A plankton-nutrient model with Holling type III response function

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Outline

- Introduction
- Model Construction
- Stability Property of different Equilria of deterministic model
- Effect of additional food source
- Stability analysis of Stochastic model and comparison with deterministic model
- Numerical Example
- Conclusions

Nutrient-Plankton

- ❖The most important feature of an ecosystem is the number of species in different tropic levels of a food web.

- ❖Living organism gradually grow and actively incorporate energy and nutrient into their biomass of their descendants.

- ❖These nutrients are obtained by either uptaking from the abiotic environment or consumption from the biomass of other organism in the food web.

Planktonic Bloom

- ❖A planktonic bloom is defined as a rapid and marked increase in the local population of plankton.

- ❖The main factors that cause blooms to occur are sunlight, nutrients, and changes in water temperature.

The Mathematical Model contd.

- Dilution rate is referred to as the water exchange rate or flushing rate when referring to open marine system (Ecological effects of wastewater: applied limnology and pollution effects By Eugene B. Welch, T. Lindell).

- The rate of nutrient exchange rate is referred to as Dilution rate. When the dilution rate is very low, the cells reach a high density as the nutrients are leaving the system at a very slow rate and the cells get ample timed to use the substrate. Thus the nutrient concentration is maintained at a low level in the system.

- On the other hand, if the dilution rate of nutrient is high, the cell density is low as they have a little time to use the substrate.

