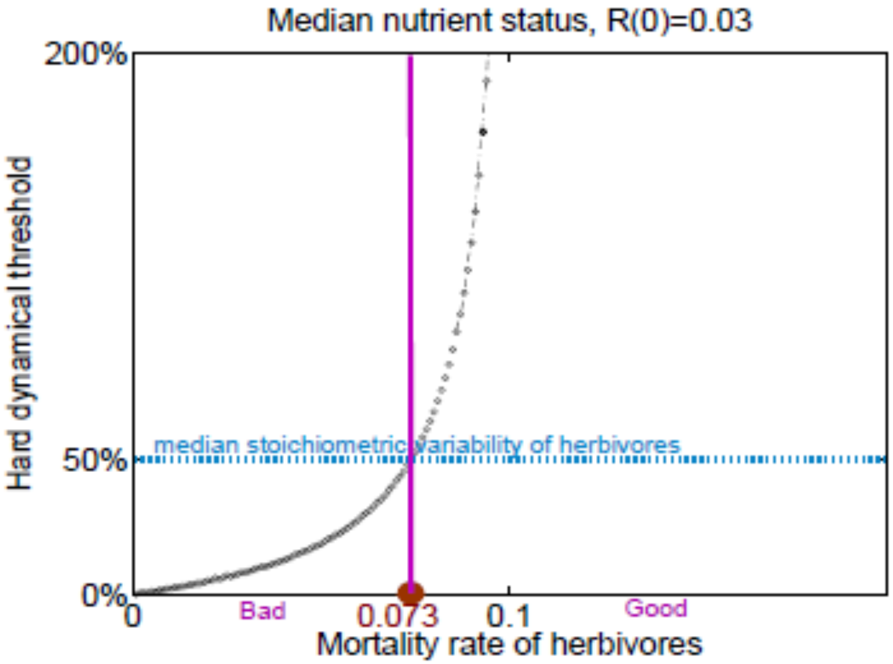
nutrient-poor

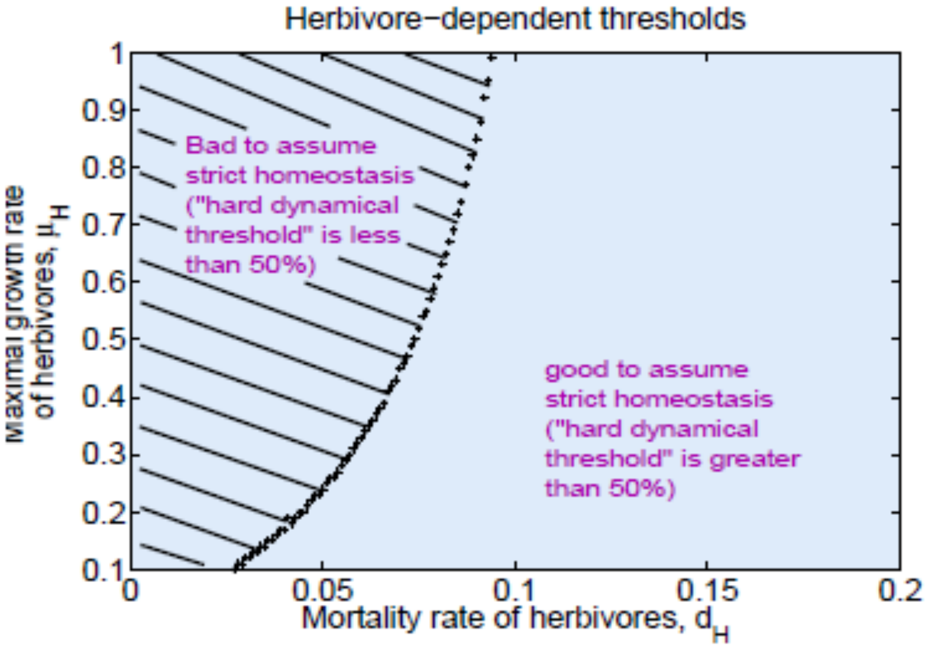
- When the nutrient is more limiting, the hypothesis is more likely valid; when the nutrient is not extremely limiting, the hard dynamical threshold is a constant.
- The threshold is independent of algal stoichiometric variability. The historic reasoning makes no sense here.





- The "homeostatic herbivores" assumption makes sense when the stoichiometric variability of herbivores is less than 67.*6%.*


Median nutrient status, R(0)=0.03
200%
50%
0%
Hard dynamical threshold
median stoichiometric variability of herbivores
0
Bad
0.073
0.1
Good
Mortality rate of herbivores


Herbivore−dependent thresholds
Bad to assume strict homeostasis ("hard dynamical threshold" is less than 50%)
good to assume strict homeostasis ("hard dynamical threshold" is greater than 50%)
maximal growth rate of herbivores, μ_H
Mortality rate of herbivores, d_H
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.05
0.1
0.15
0.2

Conclusions

- The "strict homeostasis" hypothesis sounds when the stoichiometric variability of herbivores is less than a threshold (67.6% under the median nutrient availability).

- The median herbivore's stoichiometric variability is about 50%, less than our default threshold, accepting the "strict homeostasis" hypothesis for many herbivores. Since the threshold strongly depends on herbivore's traits such as turnover rates, the hypothesis can be invalid for some herbivores.

- The hard dynamical threshold is independent of algal stoichiometric variability, rejecting the historic reasoning for the hypothesis.

- The hypothesis is more likely valid when nutrient is more limiting.

Wang, H., Sterner, R.W. and Elser, J.J., 2012. On the "strict homeostasis" assumption in ecological stoichiometry. *Ecological Modelling*, *243*, pp.81-88.

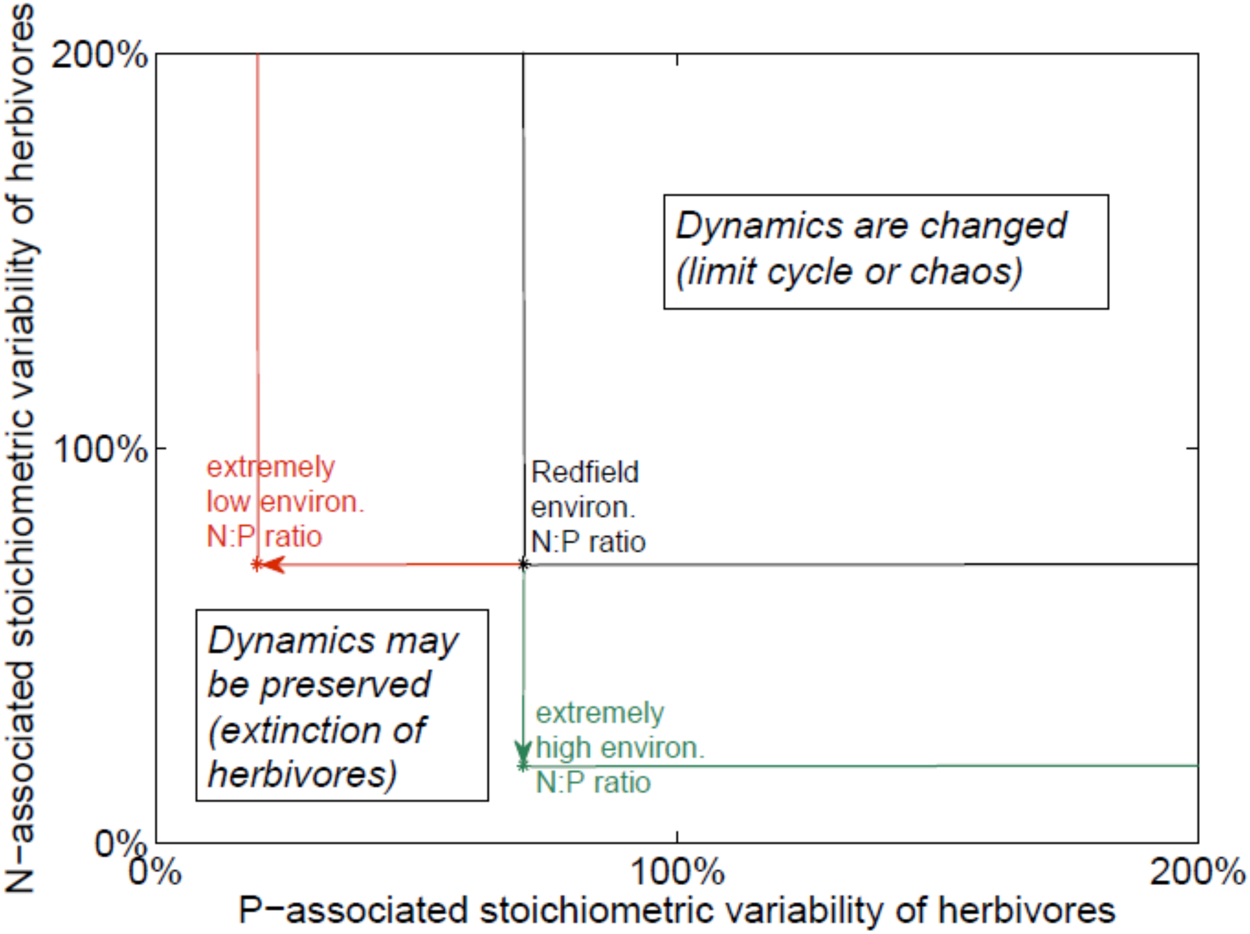
To discuss the multi-nutrient case, we consider both N- and P-associated nonhomeostasis of herbivores.

Model extension to multiple nutrients (after applying the conservation law of nutrient elements)

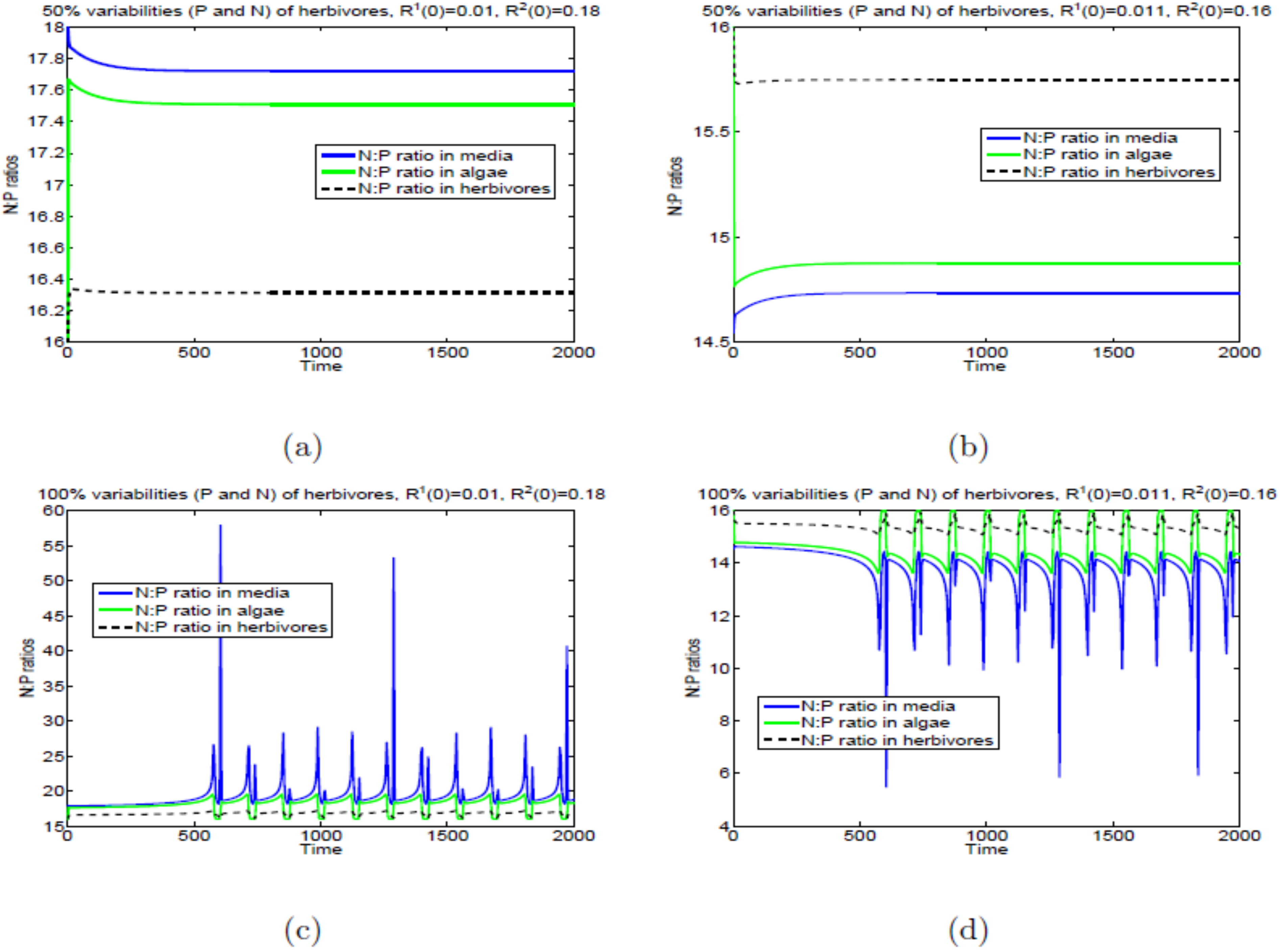
$$\begin{aligned}
\frac{dA}{dt} &= \mu_A \min_i \left(1 - \frac{Q_A^{i,min}}{Q_A^i}\right) A - d_A A - f(A)H, \\
\frac{dQ_A^i}{dt} &= \rho_A^i(Q_A^i, R^i) - \mu_A \min_i \left(1 - \frac{Q_A^{i,min}}{Q_A^i}\right) Q_A^i, \\
\frac{dH}{dt} &= \mu_H \min_i \left(1 - \frac{Q_H^{i,min}}{Q_H^i}\right) H - d_H H, \\
\frac{dQ_H^i}{dt} &= f(A)Q_A^i - \mu_H \min_i \left(1 - \frac{Q_H^{i,min}}{Q_H^i}\right) Q_H^i - \sigma_H^i(A, Q_A^i, Q_H^i).
\end{aligned}$$

where

$$\begin{aligned}
\rho_A^i(Q_A^i, R^i) &= V_A^i \left(\frac{R^i}{a_A^i + R^i}\right) \left(\frac{Q_A^{i,max} - Q_A^i}{Q_A^{i,max} - Q_A^{i,min}}\right), \\
R^i &= TR^i - AQ_A^i - HQ_H^i, \\
\sigma_H^i(A, Q_A^i, Q_H^i) &= f(A)Q_A^i \left[1 - \frac{Q_H^{i,max} - Q_H^i}{Q_H^{i,max} - Q_H^{i,min}}\right], \\
f(A) &= \frac{c_H A}{a_H + A}, \\
Q_A^{i,max} &= X_A^i Q_A^{i,min}, \\
Q_H^{i,max} &= X_H^i Q_H^{i,min},
\end{aligned}$$



Dynamics are more sensitive to N-associated stoichiometric variability when the environmental N:P ratio shifts from the Redfield ratio to be higher, while dynamics are more sensitive to P-associated stoichiometric variability when the environmental N:P shifts from the Redfield ratio to be lower.