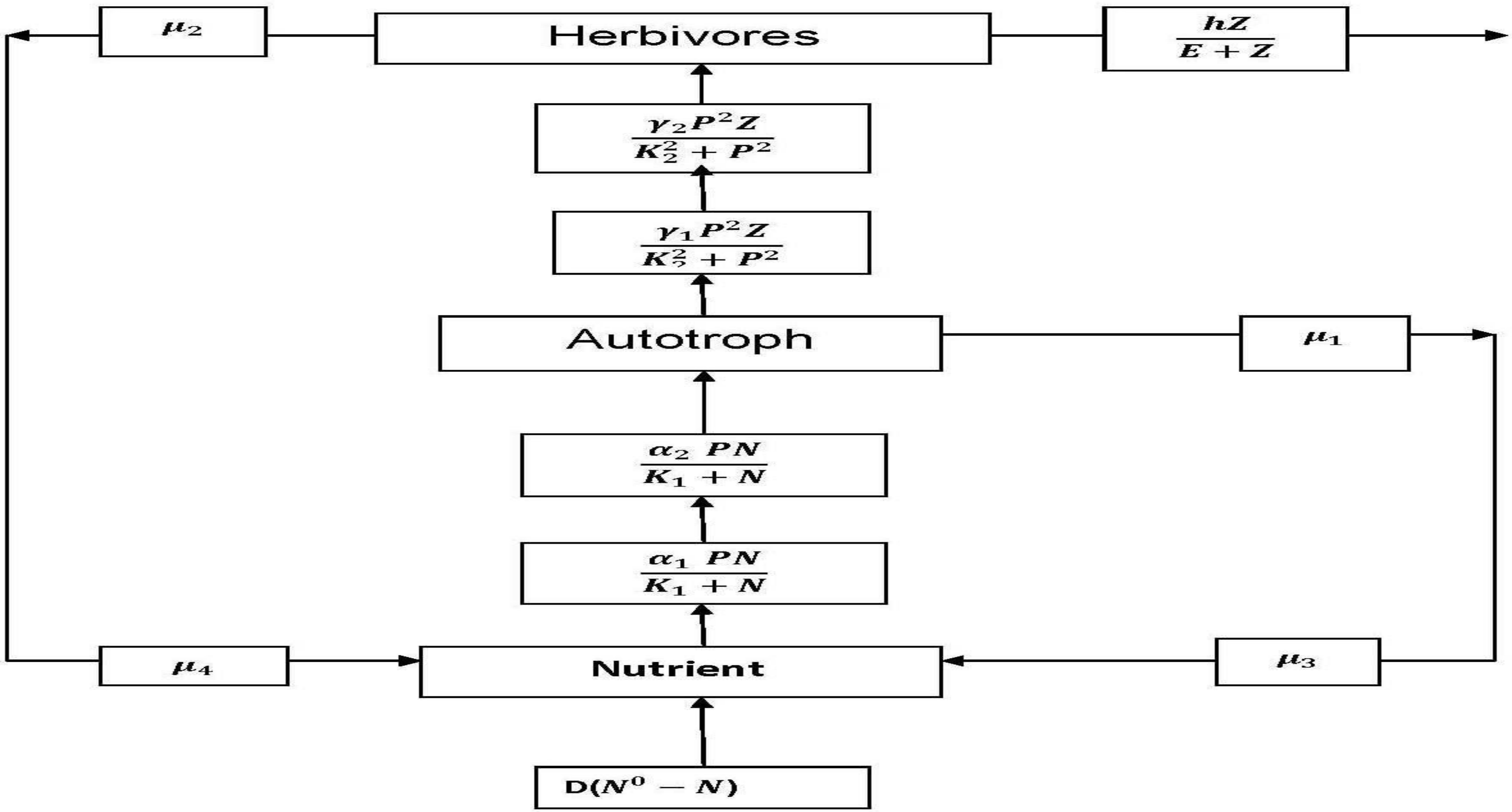
Mathematical Model

- $N(t)$ be the concentration of the nutrient at time t.
- $P(t)$ the autotroph biomass
- $Z(t)$ the number of herbivores present at time t.
- N_0 be the constant input of nutrient concentration.
- D is the dilution rate of nutrient. Its inverse $1/D$ represents the average time that nutrient and waste products spend in the system.
- α_1 and α_2 be the nutrient uptake rate for the autotroph biomass and conversion rate of nutrient for the growth of the autotroph biomass respectively ($\alpha_2 \leq \alpha_1$).
- μ and μ_2 denote respectively the mortality rates of the autotroph biomass and of the herbivore population.
- μ_3 ($\mu_3 \leq \mu$) and μ_4 ($\mu_4 \leq \mu_2$) be the nutrient recycle rates respectively coming from the dead autotroph biomass and the dead herbivore population.
- The maximal zooplankton's herbivore hunting rate is represented by γ_1 while γ_2 ($\gamma_2 \leq \gamma_1$) is its maximal herbivore conversion rate.

Mathematical Model contd.

- We choose Holling type II and type III functional forms to describe the grazing phenomena with K1 and K2 as half saturation constant.
- We also include harvesting of the top population in this food chain, at rate h.
- The harvesting is modeled via a Holling type II function with half saturation constant E, to mimic the diminishing returns obtained via constant harvesting efforts, as it commonly occurs in fisheries models.
- In addition, it has been observed that other food sources are occasionally available to phytoplankton, other than the basic nutrients N. The additional food source is vitamin B12, [7, 15, 16].
- We include the latter in our description. Thus, let rP be the phytoplankton's growth rate due to this additional vitamin supply.
- Then the autotroph biomass mortality rate is $\mu 1 = \mu - r \in R$. With these assumptions our deterministic system is

Schematic Diagram



Mathematical Model

$$
\begin{aligned}
\frac{dN}{dt} &= D(N^0 - N) - \frac{\alpha_1 PN}{K_1 + N} + \mu_3 P + \mu_4 Z \equiv F_1(N, P, Z) \\
\frac{dP}{dt} &= \frac{\alpha_2 PN}{K_1 + N} - \frac{\gamma_1 P^2 Z}{K_2^2 + P^2} - \mu_1 P \equiv F_2(N, P, Z) \\
\frac{dZ}{dt} &= \frac{\gamma_2 P^2 Z}{K_2^2 + P^2} - \mu_2 Z - \frac{hZ}{E + Z} \equiv F_3(N, P, Z). \qquad (1)
\end{aligned}
$$

Some basic results

The system (1) possesses the following three equilibria: the nutrient-only equilibrium $E_0 = (N^0, 0, 0)$, the zooplankton-free equilibrium $E_1 = (N_1, P_1, 0)$ and possibly the coexistence of the three populations, $E^* = (N^*, P^*, Z^*)$.

Some basic results

The nutrient-only equilibrium

E_0 is always feasible; the Jacobian (2) evaluated at this equilibrium has the eigenvalues $-D < 0$, $-(hE^{-1} + \mu_2) < 0$ and $\mu_1(R_0 - 1)$, where R_0 is defined below. Thus for $\mu_1 < 0$ this equilibrium is never stable, while for $\mu_1 > 0$, E_0 is locally asymptotically stable if and only if

$$\boxed{R_0 := \frac{\alpha_2 N^0}{\mu_1(K_1 + N^0)} < 1.}$$

Some basic results

The zooplankton-free equilibrium

At E_1 the population levels are

$$N_1 = \frac{\mu_1 K_1}{\alpha_2 - \mu_1}, \quad P_1 = \frac{D\alpha_2[N^0\alpha_2 - (N^0 + K_1)\mu_1]}{(\alpha_2 - \mu_1)[\alpha_1\mu_1 - \mu_3\alpha_2]}.$$

Therefore for $\mu_1 \geq 0$ this equilibrium is feasible if $\alpha_2 > \mu_1$ and either one the two alternative conditions hold:

$$\mu_1 \frac{N^0 + K_1}{N^0} \leq \alpha_2 < \alpha_1 \frac{\mu_1}{\mu_3}; \quad \alpha_1 \frac{\mu_1}{\mu_3} < \alpha_2 \leq \mu_1 \frac{N^0 + K_1}{N^0}.$$

Stability of E_1 is then ensured by

$$R_1 = \frac{\gamma_2 E D^2 \alpha_2^2 M^2}{J^2 + D^2\alpha_2^2 M^2(\mu_2 E + h)} < 1,$$

Some basic results

The coexistence equilibrium

The coexistence equilibrium $E^* = (N^*, P^*, Z^*)$ cannot be found explicitly, since

$$N^* = \frac{(\gamma_1 P^* Z^* + \mu_1(K_2^2 + P^{*2}))K_1}{(\alpha_2 - \mu_1)(K_2^2 + P^{*2}) - \gamma_1 P^* Z^*}, \quad Z^* = \frac{(K_2^2 + P^{*2})h}{(\gamma_2 - \mu_2)P^{*2} - K_2^2\mu_2} - E.$$

For feasibility

$$h > \frac{E[(\gamma_2 - \mu_2)P^{*2} - K_2^2\mu_2]}{K_2^2 + P^{*2}}, \quad \alpha_2 > \mu_1 + \frac{\gamma_1 P^* Z^*}{K_2^2 + P^{*2}}.$$