50% variabilities (P and N) of herbivores, R¹(0)=0.01, R²(0)=0.18
N:P ratios
Time
N:P ratio in media
N:P ratio in algae
N:P ratio in herbivores
18
17.8
17.6
17.4
17.2
17
16.8
16.6
16.4
16.2
16
0
500
1000
1500
2000
50% variabilities (P and N) of herbivores, R¹(0)=0.011, R²(0)=0.16
N:P ratios
Time
N:P ratio in media
N:P ratio in algae
N:P ratio in herbivores
16
15.5
15
14.5
0
500
1000
1500
2000
100% variabilities (P and N) of herbivores, R¹(0)=0.01, R²(0)=0.18
N:P ratios
Time
N:P ratio in media
N:P ratio in algae
N:P ratio in herbivores
60
55
50
45
40
35
30
25
20
15
0
500
1000
1500
2000
100% variabilities (P and N) of herbivores, R¹(0)=0.011, R²(0)=0.16
N:P ratios
Time
N:P ratio in media
N:P ratio in algae
N:P ratio in herbivores
16
14
12
10
8
6
4
0
500
1000
1500
2000

(a)

(b)

(c)

(d)

We assume turnover rates increase proportionally with a same rate: the intrinsic growth rate $\mu_H = 0.5\alpha$ and the per capita mortality rate $d_H = 0.08\alpha$, and then we decrease or increase α from one.

$\alpha =$	0.5	0.6	0.7	0.8	0.9	1	1.1	1.2	1.3
Threshold	25.6%	31.6%	37.6%	43.6%	52.6%	70.6%	100.6%	175.6%	>200%

When the turnover rates are small, the sensitivity of the threshold is low; when the turnover rates are large, the sensitivity of the threshold is high. When the turnover multiplier α increases, the threshold increases and thus the "strict homeostasis" hypothesis is more likely valid.

Wang, H., Sterner, R.W. and Elser, J.J., 2012. On the "strict homeostasis" assumption in ecological stoichiometry. *Ecological Modelling*, *243*, pp.81-88.

What is the impact of light intensity?

Critical thresholds other than the hard dynamical threshold?

Light dependent algal growth

- Loladze et al. have taken carrying capacity increase to be equivalent to light increase
- This may not be true since when algal density increases, the medium gets denser (greener)
- Lambert-Beer law must include density dependence in attenuation coefficient
- Lambert-Beer law - light intensity will drop in an exponential form, when random scatters are present.
  - Generally true for *dilute* media. Here, *k* is absorption coefficient and I_{in} is the light at z=0.

$$I = I_{in}e^{-kz}$$

- Assume well-mixed condition, i.e., algae are uniformly mixed throughout the medium
- $k=K_{bg}+K_A A$

Different light intensities leads to different green discolorations of the medium, owing to more algal growth

Light dependent algal growth

- Under the well-mixed argument, we see that the algal growth rate will depend not only on nutrient uptake rate from Droop's equation, but also on the integrated light energy available to the algae

$$
\begin{aligned}
b_A &= \mu_A \min\left(1-\frac{Q_A^{\min}}{Q_A}, \frac{1}{z_m}\int_0^{z_m}\frac{I(z,A)}{I(z,A)+D}\,dz\right)\\
&= \mu_A \min\left(1-\frac{Q_A^{\min}}{Q_A}, \frac{1}{z_m(K_{bg}+K_A A)}\ln\frac{D+I_{in}}{D+I(z_m,A)}\right)
\end{aligned}
$$

Wang, H., Lu, Z. and Raghavan, A., 2018. Weak dynamical threshold for the "strict homeostasis" assumption in ecological stoichiometry. *Ecological Modelling*, *384*, pp.233-240.

New model with light dependence

$$\frac{\mathrm{dR}}{\mathrm{dt}} = -\rho_A(Q_A, R)A + \sigma_H(A, Q_A, Q_H)H + Q_A d_A A + Q_H d_H H, \tag{1}$$

$$\frac{\mathrm{dA}}{\mathrm{dt}} = \mu_A \min\left[1 - \frac{Q_A^{\min}}{Q_A}, \frac{1}{z_m}\int_0^{z_m} \frac{I(z, A)}{I(z, A) + L}\mathrm{dz}\right]A - f(A)H - d_A A, \tag{2}$$

$$\frac{\mathrm{dQ}_A}{\mathrm{dt}} = \rho_A(Q_A, R) - \mu_A \min\left[1 - \frac{Q_A^{\min}}{Q_A}, \frac{1}{z_m}\int_0^{z_m} \frac{I(z, A)}{I(z, A) + L}\mathrm{dz}\right]Q_A, \tag{3}$$

$$\frac{\mathrm{dH}}{\mathrm{dt}} = \min\left[\mu_H\left(1 - \frac{Q_H^{\min}}{Q_H}\right), \hat{e}f(A)\right]H - d_H H, \tag{4}$$

$$\frac{\mathrm{dQ}_H}{\mathrm{dt}} = f(A)Q_A - \min\left[\mu_H\left(1 - \frac{Q_H^{\min}}{Q_H}\right), \hat{e}f(A)\right]Q_H - \sigma_H(A, Q_A, Q_H), \tag{5}$$

$$\rho_A(Q_A, R) = V_A\left(\frac{R}{a_A + R}\right)\left(\frac{Q_A^{\max} - Q_A}{Q_A^{\max} - Q_A^{\min}}\right),$$

$$\sigma_H(A, Q_A, Q_H) = f(A)Q_A\left[1 - \frac{Q_H^{\max} - Q_H}{Q_H^{\max} - Q_H^{\min}}\right],$$

$$I(z, A) = I_{\mathrm{in}}e^{-(K_{\mathrm{bg}}+\mathrm{k}A)z},$$

$$f(A) = \frac{c_H A}{a_H + A},$$

$$Q_A^{\max} = X_A Q_A^{\min},$$

$$Q_H^{\max} = X_H Q_H^{\min}.$$

Wang, H., Lu, Z. and Raghavan, A., 2018. Weak dynamical threshold for the “strict homeostasis” assumption in ecological stoichiometry. *Ecological Modelling*, *384*, pp.233-240.

New model with light-dependent term

- The model is reducible to 4d via the conservation law

$$TR(t) = R(t) + A(t)Q_A(t) + H(t)Q_H(t) = \text{constant}$$

- The point (A=0, $Q_A = Q_a^{min}$, H =0, $Q_H = Q_H^{min}$) is a saddle point
- Herbivores go extinct if one of the following holds:
  - Strong light and “low” stoichiometric variability

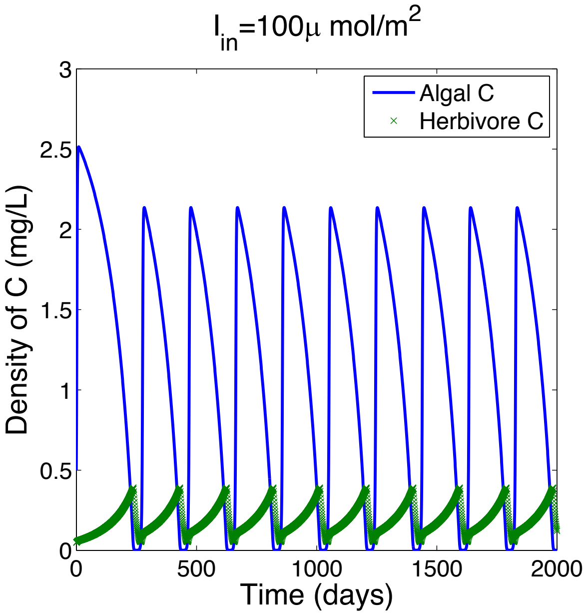
$$I_{in} \to \infty, \qquad \chi_H \approx 1$$

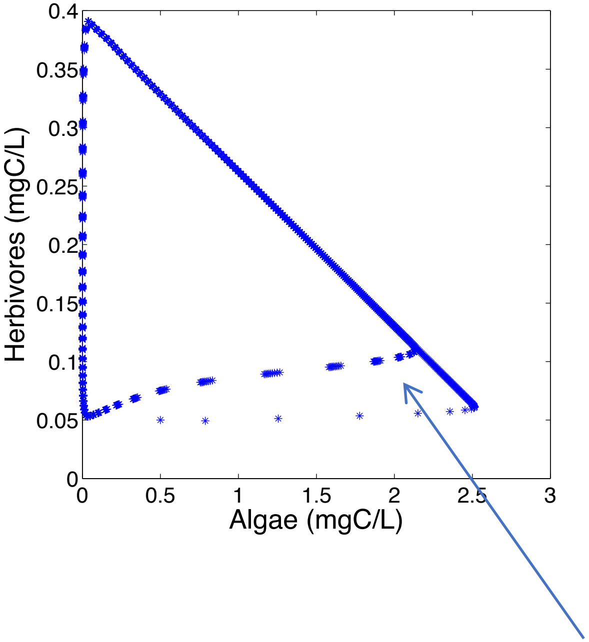
  - Very low light condition, any stoichiometric variability

$$I_{in} \to 0$$

- Model reduction admits Loladze-Kuang-Elser like bifurcation diagram for fixed herbivore quota ($Q_H > Q_H^{min}$)

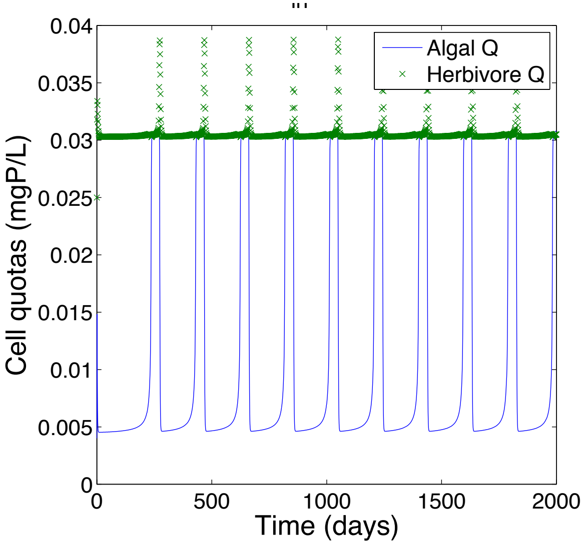
Basic dynamics with light dependence





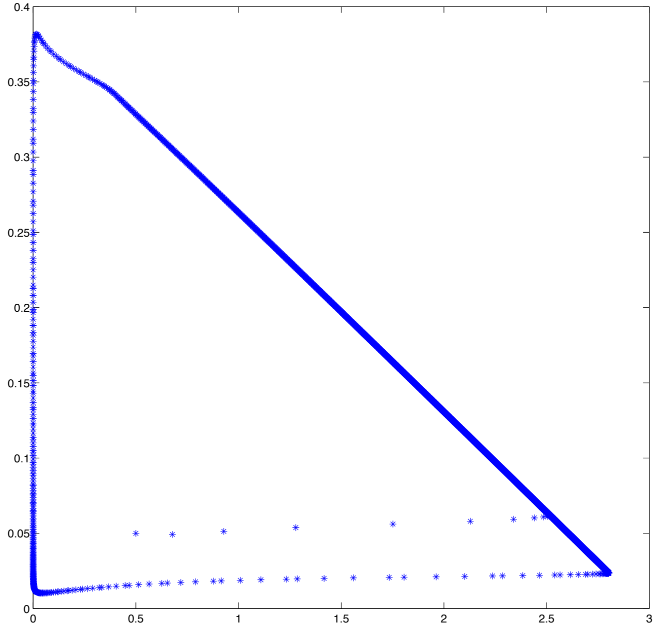
Regular periodic orbit

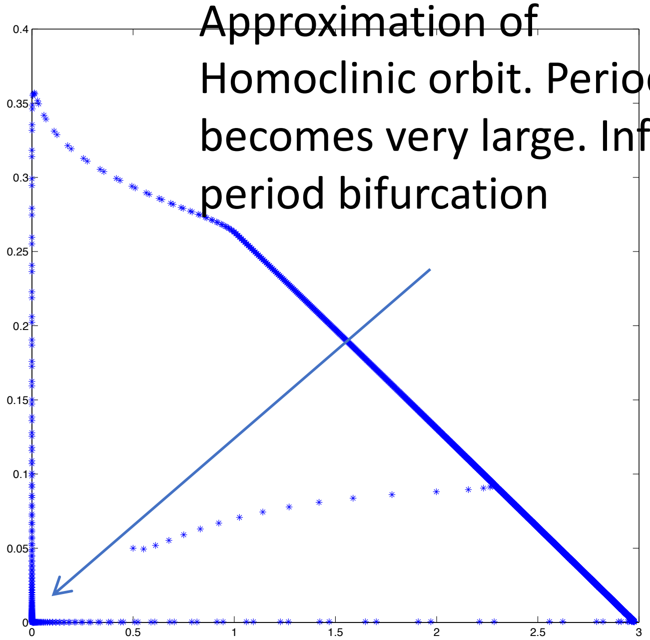
R(0) = 0.01 mgP/L



Under strong light, we have regular predator-prey type dynamics

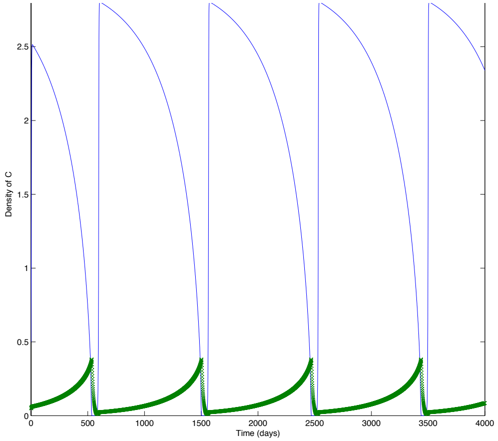
Homoclinic orbits and bifurcations



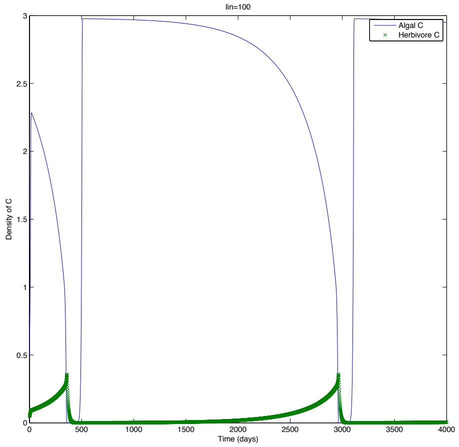


Approximation of Homoclinic orbit. Period becomes very large. Infinite period bifurcation