Stability analysis

$$V = \begin{bmatrix} -D - \frac{\alpha_1 K_1 P}{(K_1+N)^2} & -\frac{\alpha_1 N}{K_1+N} + \mu_3 & \mu_4 \\ \frac{K_1 \alpha_2 P}{(K_1+N)^2} & \frac{\alpha_2 N}{K_1+N} - \frac{2K_2^2 \gamma_1 Z\ P}{(K_2^2+P^2)^2} - \mu_1 & -\frac{\gamma_1 P^2}{K_2^2+P^2} \\ 0 & \frac{2K_2^2 \gamma_2 P\ Z}{(K_2^2+P^2)^2} & \frac{\gamma_2 P^2}{K_2^2+P^2} - \mu_2 - \frac{Eh}{(E+Z)^2} \end{bmatrix}$$

Stability of E_1 is then ensured by

$$R_0 := \frac{\alpha_2 N^0}{\mu_1 (K_1 + N^0)} < 1.$$

Stability of E_1 is then ensured by

$$R_1 = \frac{\gamma_2 E D^2 \alpha_2^2 M^2}{J^2 + D^2 \alpha_2^2 M^2 (\mu_2 E + h)} < 1,$$

Stability analysis of positive interior equilibrium E *

The characteristic equation is

$$y^3 + A_1 y^2 + A_2 y + A_3 = 0$$

where $A_1 = -\mathrm{tr}(V) = (V_{11} + V_{22} + V_{33})$, $A_2 = M_2(V) := V_{11}V_{22} + V_{22}V_{33} + V_{11}V_{33} - V_{23}V_{32} - V_{12}V_{21}$; $A_3 = \det(V) = V_{11}V_{23}V_{32} + V_{12}V_{21}V_{33} - V_{11}V_{22}V_{33} - V_{13}V_{21}V_{32}$.

By the Routh–Hurwitz criteria, all roots of above equation have negative real parts if and only if

$A_1 > 0$, $A_3 > 0$ and $A_1 A_2 - A_3 > 0$.

Analysis of globally asymptotically stable at E_1

$$W(N,P) = \int_{N_1}^{N} \frac{x - N_1}{x} dx + \frac{\alpha_1 N_1 - \mu_3 (K_1 + N_1)}{\alpha_2 N_1} \int_{P_1}^{P} \frac{x - P_1}{x} dx.$$

Estimating from above its time derivative along the trajectories of the sub-system (1) with $Z = 0$, we find

$$\frac{dW}{dt} = (N - N_1)\left[\frac{D(N^0 - N)}{N} - \frac{D(N^0 - N_1)}{N_1} - P\left(\frac{\alpha_1}{K_1 + N} - \frac{\mu_3}{N}\right)\right.$$
$$\left. + P_1\left(\frac{\alpha_1}{K_1 + N_1} - \frac{\mu_3}{N_1}\right) + \left(\frac{\alpha_1}{K_1 + N_1} - \frac{\mu_3}{N_1}\right)\left(\frac{K_1}{K_1 + N}\right)(P - P_1)\right]$$
$$\leq -(N - N_1)^2 \frac{D}{N} - \frac{(N - N_1)^2}{N N_1}[P\mu_3 + D(N^0 - N_1)].$$

Thus, if $N_1 < N^0$, which is the very first inequality in (4), the second term is negative and the derivative also.

Direction of Hopf Bifurcation

Theorem: 1. The parameter μ_{22} determines the direction of the Hopf-bifurcation. If $\mu_{22} > 0$ (< 0) then the Hopf-bifurcation is supercritical (subcritical) and the bifurcating periodic solutions exists for $h > h^*$.
The stability and the period of the bifurcating periodic solutions are respectively determined by the parameters β_2 and τ_2 defined in the proof. The solutions are orbitally stable (unstable) if $\beta_2 < 0$ (> 0) and the period increases (decreases) if $\tau_2 > 0$ (< 0).

stochastic model

- A linear stochastic process is formulated as an approximation to a nonlinear ecosystem model. The formulation traces a chemical nutrient as it undergoes random exchanges between the phytoplankton, zooplankton, and the euphotic zone of an aquatic ecosystem.

- The formulation of a linear process allows the derivation of a partial-differential equation for the cumulant-generating function of the process. The use of this equation leads to a system of linear, deterministic differential equations for the cumulants of the process.

Stochastic model

$$
\begin{aligned}
dN &= F_1(N, P, Z)dt + \sigma_1(N - N^*)d\xi_t^1, \\
dP &= F_2(N, P, Z)dt + \sigma_2(P - P^*)d\xi_t^2, \\
dZ &= F_3(N, P, Z)dt + \sigma_3(Z - Z^*)d\xi_t^3
\end{aligned}
$$

where σ_1, σ_2 and σ_3 are real constants, known as the intensities of environmental fluctuations, $\xi_t^i = \xi_i(t)$, $i = 1, 2, 3$ are standard Wiener processes independent of each other [21].

Some basic results

Theorem 2. Assume that the functions $\Theta(U,t) \in C_3(\Omega)$ and L_Θ satisfy the inequalities

$$r_1|U|^\alpha \leq \Theta(U,t) \leq r_2|U|^\alpha,$$
$$L_\Theta(U,t) \leq -r_3|U|^\alpha, \quad r_i > 0, \ i = 1,2,3, \ \alpha > 0.$$

Then the trivial solution of $\quad dU(t) = F_L(U(t))dt + g(U(t))d\xi(t),$

is exponentially α-stable for all time $t \geq 0$.

Some basic results

Theorem 3. Assume $V_{ij} < 0$, $i, j = 1, 2, 3$, and that for some positive real values of ω_k, $k = 1, 2$, the following inequality holds

$$[2(1+\omega_2)V_{22} + 2V_{32}\omega_2 + (1+\omega_2)\sigma_2^2]\,[2V_{13}\omega_1 + 2V_{23}\omega_1 + 2V_{33}(\omega_1+\omega_2) + (\omega_1+\omega_2)\sigma_3^2] > [V_{12}\omega_1 + V_{22}\omega_2 + V_{23}(1+\omega_2) + V_{32}(\omega_1+\omega_2) + V_{33}\omega_2]^2 . \quad (18)$$

Then if $\sigma_1^2 < -2V_{11}$, it follows that

$$\sigma_2^2 < -\frac{2V_{22}(1+\omega_2) + 2V_{32}\omega_2}{1+\omega_2}, \quad \sigma_3^2 < -\frac{2V_{13}\omega_1 + 2V_{23}\omega_1 + 2V_{33}(\omega_1+\omega_2)}{\omega_1+\omega_2}, \quad (19)$$

where

$$\omega_1{}^* = \frac{V_{21}}{V_{13} + V_{11} + V_{33} - V_{12} - V_{32}}, \quad \omega_2{}^* = \frac{V_{11} + V_{13} + V_{33}}{V_{12} - (V_{13} + V_{11} + V_{33}) + V_{32}}, \quad (20)$$

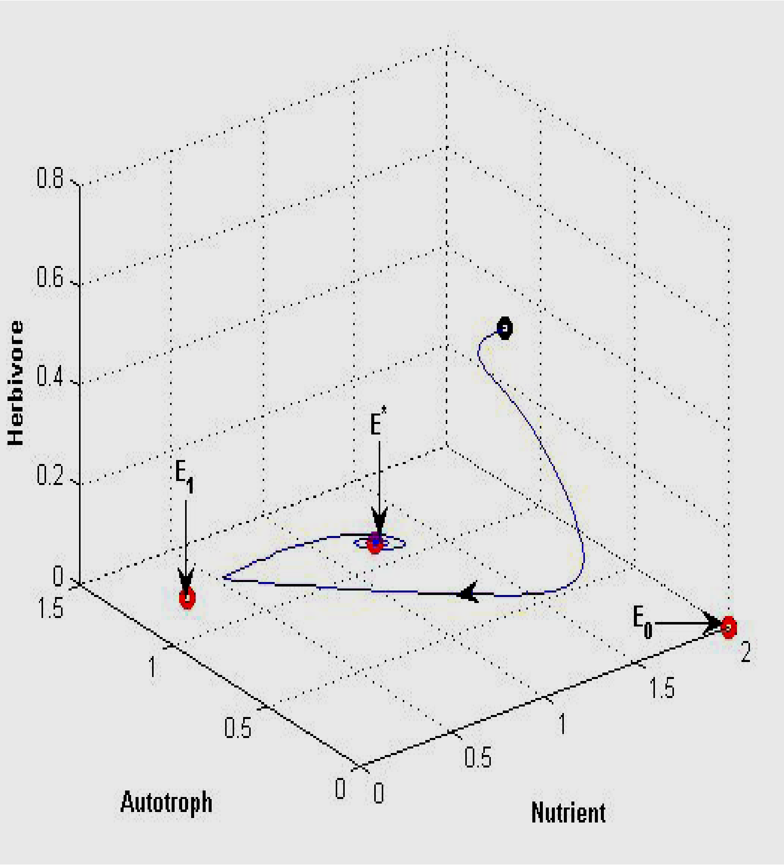
and the zero solution of system (12) is asymptotically mean square stable.

The table representing thresholds and stability of steady states

Thresholds (R_0, R_1)	$(N_0, 0, 0)$	$(N_1, P_1, 0)$	(N^*, P^*, Z^*)
$R_0 < 1$	Asymptotically stable	Not feasible	Not feasible
$R_0 > 1,\ R_1 < 1$	Unstable	Asymptotically stable	Not feasible
$R_1 > 1$	Unstable	Unstable	Asymptotically stable

Table 2 (Set of parametric values)