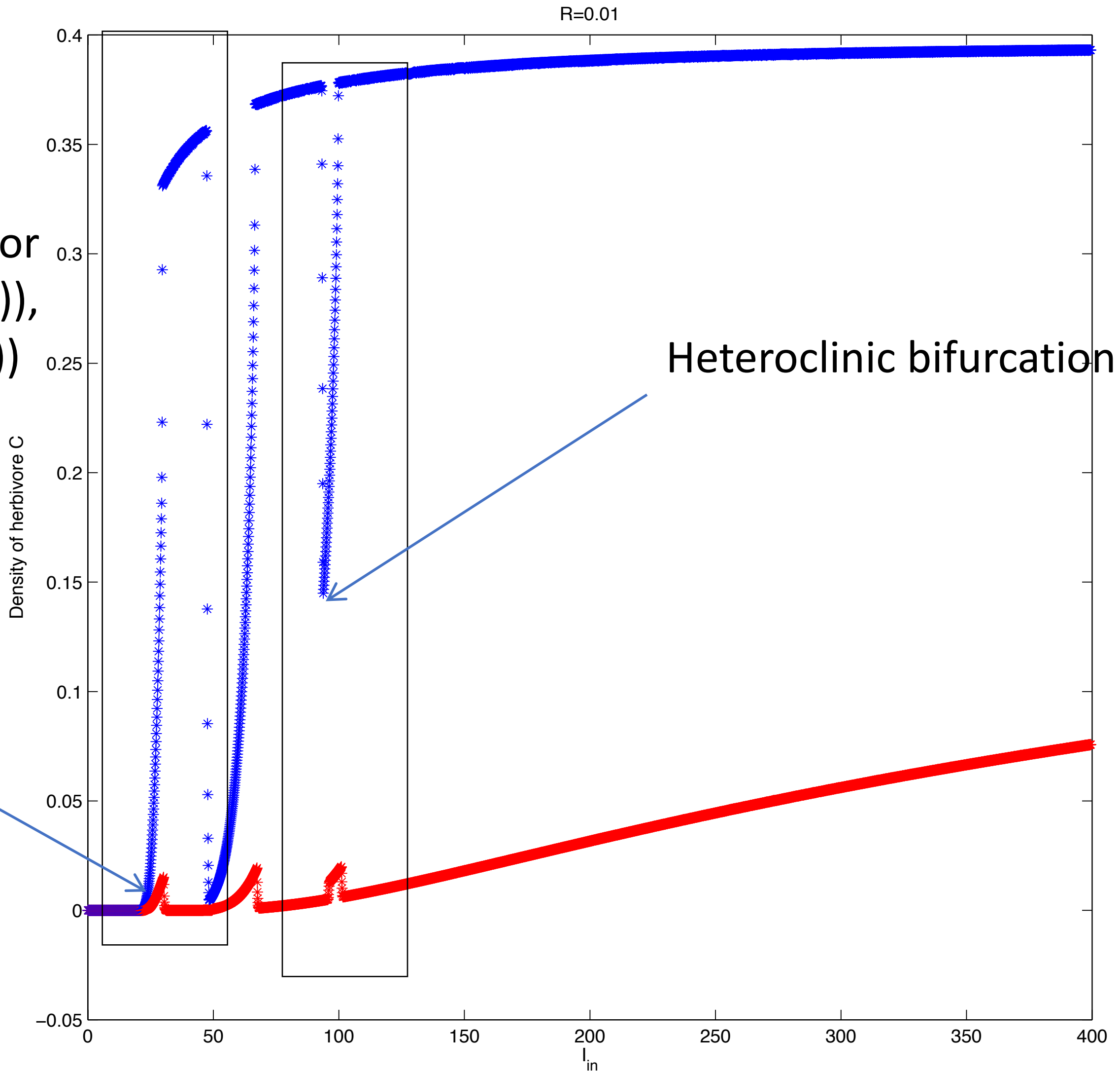
I_{in}=55µmol/m^2
R(0) = 0.01 mgP/



I_{in} =48µmol/m^2
R(0) = 0.01 mgP/L



Homoclinic bifurcations, the low nutrient case R(0) = 0.01 mgP/L



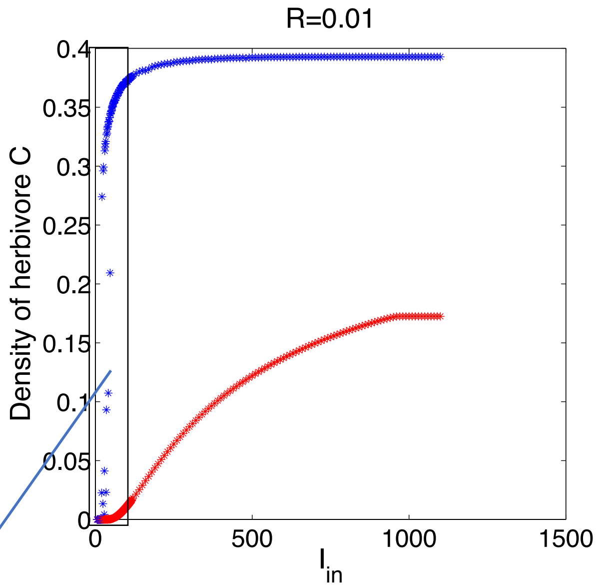
Bifurcation Diagram for max(herbivores(t->∞)), min(herbivores(t->∞))

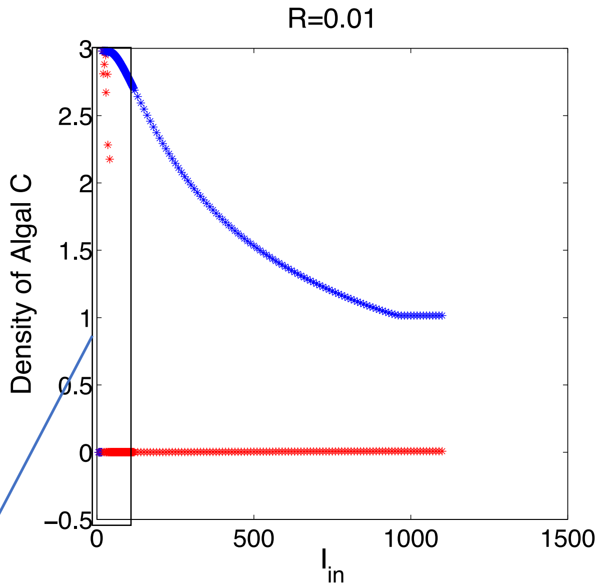
Heteroclinic bifurcation

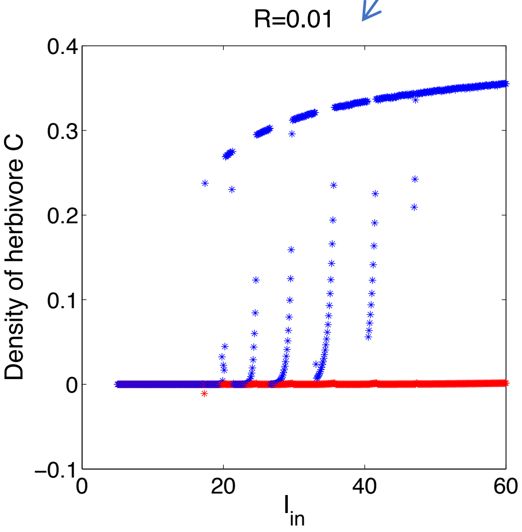
Series of homoclinic bifurcations

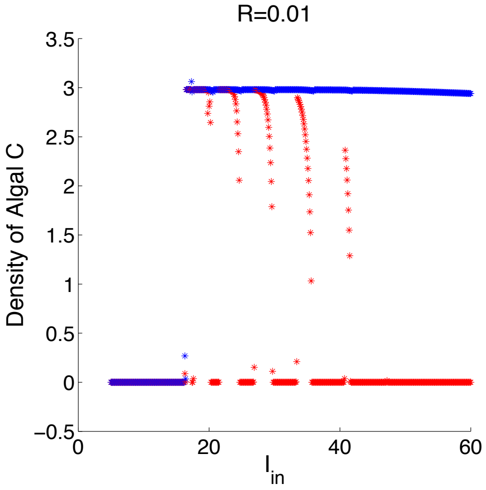
Homoclinic bifurcations, the low nutrient case R(0) = 0.01 mgP/L

Bifurcation Diagram for max(algae(t->∞)), min(algae(t->∞))



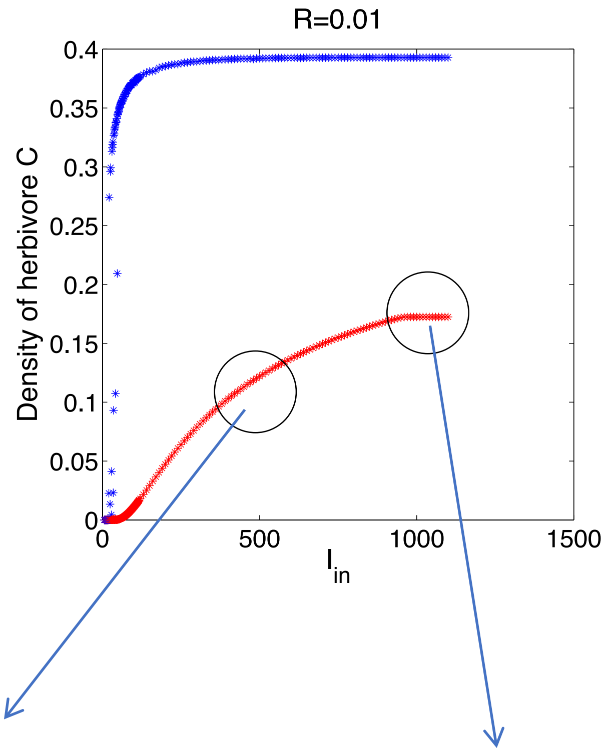


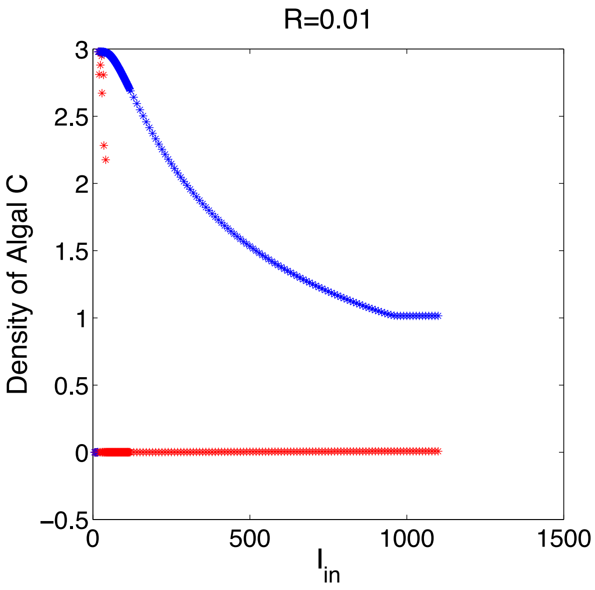




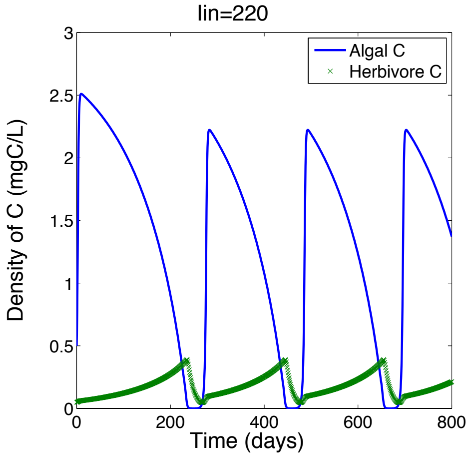
Bifurcation Diagram for max(herbivores(t->∞)), min(herbivores(t->∞))

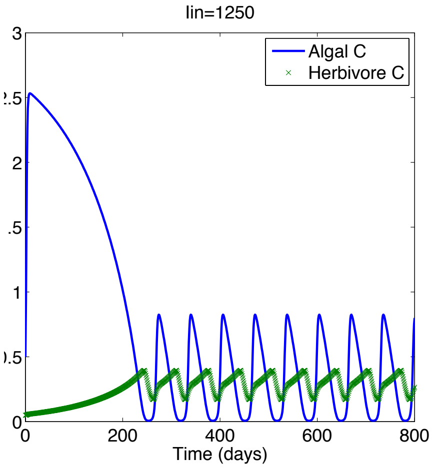
Bifurcation Diagram for
max(algae(t->∞)),
min(algae(t->∞))