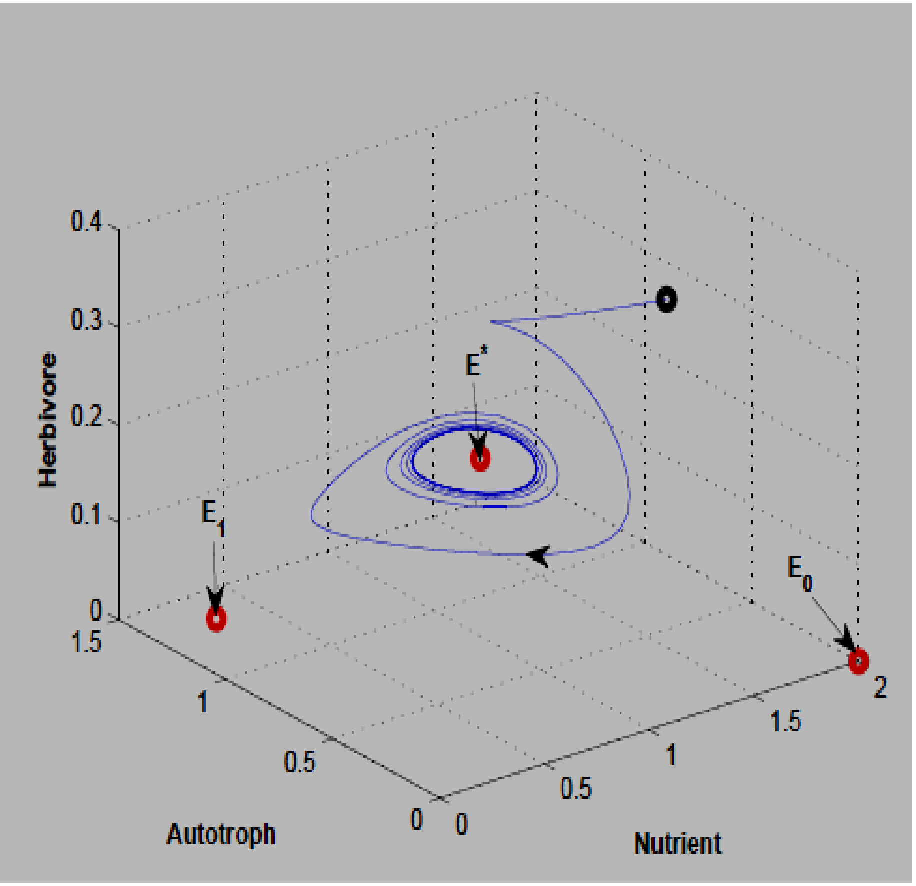
Parameter	Definition	Value	Unit
N^0	Constant input of nutrient	2.0	$mgml^{-1}$
D	Dilution rate of nutrient	0.5	day^{-1}
α_1	Nutrient uptake rate for the autotroph biomass	1.6	day^{-1}
α_2	Nutrient conversion rate for the growth of autotroph	1.2	day^{-1}
γ_1	Autotroph biomass uptake rate for the herbivore	1	day^{-1}
γ_2	Autotroph biomass conversion rate for the herbivore	0.9	day^{-1}
μ_1	Mortality rate of autotroph biomass	0.6	day^{-1}
μ_2	Mortality rate of herbivore	0.4	day^{-1}
μ_3	Nutrient Recycle rate due to the death autotroph biomass	0.1	day^{-1}
μ_4	Nutrient recycle rate due to the death of herbivore	0.1	day^{-1}
K_1	Half saturation constant for autotroph	0.3	$mgml^{-1}$
K_2	Half saturation constant for herbivore	0.3	$mgml^{-1}$
h	Harvesting rate of herbivore population	0.4	day^{-1}
E	Effort required to harvest the herbivores	1.0	day^{-1}

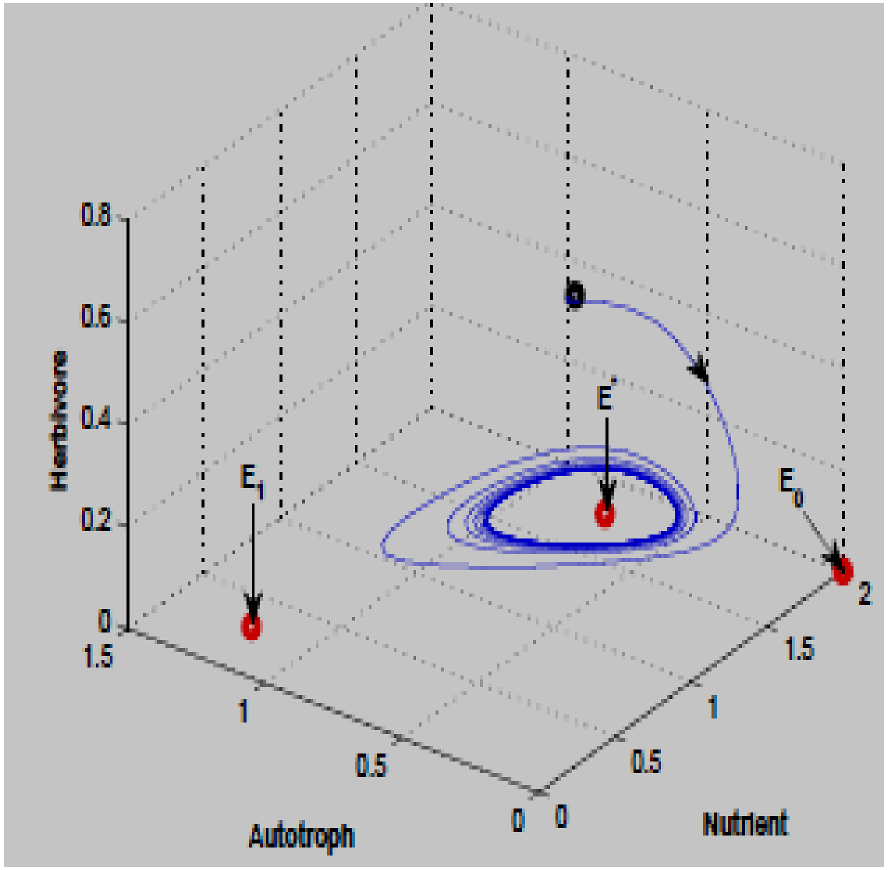


The equilibrium point E^* (0.7297, 0.6331, 0.1941)is stable with −0.5081, -0.0327+i0.3106, -0.0327-i0.3106, for the parametric values as given in the Table 2

The plot is obtained for the reference parameter values given in Table 2, but with D = 0.55.