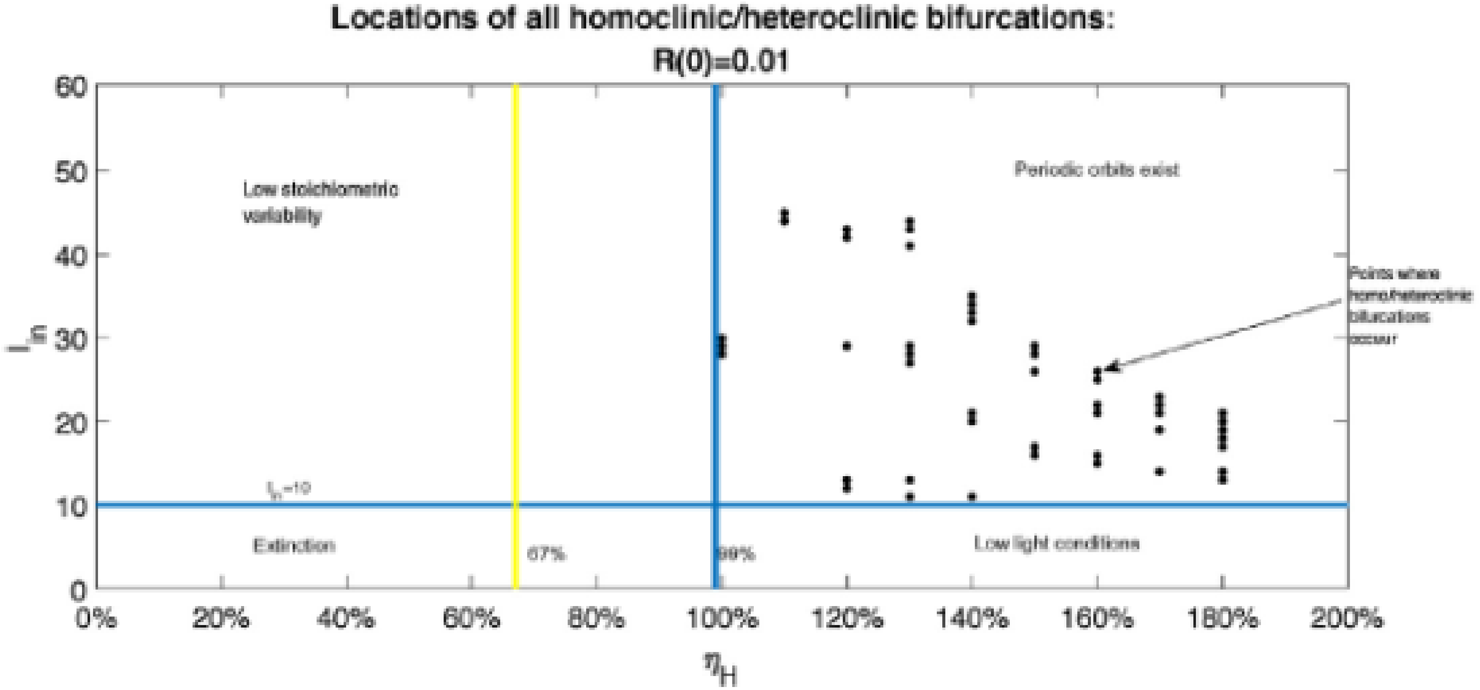


Bifurcation Diagram for
max(herbivores(t->∞)),
min(herbivores(t->∞))



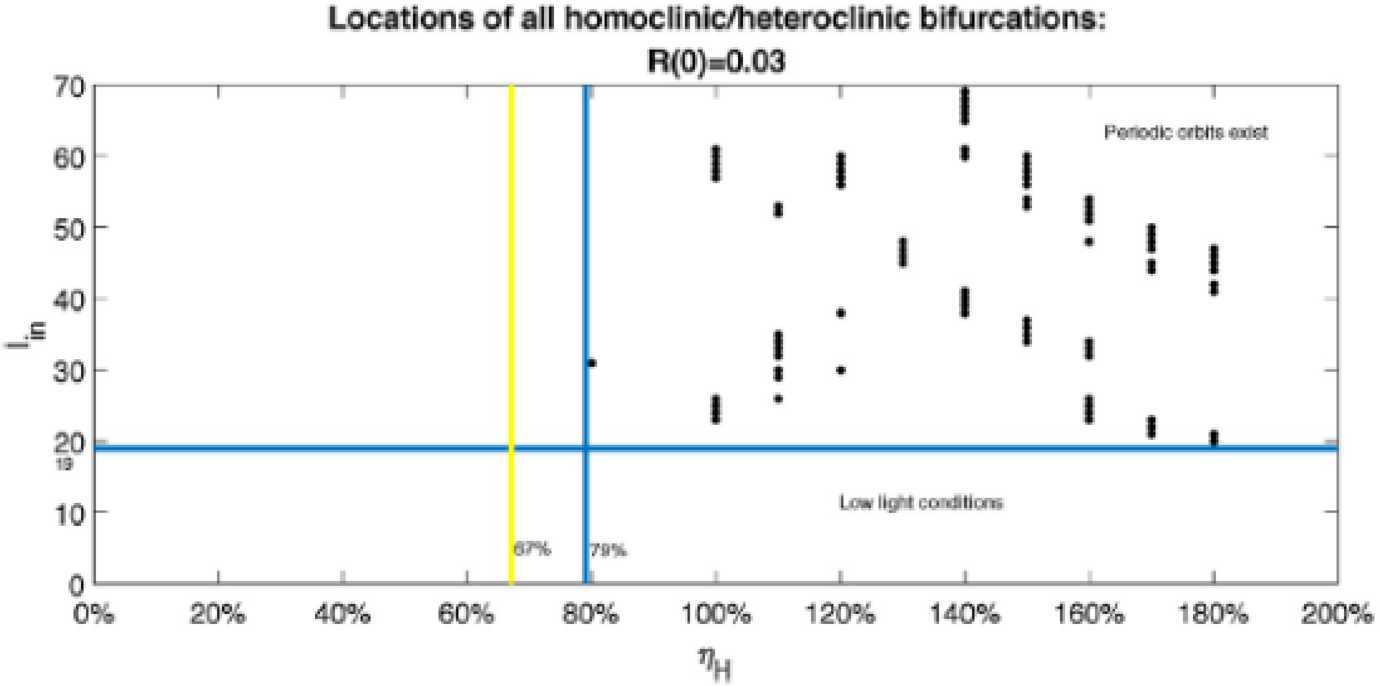


Low nutrient



Locations of all homoclinic/heteroclinic bifurcations: R(0)=0.01

High nutrient



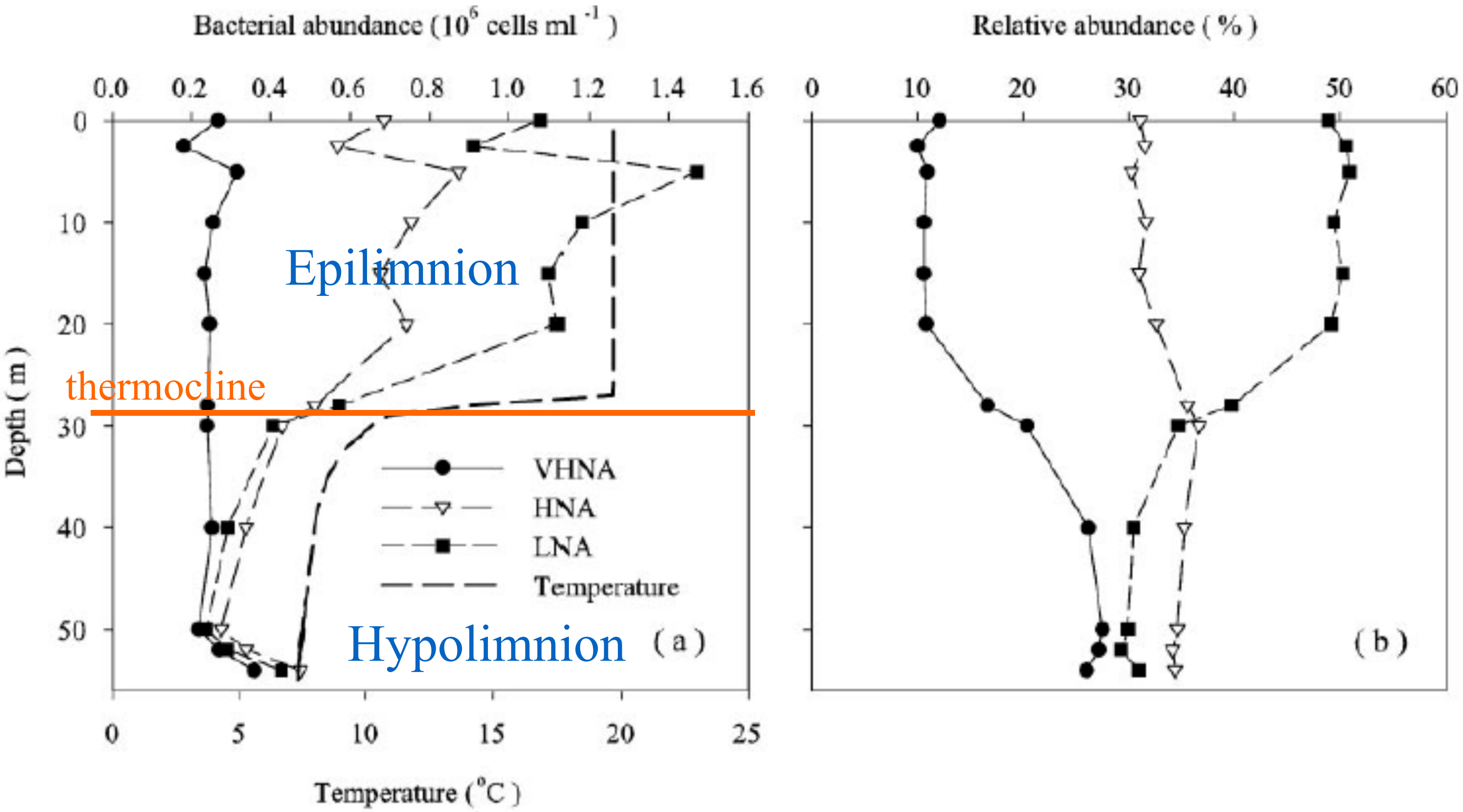
Locations of all homoclinic/heteroclinic bifurcations: R(0)=0.03

Concluding Remarks

- The validity of the strict homeostasis condition is worth questioning.
- The “weak dynamical threshold” for stoichiometric variability is 79–99% as opposed to the “hard dynamical threshold” 67% on “strict homeostasis”.
- Introduction of light creates very interesting dynamics such as homoclinic orbits and heteroclinic orbits.
- Even in the presence of high quality food and reasonable stoichiometric variability, it is possible for herbivores to go extinct (with stochasticity) via falling into a homoclinic orbit. This is a remarkable situation. Experimental results are vulnerable?

Dynamics of Stoichiometric Bacteria-Algae Interactions in the Epilimnion

Hao Wang, Hal L. Smith, Yang Kuang, and James J. Elser. 2007.
Dynamics of Stoichiometric Bacteria-Algae Interactions in the Epilimnion.
SIAM J. Appl. Math, Vol. 68, pp. 503-522.

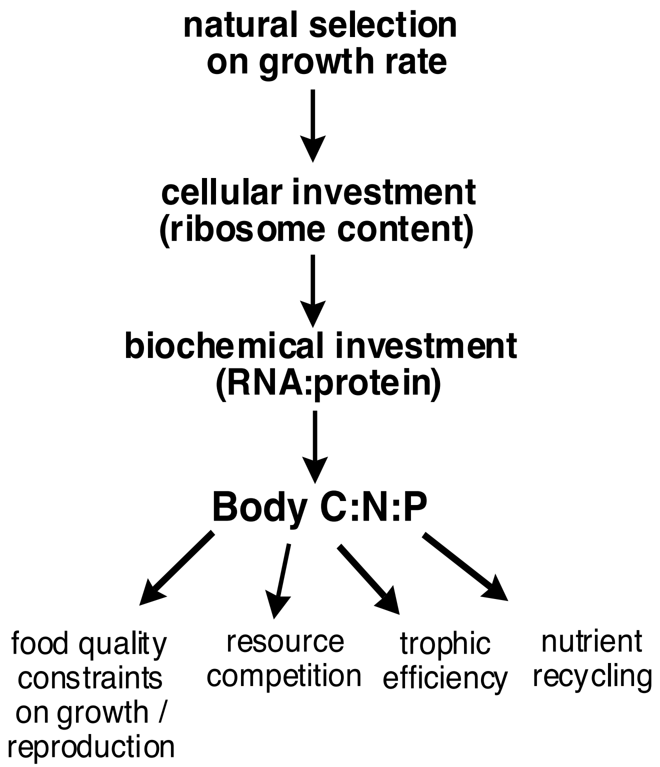


(Nishimura et al 2005, Applied and Environmental Microbiology)

Bacterial Strains

- LNA: bacterial strain with low nucleic acid contents.
- HNA: bacterial strain with high nucleic acid contents.
- VHNA: bacterial strain with very high nucleic acid contents.

The Growth Rate Hypothesis



natural selection on growth rate

cellular investment (ribosome content)

biochemical investment (RNA:protein)

Body C:N:P

food quality constraints on growth / reproduction

resource competition

trophic efficiency

nutrient recycling

VHNA + HNA vs LNA

Previous claim LNA is less active, or dormant.

Observation In late August of Lake Biwa, LNA grows faster than VHNA and HNA.

Hypothesis Probably P-limitation is severe at that time and LNA has higher nutrient uptake efficiency or lower requirements for P.

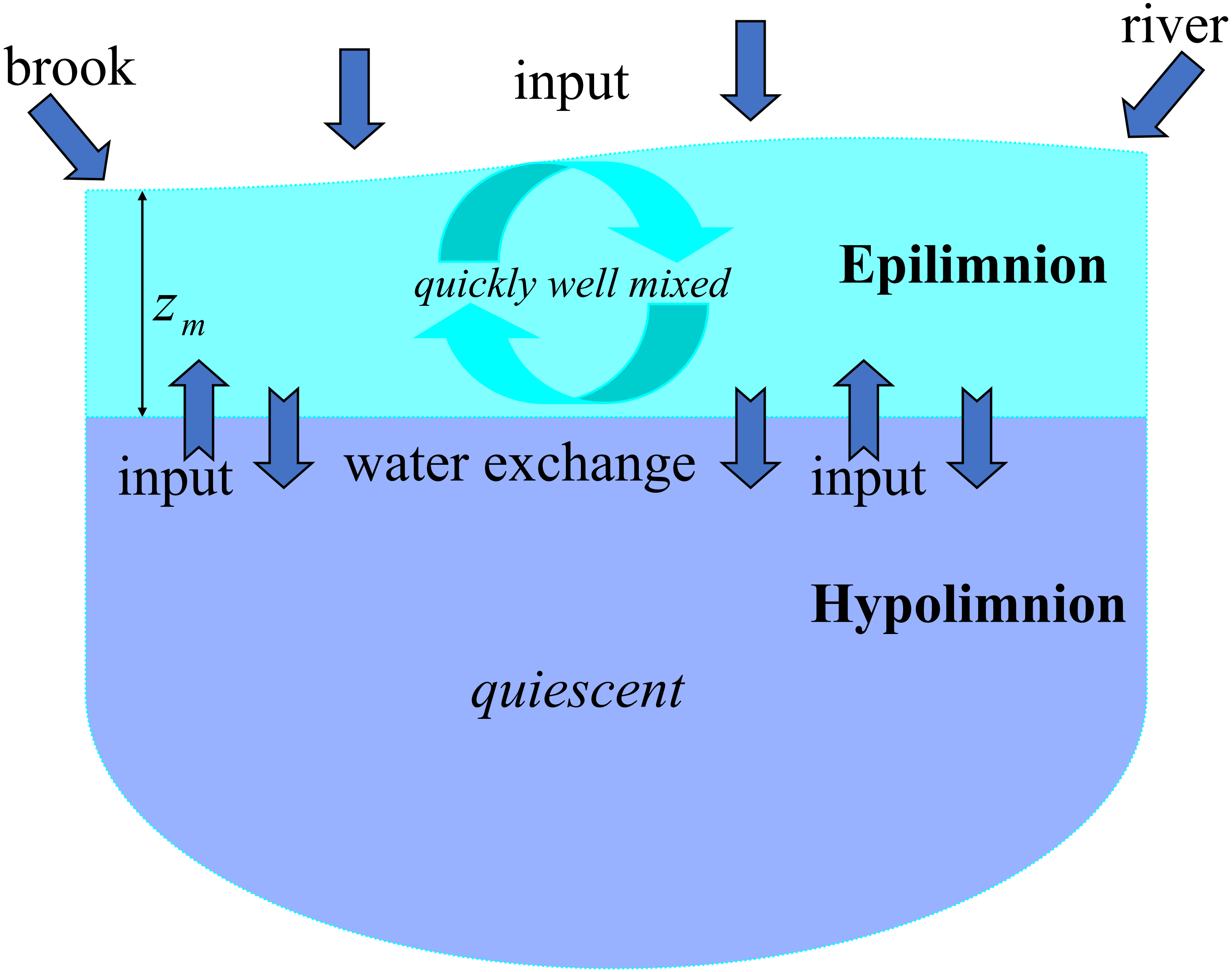
(Nishimura et al 2005, Applied and Environmental Microbiology)

In Lake Biwa,

Phosphorus is the most limiting element for species.

Organic Carbon is mainly from exudation of algae.

A Lake System



brook

input

river

z_m

quickly well mixed

Epilimnion

input

water exchange

input

Hypolimnion

quiescent

Scenario The Epilimnion is quickly well mixed in the sense that it is well mixed over night.

Assumption The Epilimnion is well mixed immediately in the time scale ‘days’.

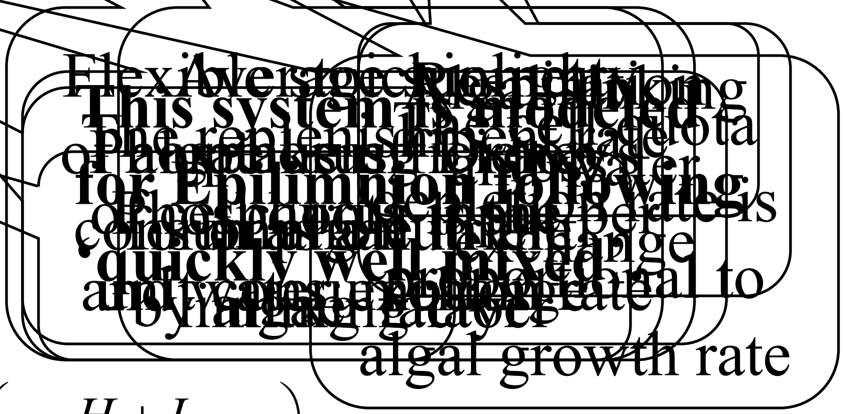
First, algae without bacteria

Algae

Cell Quota

DIP

$$
\begin{aligned}
\frac{dA}{dt} &= \mu_A A \boxed{\left(1-\frac{Q_m}{Q}\right)} \boxed{\frac{1}{z_m}\int_0^{z_m} \frac{I(s,A)}{I(s,A)+H}\,ds} - \boxed{l_m A} - \boxed{\frac{\nu + D}{z_m} A} \\
\frac{dQ}{dt} &= \boxed{\rho(Q,P)} - \boxed{\mu_A Q \left(1-\frac{Q_m}{Q}\right) \frac{1}{z_m}\int_0^{z_m} \frac{I(s,A)}{I(s,A)+H}\,ds} \\
\frac{dP}{dt} &= \boxed{\frac{D}{z_m}(P_{in}-P)} - \boxed{\rho(Q,P)A}
\end{aligned}
\tag{3.1}
$$



[illegible]

algal growth rate

where

$$I(s,A) = I_{in} \exp[-(kA + K_{bg})s]$$

$$\int_0^{z_m} \frac{I(s,A)}{I(s,A)+H}\,ds = \frac{1}{kA+K_{bg}} \ln\left(\frac{H+I_{in}}{H+I(z_m,A)}\right)$$

$$\rho(Q,P) = \rho_{\max}\left(\frac{Q_M - Q}{Q_M - Q_m}\right)\frac{P}{M+P}$$

Lemma 1. $Q_m < Q < Q_M$, whenever $Q_m < Q(0) < Q_M$.

Since positivity of all the variables holds obviously, we analyze the system (3.1) on the positively invariant set $\Omega = \{(A, Q, P) \in \Re^3_+ \big| A \geq 0, Q_m \leq Q \leq Q_M, P \geq 0\}$.

Theorem 2. Dissipativity holds. Let $S = AQ + P$, which is the total phosphorus of the system (3.1), then $\limsup_{t \to \infty} S(t) \leq P_{in}$. Therefore, $\wp = \{(A, Q, P) \in \Omega \big| AQ + P \leq P_{in}\}$ is a globally attracting region which all nonnegative solutions eventually enter and stay.

Theorem 3. The basic reproductive number for algae is

$$R_0 = \frac{\mu_A h(0)(1 - Q_m / Q)}{l_m + \frac{\nu + D}{z_m}}$$

where $h(A) = \dfrac{1}{z_m} \displaystyle\int_0^{z_m} \frac{I(s,A)}{I(s,A) + H} ds$.

Then the algae extinction steady state $E_0 = (0, \hat{Q}, P_{in})$ is

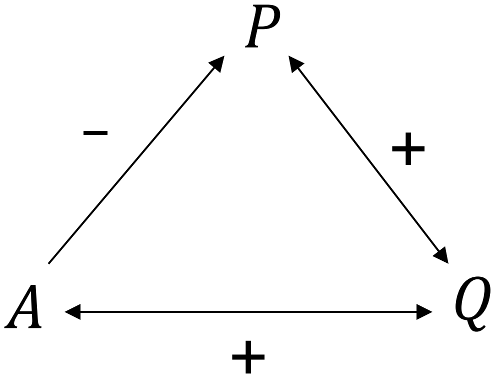
(1) locally asymptotically stable when $R_0 < 1$;

(2) unstable when $R_0 > 1$.

Theorem 4. $R_0 < 1$ implies E_0 is globally asymptotically stable. $R_0 > 1$ implies there exists a unique positive steady state E^* and algae uniformly persist : there exists $\varepsilon > 0$ such that $\liminf_{t\to\infty} A(t) > \varepsilon$ for all solutions with $A(0) > 0$.

Proof : Apply theory of monotone dynamical systems to prove the global stability. One dimension reduction.

competitive system



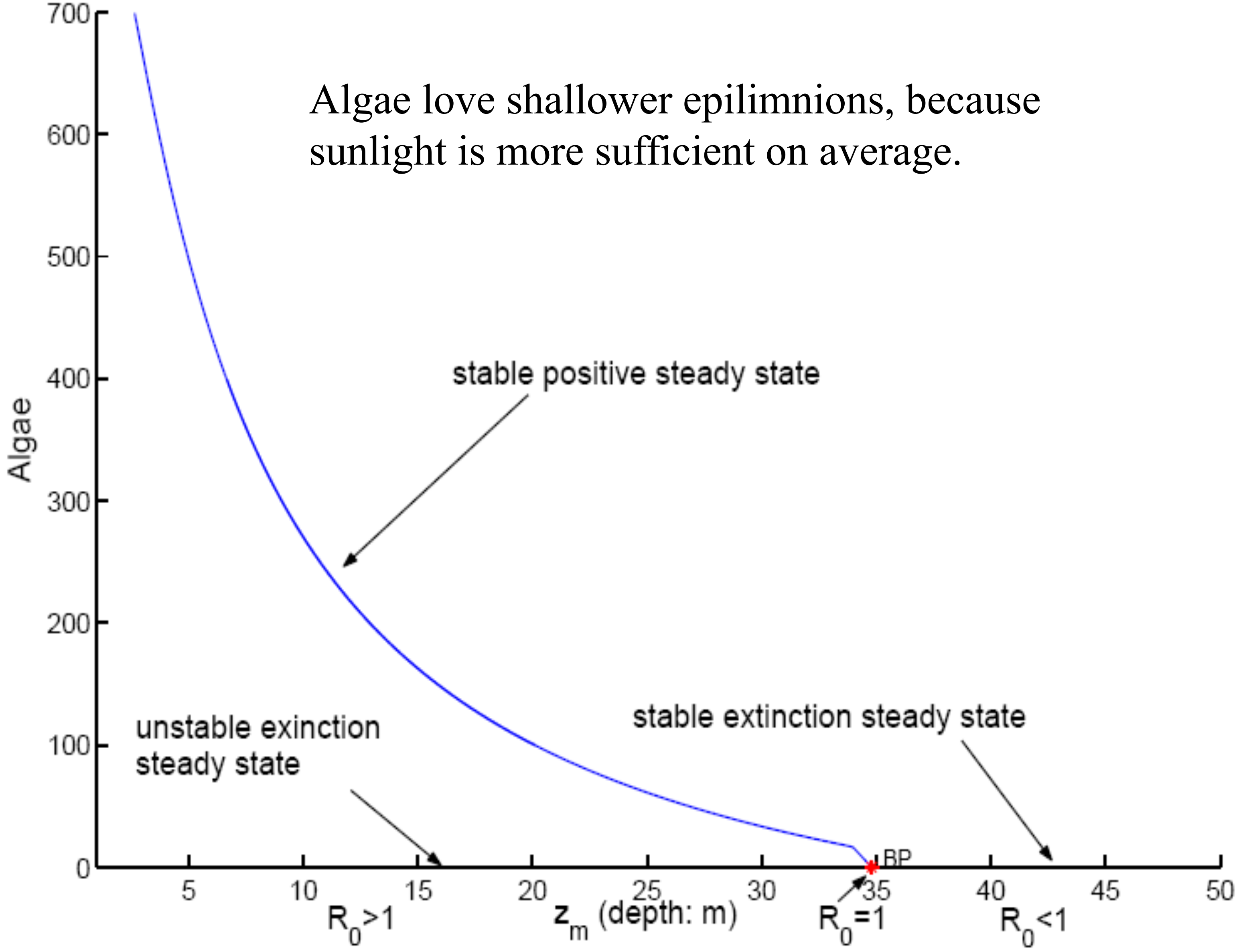
(H. L. Smith, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems, Math. Surveys Monogr. 41, AMS, Providence, RI, 1995)*

Theorem 5. E^* is globally asymptotically stable for the planar system obtained from the system (3.1) by setting $dQ/dt = 0$, when R_0>1. (Quasi-steady state approximation, since the algal cell quota changes much faster than other variables) Proof: Dulac + Poincaré–Bendixson

Theorem 6. E^* is globally asymptotically stable when $R_0 > 1$ and $l_m = \nu = 0$.

Proof: All nonnegative solutions asymptotically approach the surface $P+AQ=P_{in}$; E^* is globally asymptotically stable on the surface $P+AQ=P_{in}$ when R_0>1.

(Global stability is true whenever these two parameters are sufficiently small.)