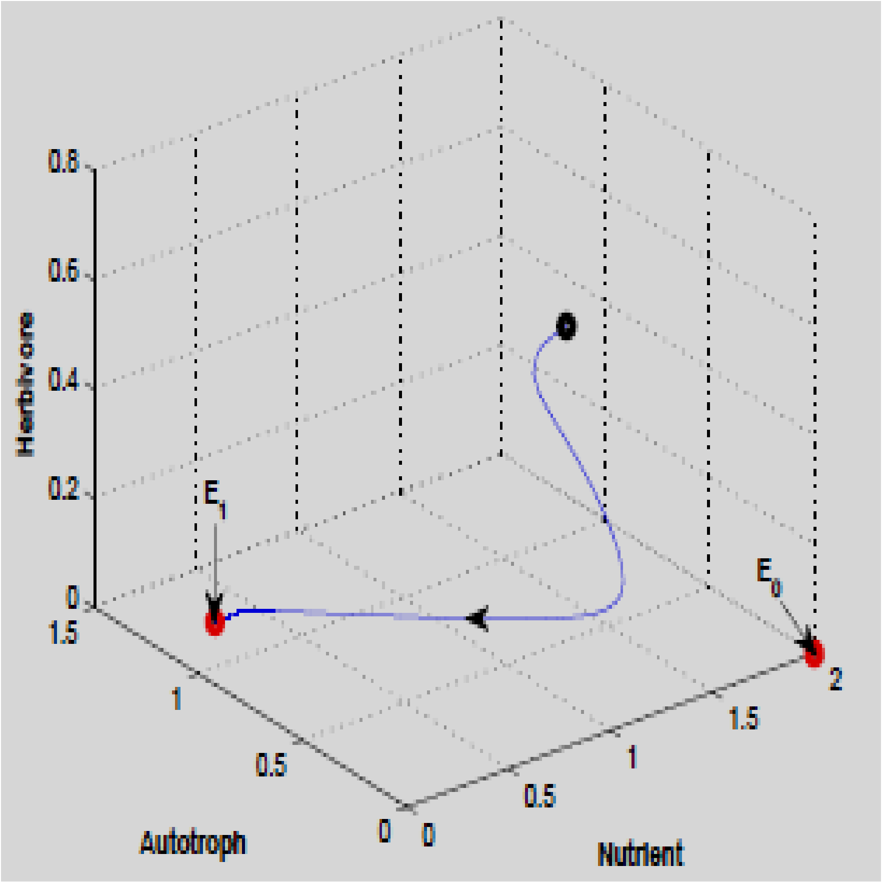
The plot is obtained for the reference parameter values given in Table 2 with h = 0.2. (Right)

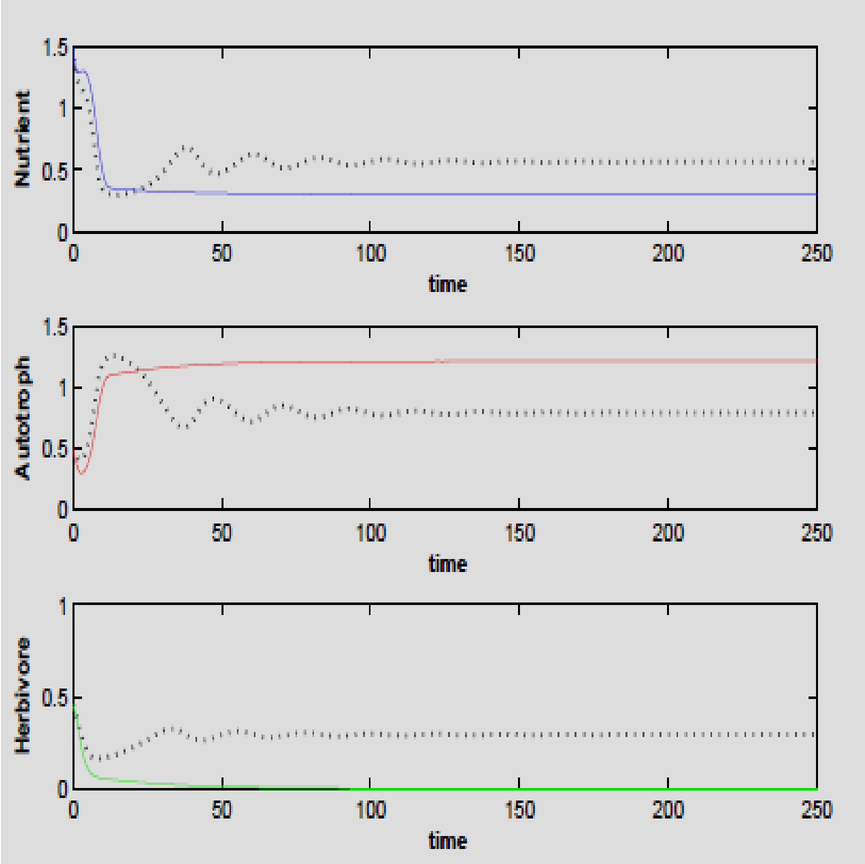




The plot is obtained for the reference parameter values given in Table 2 with h = 0.5. (left)

The plot is obtained for the reference parameter values given in Table 2, but with h = 0.5; in addition we take r = 0, the continuous line, and r = 0.14, the dotted line. (right)