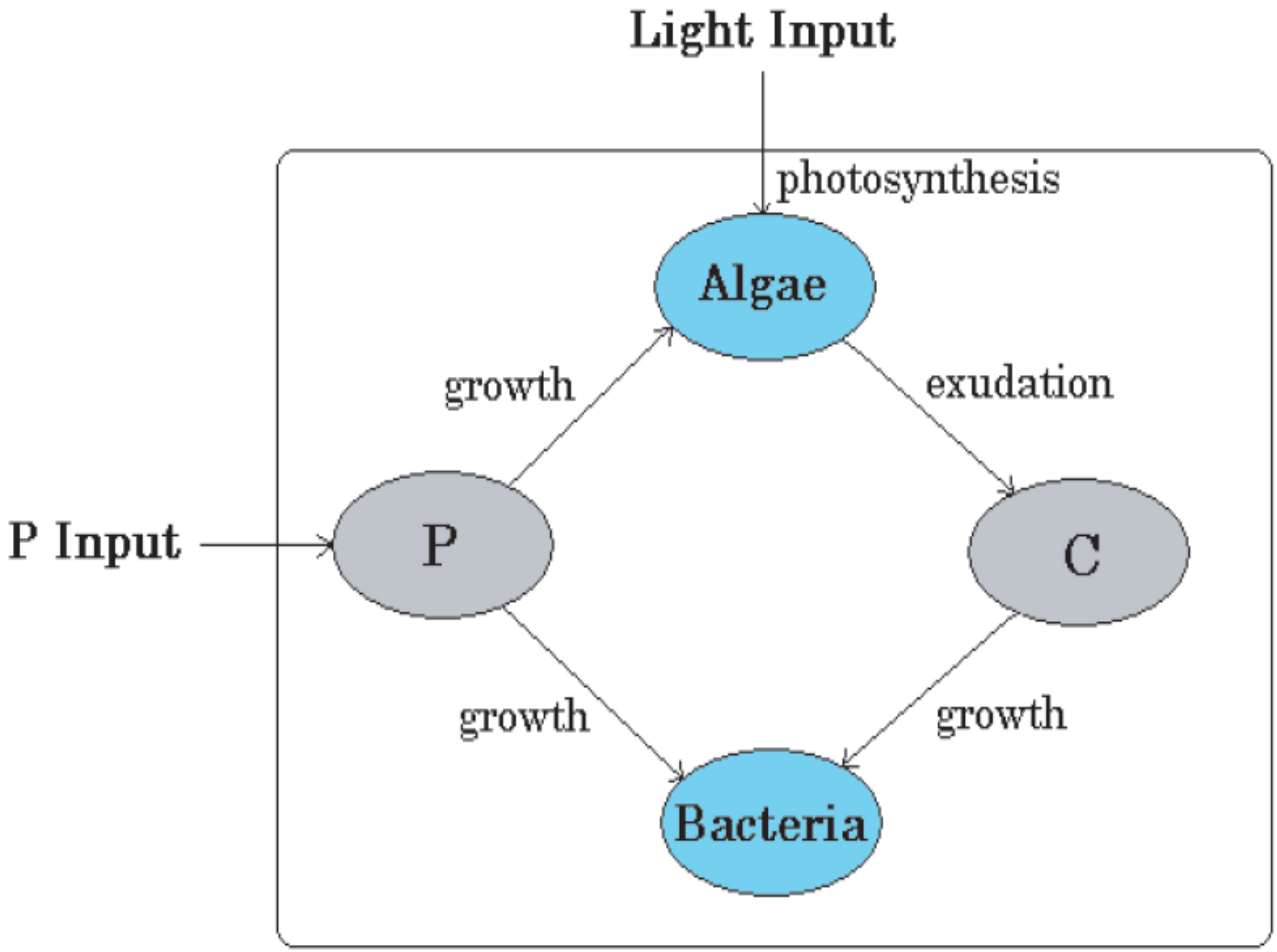
Algae love shallower epilimnions, because sunlight is more sufficient on average.

stable positive steady state

unstable exinction steady state

stable extinction steady state

Second, algae with bacteria



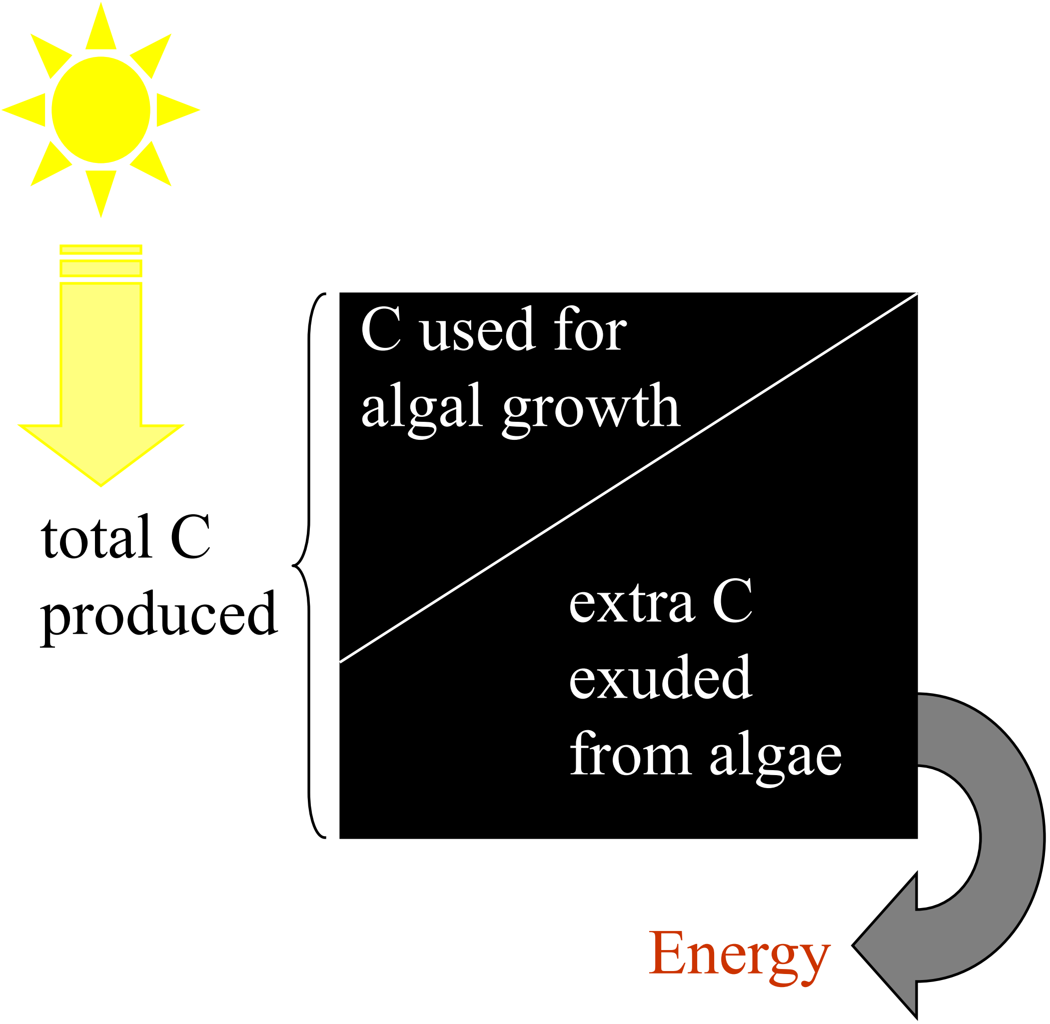
Homeostasis

Scenario Algae have flexible (P:C) whereas bacteria have relatively fixed (P:C).

Assumption (P:C) in bacterial cells is fixed.

W. Makino, J. B. Cotner, R. W. Sterner and J. J. Elser, *Are bacteria more like plants or animals? Growth rate and resource dependence of bacterial C:N:P stoichiometry*, Functional Ecology, 17 (2003), pp. 121-130.

DOC Exudation by Algae



total C
produced

C used for
algal growth

extra C
exuded
from algae

Energy

The exudation rate of DOC by algae is the difference between the potential growth rate attained when growth is not mineral nutrient limited,

$\mu_A A \frac{1}{z_m}\int_0^{z_m} \frac{I(s,A)}{I(s,A)+H}\,ds$, and actual growth rate,

$$\mu_A A\left(1-\frac{Q_m}{Q}\right)\frac{1}{z_m}\int_0^{z_m} \frac{I(s,A)}{I(s,A)+H}\,ds \ .$$

Therefore, the exudation rate is

$$\mu_A A \frac{Q_m}{Q}\frac{1}{z_m}\int_0^{z_m} \frac{I(s,A)}{I(s,A)+H}\,ds \ .$$

Algae with one bacterial strain

$$
\begin{aligned}
\frac{dA}{dt} &= \mu_A A\left(1-\frac{Q_m}{Q}\right)\frac{1}{z_m}\int_0^{z_m}\frac{I(s,A)}{I(s,A)+H}\,ds - l_m A - \frac{\nu+D}{z_m}A \\
\frac{dQ}{dt} &= \rho(Q,P) - \mu_A Q\left(1-\frac{Q_m}{Q}\right)\frac{1}{z_m}\int_0^{z_m}\frac{I(s,A)}{I(s,A)+H}\,ds \\
\frac{dP}{dt} &= \frac{D}{z_m}(P_{in}-P) - \rho(Q,P)A - \boxed{\theta\mu_B Bf(P)g(C)} \qquad (2.2) \\
\frac{dB}{dt} &= \boxed{\mu_B Bf(P)g(C)} - \boxed{(\mu_r+\mu_g)B} - \boxed{\frac{D}{z_m}B} \\
\frac{dC}{dt} &= \boxed{\mu_A A\frac{Q_m}{Q}\frac{1}{z_m}\int_0^{z_m}\frac{I(s,A)}{I(s,A)+H}\,ds} - \boxed{\frac{\mu_B}{r}Bf(P)g(C)} - \boxed{\frac{D}{z_m}C}
\end{aligned}
$$

Consumptions by bacteria

Water exchange

Bacterial growth

Exudation by Algae

Respiration and grazing

We analyze the system (2.2) on the positively invariant set
$\Omega = \{(A, Q, P, B, C) \in \Re_+^5 \,\big|\, A \ge 0, Q_m \le Q \le Q_M, P \ge 0, B \ge 0, C \ge 0\}$.

The basic reproductive number for bacteria is $R_1 = \dfrac{\mu_B f(\bar{P}) g(\bar{C})}{\mu_r + \mu_g + \frac{D}{z_m}}$,
where $\bar{P}, \bar{C}$ are components of E^* in the system (3.1). This is calculated from the linear approximation (Jacobian matrix).

Theorem 7. Dissipativity of the system (2.2) holds.

That is, $\limsup_{t\to\infty} R(t) \le P_{in}, \limsup_{t\to\infty} C(t) \le \frac{z_m \mu_A P_{in}}{DQ_m}$, where

$R = AQ + P + \theta B$ is the total phosphorus in the lake system.

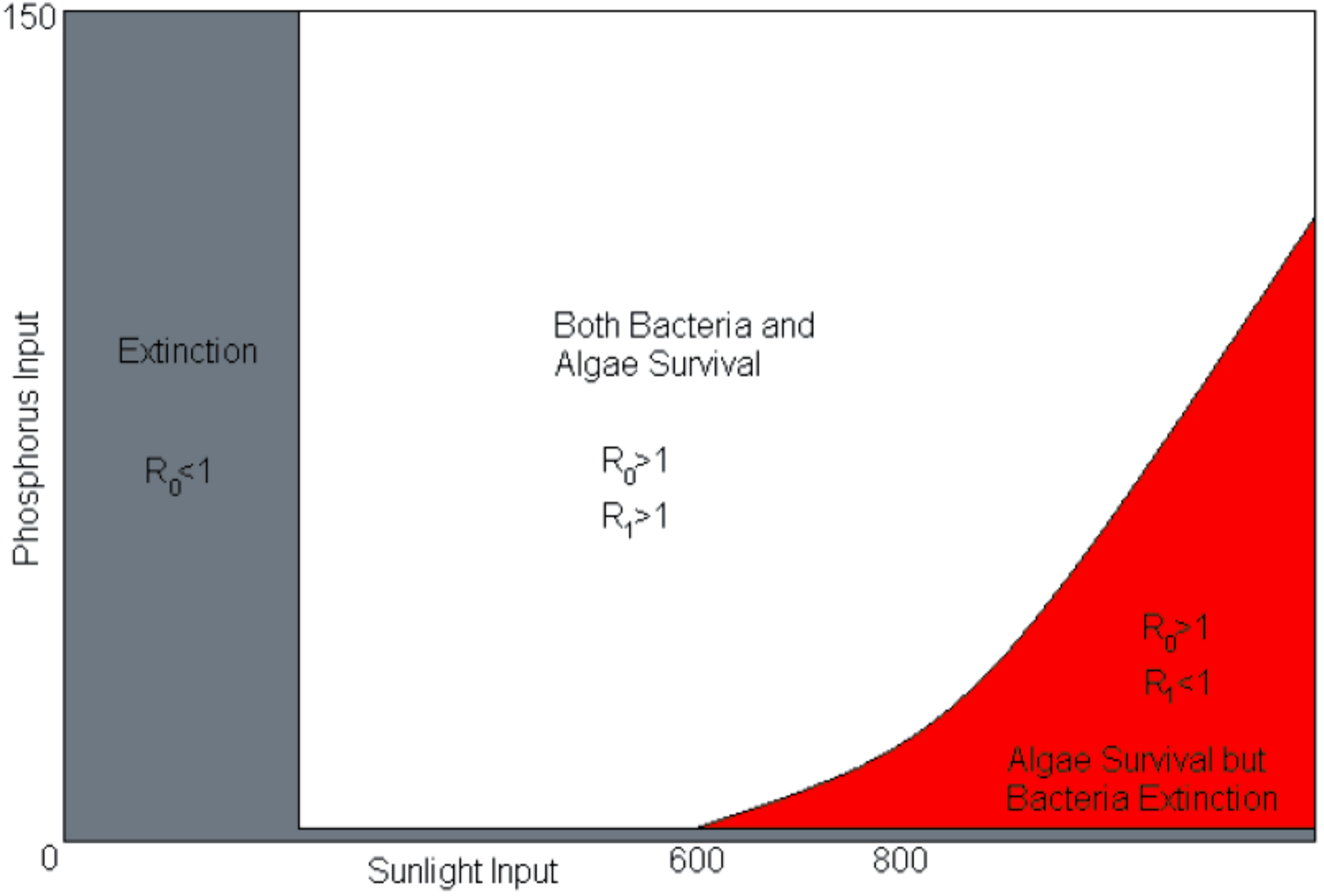
Therefore, $\wp = \{(A, Q, P, B, C) \in \Omega \big| AQ + P + \theta B \le P_{in}, C \le \frac{z_m \mu_A P_{in}}{DQ_m}\}$

is a globally attracting region.