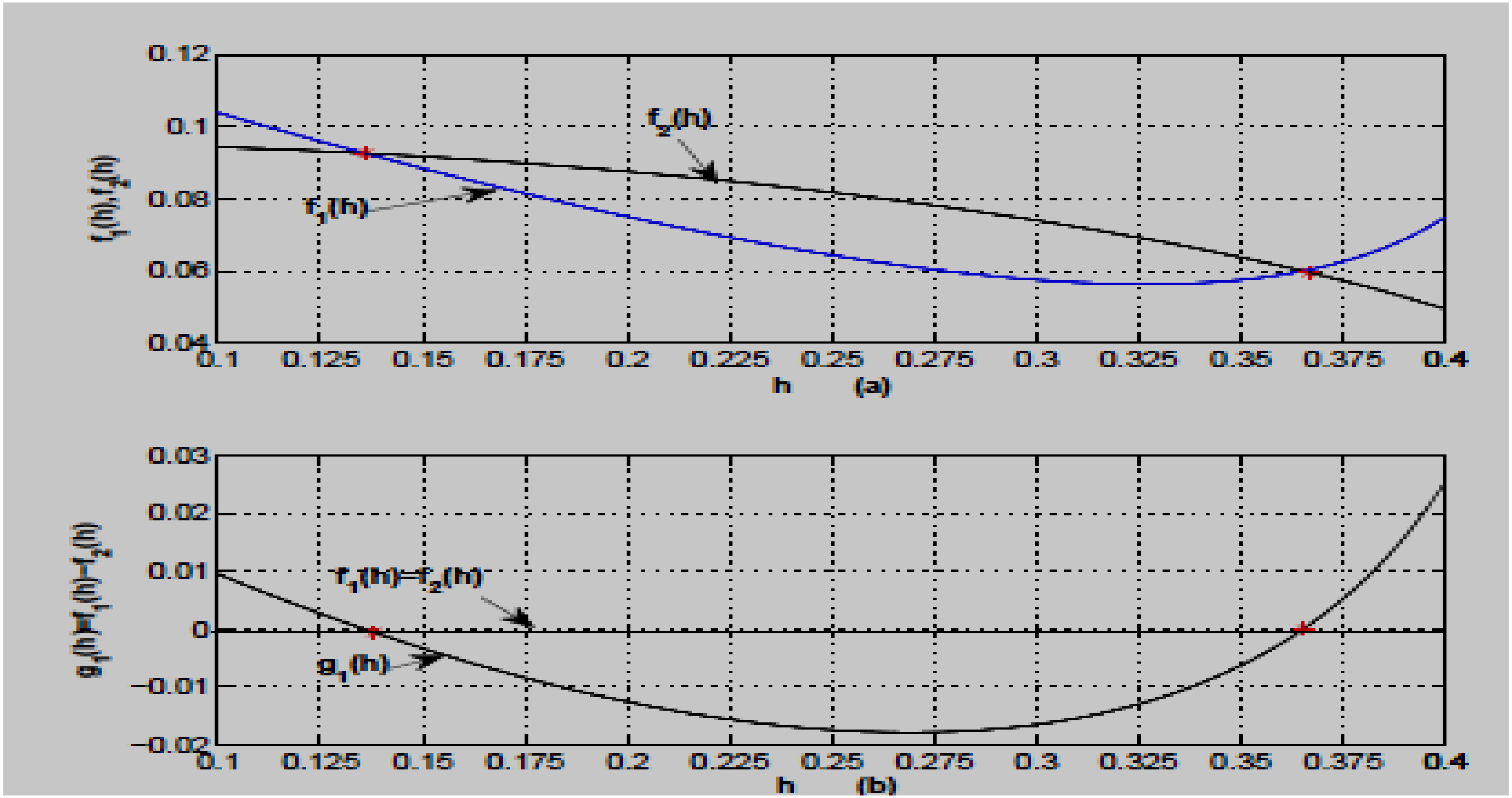




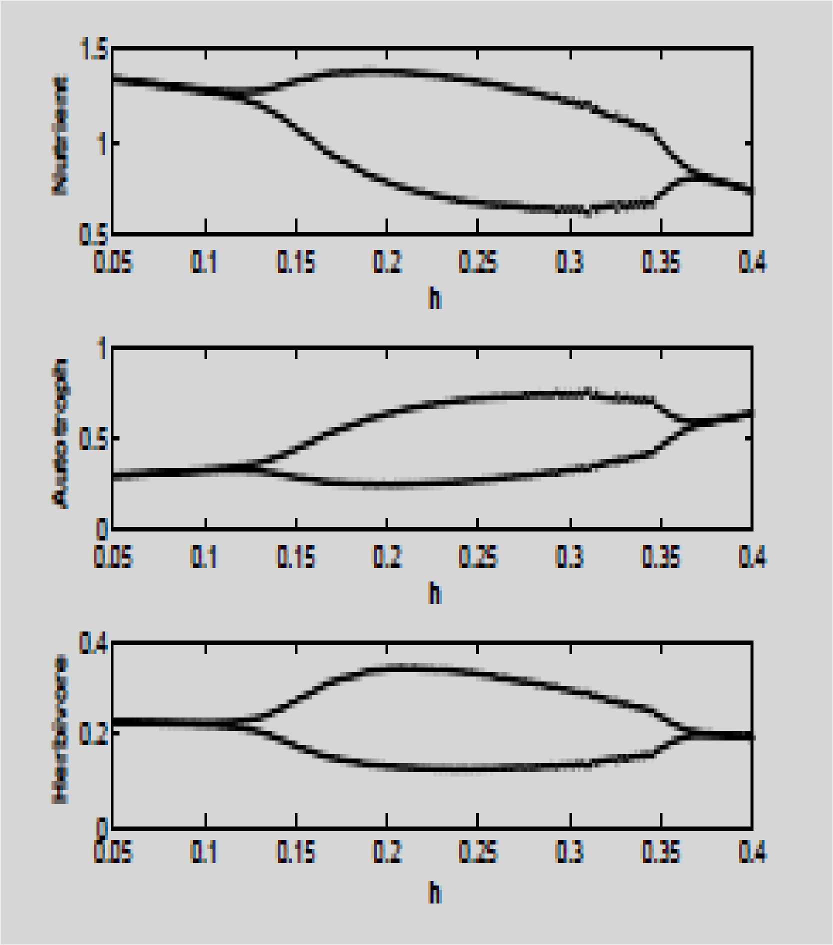
Bifurcation Analysis

- It is observed that $f1(h) = A1(h)A2(h)$ and $f2(h) = A3$ intersect at $h = 0.135$ and $h = 0.368$ indicating that the system (1) changes its stability when the parameter h crosses the thresholds $h* = 0.135$ and 0.368.
- Moreover, for $h > 0.135$ we see that $f1(h) < f2(h)$ the system (1) unstable at $E*$.
- On the other hand, for $h > 0.368$ we observe that $f1(h) > f2(h)$, satisfying the condition of stability at $E*$.