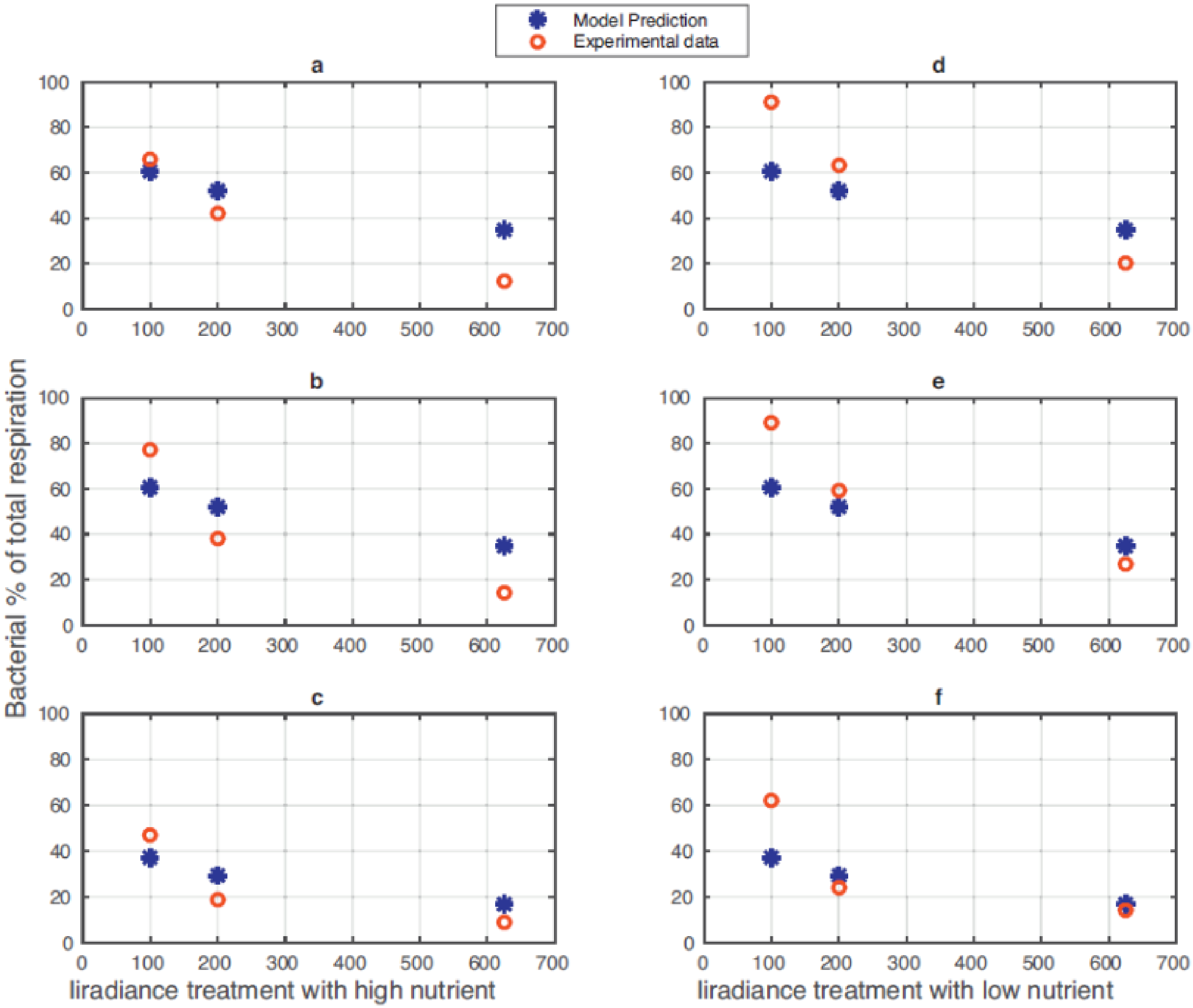
Theorem 8. When $\mu_A h(0) < \frac{D}{z_m}, \lim_{t\to\infty} A(t) = \lim_{t\to\infty} B(t) = 0$.

(i.e. the extinction steady state $(0, \hat{Q}, P_{in}, 0, 0)$ is globally asymptotically stable, or both algae and bacteria go extinct)

Note : The condition in this theorem implies $R_0 < 1$.

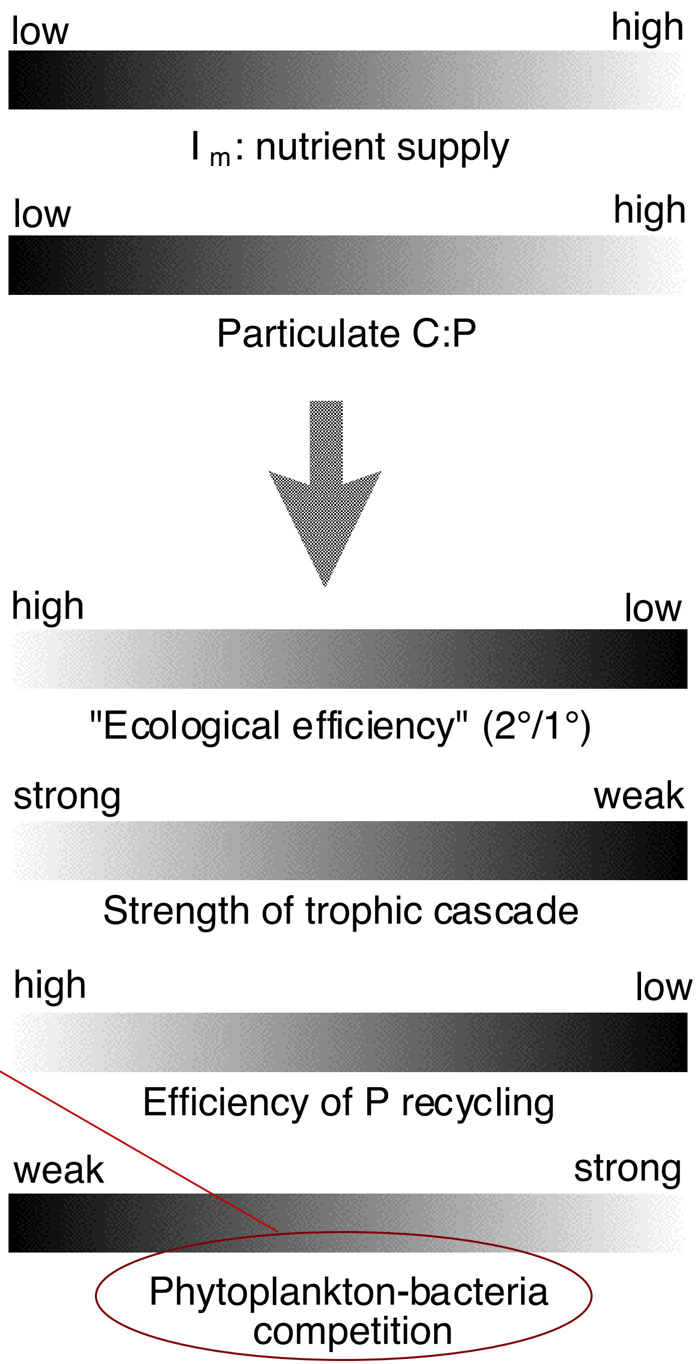

150
Phosphorus Input
Extinction
$R_0<1$
Both Bacteria and Algae Survival
$R_0>1$
$R_1>1$
$R_0>1$
$R_1<1$
Algae Survival but Bacteria Extinction
0
Sunlight Input
600
800

Respiration data fitting



Alijani, M.K., Wang, H. and Elser, J.J., 2015. Modeling the bacterial contribution to planktonic community respiration in the regulation of solar energy and nutrient availability. *Ecological complexity*, *23*, pp.25-33.

The Light:Nutrient Hypothesis: Consequences


low high

I_m: nutrient supply

low high

Particulate C:P

high low

"Ecological efficiency" (2°/1°)

strong weak

Strength of trophic cascade

high low

Efficiency of P recycling

weak strong

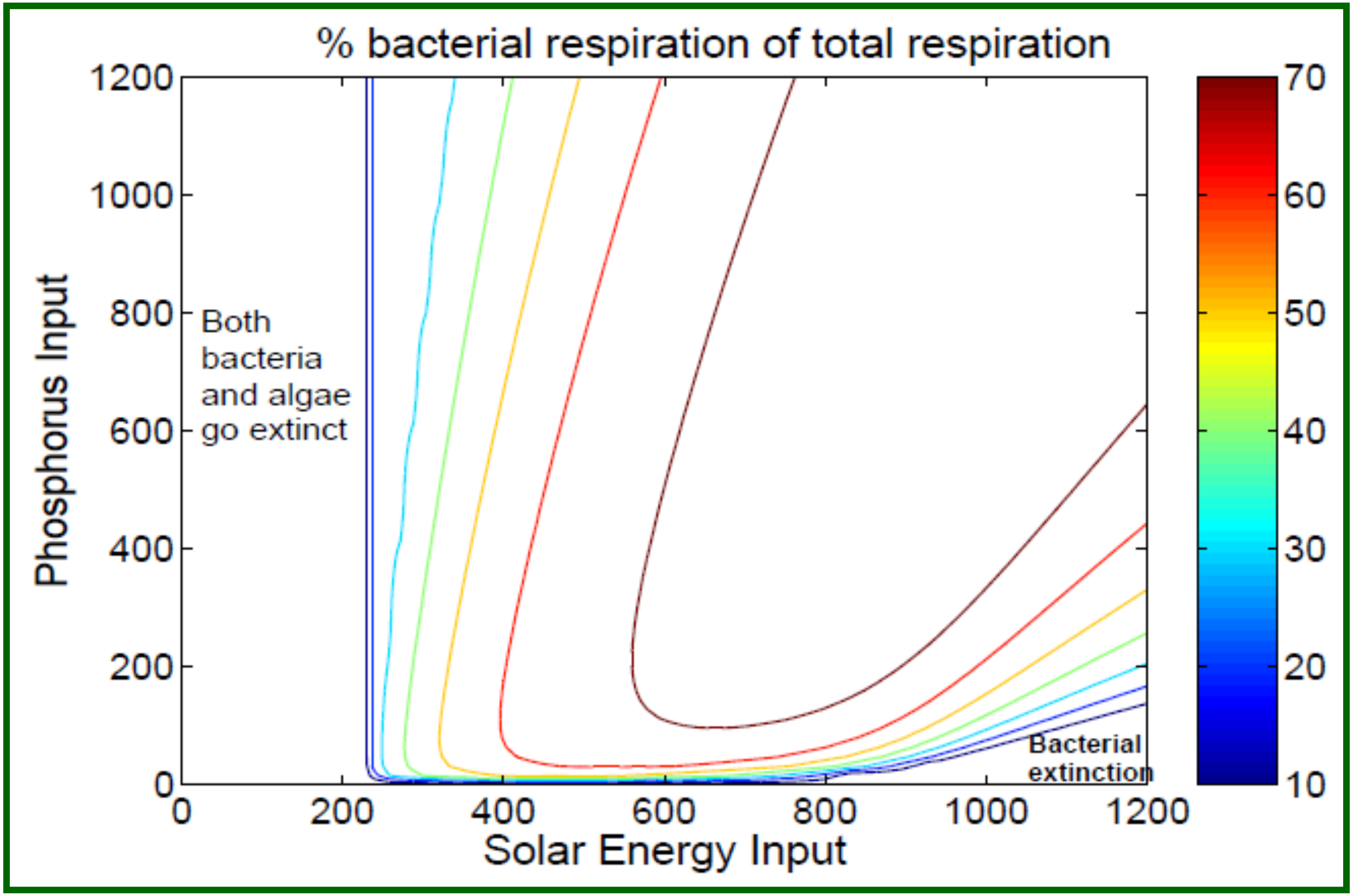
Phytoplankton-bacteria competition

Wang, H., Smith, H.L., Kuang, Y. and Elser, J.J., 2007. Dynamics of stoichiometric bacteria-algae interactions in the epilimnion. *SIAM Journal on Applied Mathematics*, *68*(2), pp.503-522.

Alijani, M.K., Wang, H. and Elser, J.J., 2015. Modeling the bacterial contribution to planktonic community respiration in the regulation of solar energy and nutrient availability. *Ecological complexity*, *23*, pp.25-33.

Based on: Sterner, R.W., J.J. Elser, E.J. Fee, S.J. Guildford, and T.H. Chrzanowski. 1997. The light:nutrient balance in lakes: the balance of energy and materials affects ecosystem structure and process. Am. Nat. **150**: 663-684.

Light-nutrient hypothesis



Alijani, M.K., Wang, H. and Elser, J.J., 2015. Modeling the bacterial contribution to planktonic community respiration in the regulation of solar energy and nutrient availability. *Ecological complexity*, *23*, pp.25-33.

Now, competing bacterial strains

$$\frac{dA}{dt} = \mu_A A\left(1-\frac{Q_m}{Q}\right)\frac{1}{z_m}\int_0^{z_m}\frac{I(s,A)}{I(s,A)+H}\,ds - l_m A - \frac{\nu+D}{z_m}A$$

$$\frac{dQ}{dt} = \rho(Q,P) - \mu_A Q\left(1-\frac{Q_m}{Q}\right)\frac{1}{z_m}\int_0^{z_m}\frac{I(s,A)}{I(s,A)+H}\,ds$$

$$\frac{dP}{dt} = \frac{D}{z_m}(P_{in}-P) - \rho(Q,P)A - [\theta_1\mu_1 B_1 f_1(P) - \theta_2\mu_2 B_2 f_2(P)]g(C)$$

$$\frac{dB_1}{dt} = \mu_1 B_1 f_1(P)g(C) - (\mu_r+\mu_g)B_1 - \frac{D}{z_m}B_1$$ HNA

$$\frac{dB_2}{dt} = \mu_2 B_2 f_2(P)g(C) - (\mu_r+\mu_g)B_2 - \frac{D}{z_m}B_2$$ LNA

$$\frac{dC}{dt} = \mu_A A\frac{Q_m}{Q}\frac{1}{z_m}\int_0^{z_m}\frac{I(s,A)}{I(s,A)+H}\,ds - \frac{1}{r}[\mu_1 B_1 f_1(P) - \mu_2 B_2 f_2(P)]g(C) - \frac{D}{z_m}C$$

VHNA + HNA vs LNA

Previous claim LNA is less active, or dormant.

Observation In late August of Lake Biwa, LNA grows faster than VHNA and HNA.

Hypothesis Probably P-limitation is severe at that time and LNA has higher nutrient uptake efficiency or lower requirements for P.

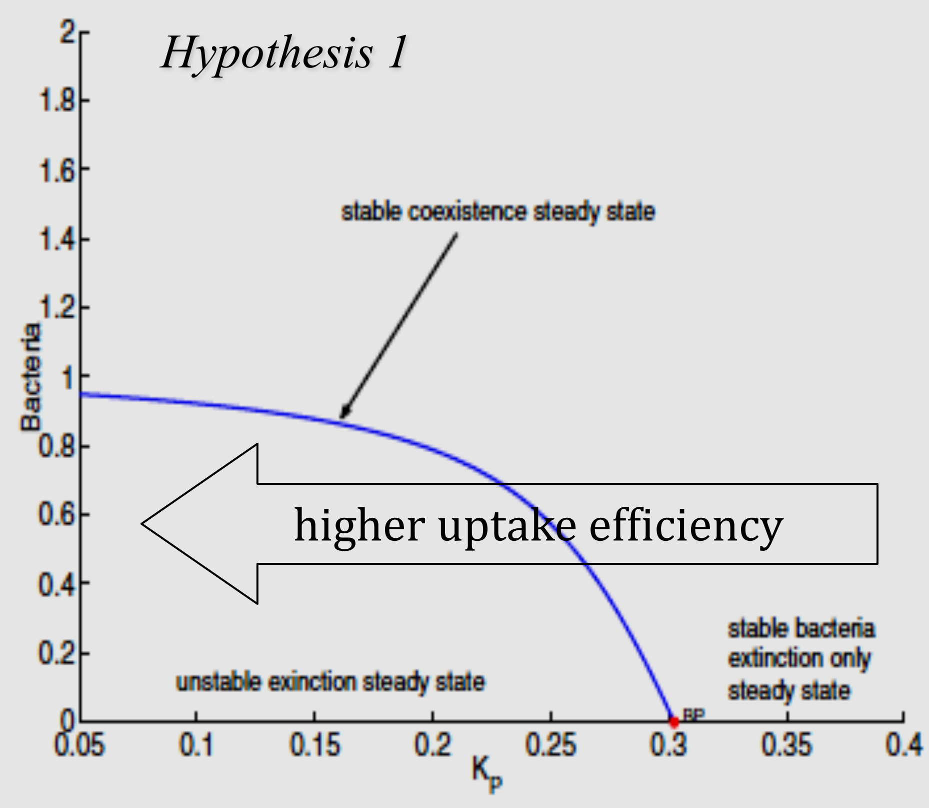
(Nishimura et al 2005, Applied and Environmental Microbiology)

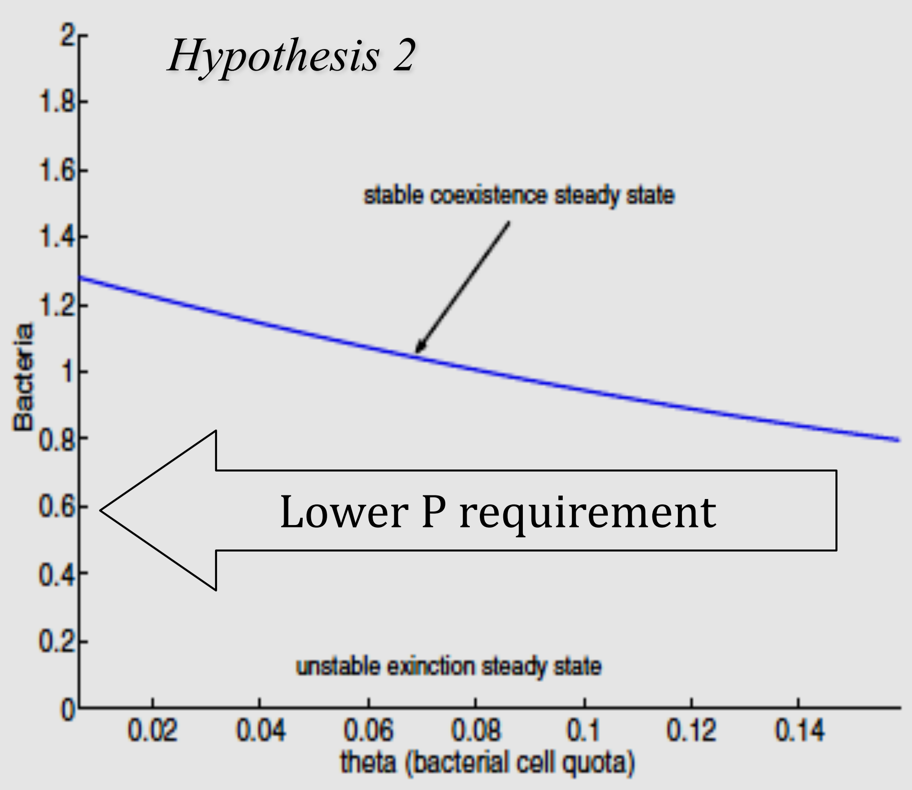
Hypothesis 1

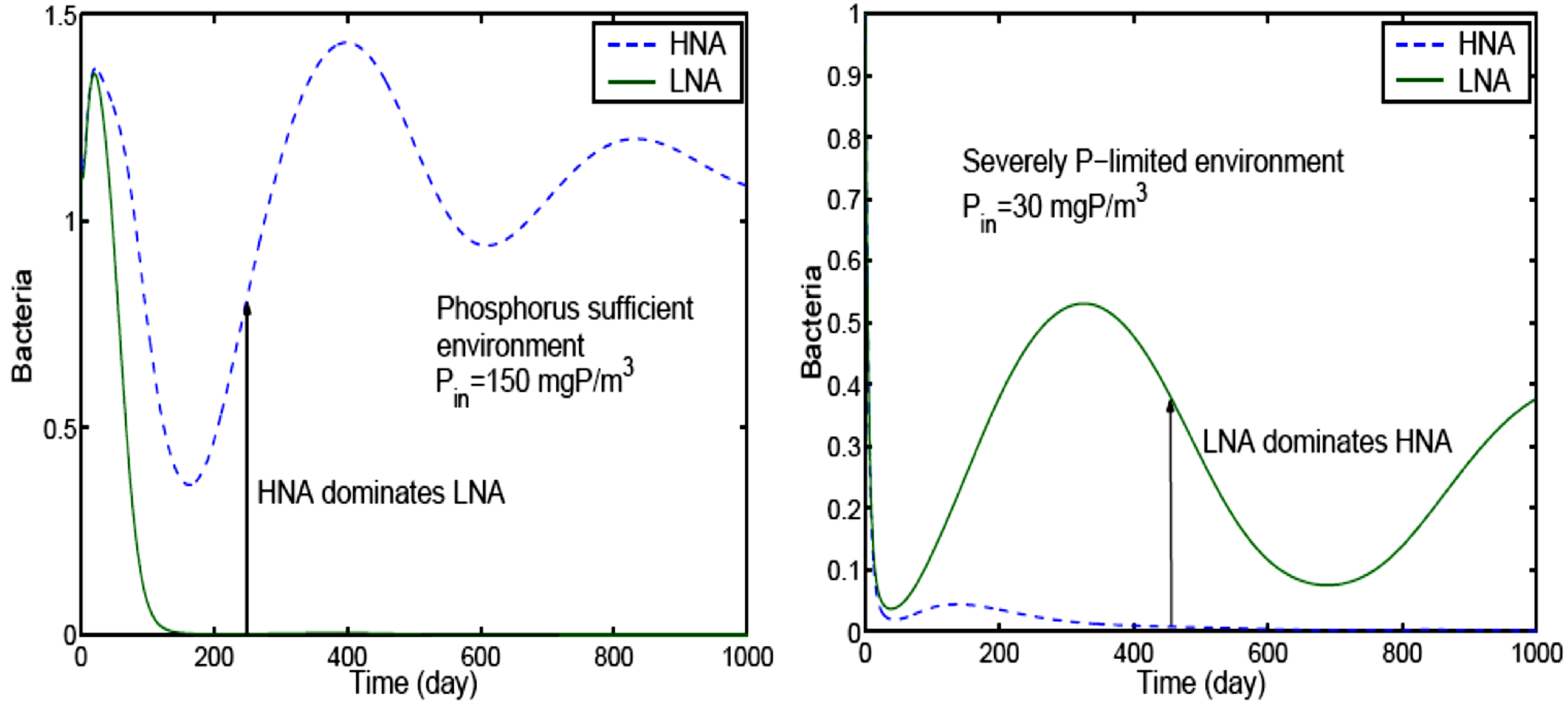
“higher nutrient uptake efficiency” ⇔
“lower half-saturation constant for P”

Hypothesis 2

“lower requirements for P” ⇔
“smaller cell quota”


Hypothesis 1
stable coexistence steady state
higher uptake efficiency
unstable exinction steady state
stable bacteria extinction only steady state
BP
Bacteria
K_P
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4


Hypothesis 2
stable coexistence steady state
Lower P requirement
unstable exinction steady state
Bacteria
theta (bacterial cell quota)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
0.02
0.04
0.06
0.08
0.1
0.12
0.14



Both of those seemingly conflict views can be true under different environments.

Take home messages

It is important to incorporate nutrients as a new dimension into the models of food webs

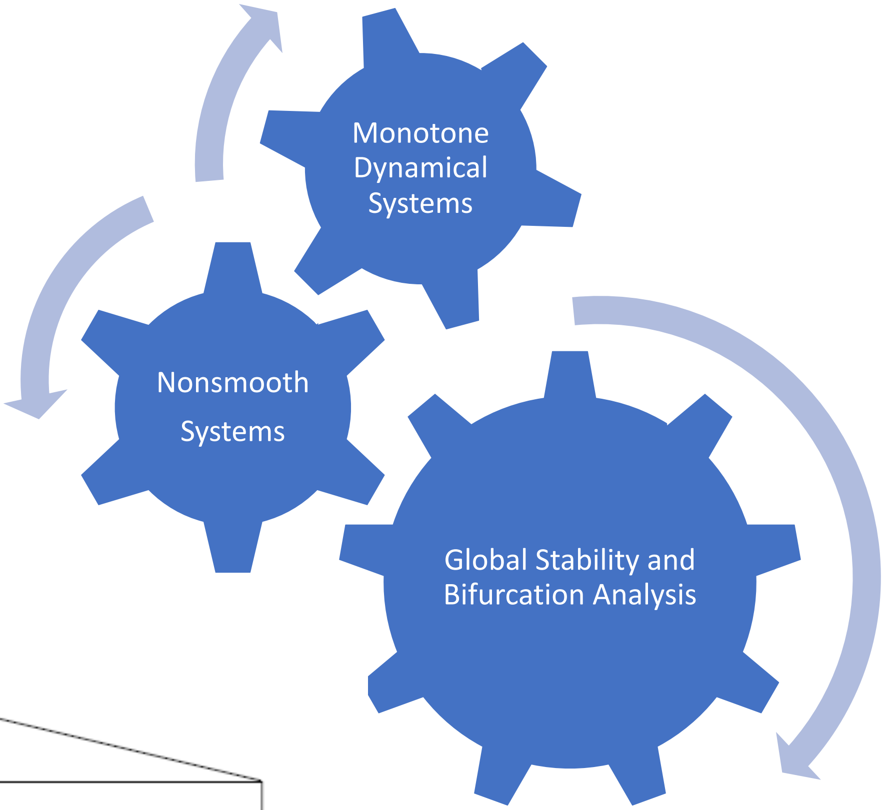
Light:nutrient balance can play a critical role in food webs

The increase of light increases plant’s quantity but decreases its quality

In many cases, there are trade-offs in species competition

Abstract mathematical theorems can be applied to realistic biological models

Mathematics inside ES



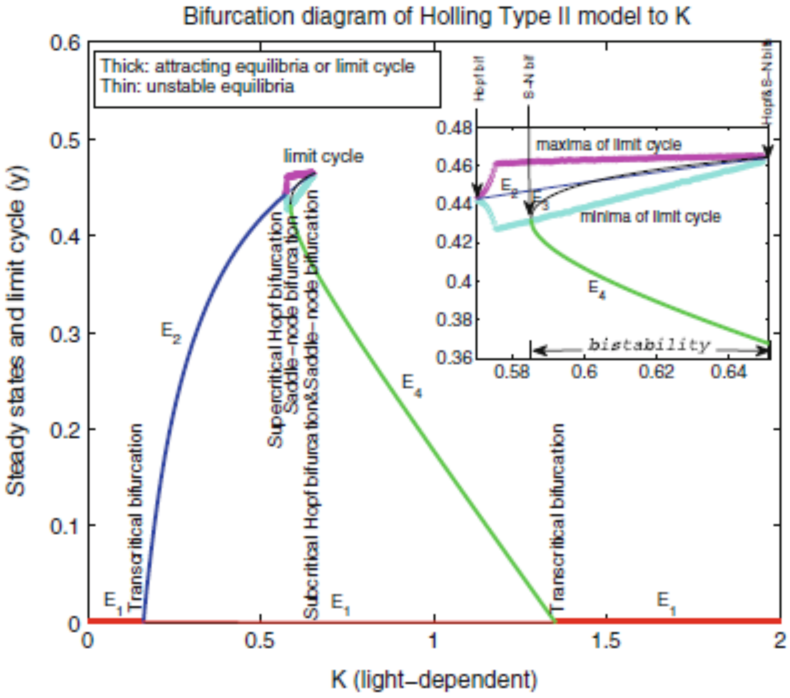
Monotone Dynamical Systems

Nonsmooth Systems

Global Stability and Bifurcation Analysis

⋮

⋮



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