Figure 5: (a) The two curves $f_1(h)$, $f_2(h)$, intersect at the $h = h^*$ (red star). (b) The tangent to the curve $g_1(h) = f_1(h) - f_2(h)$ at $h = h^*$ is not parallel to the h axis.



Bifurcation diagrams in terms of h (Left)
Bifurcation diagrams in terms of N^0 (Right)



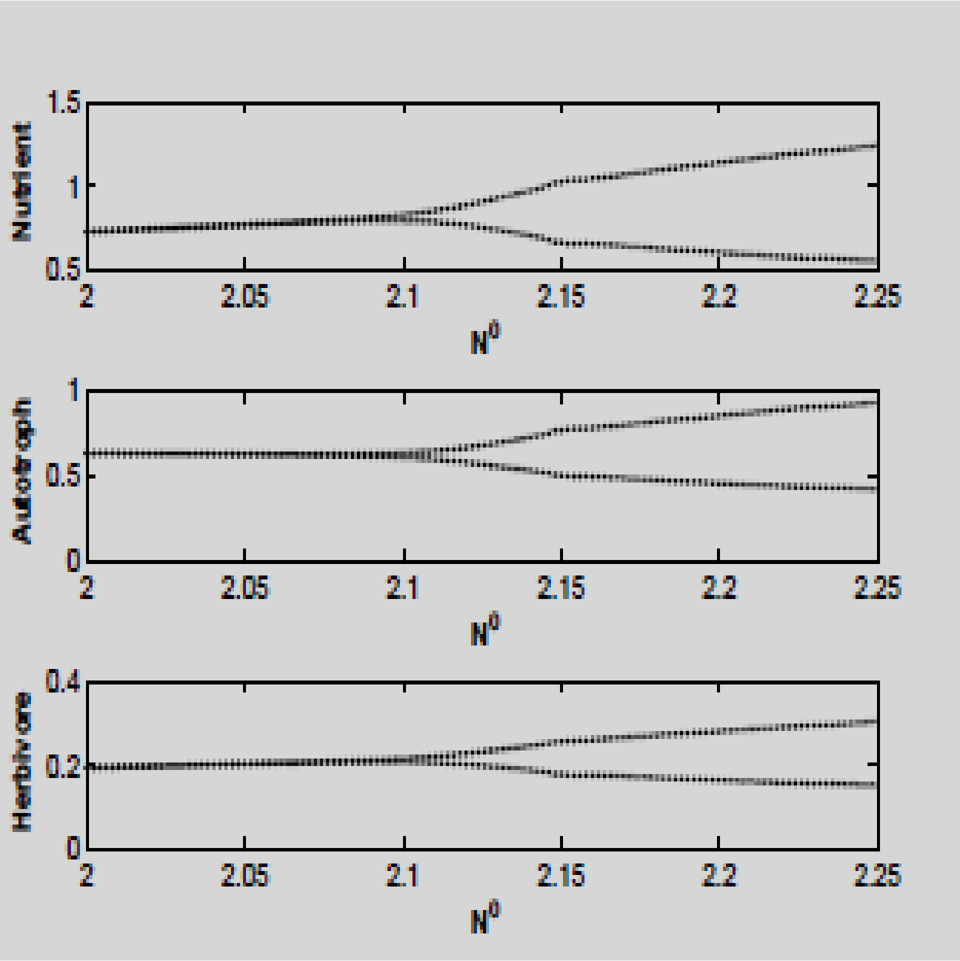


Figure 6: (a) The two curves $f_1(N^0)$, $f_2(N^0)$, intersect at the $N^0 = N^{0*}$ (red star). (b) The tangent to the curve $g_1(N^0) = f_1(N^0) - f_2(N^0)$ at $N^0 = N^{0*}$ is not parallel to the N^0 axis.

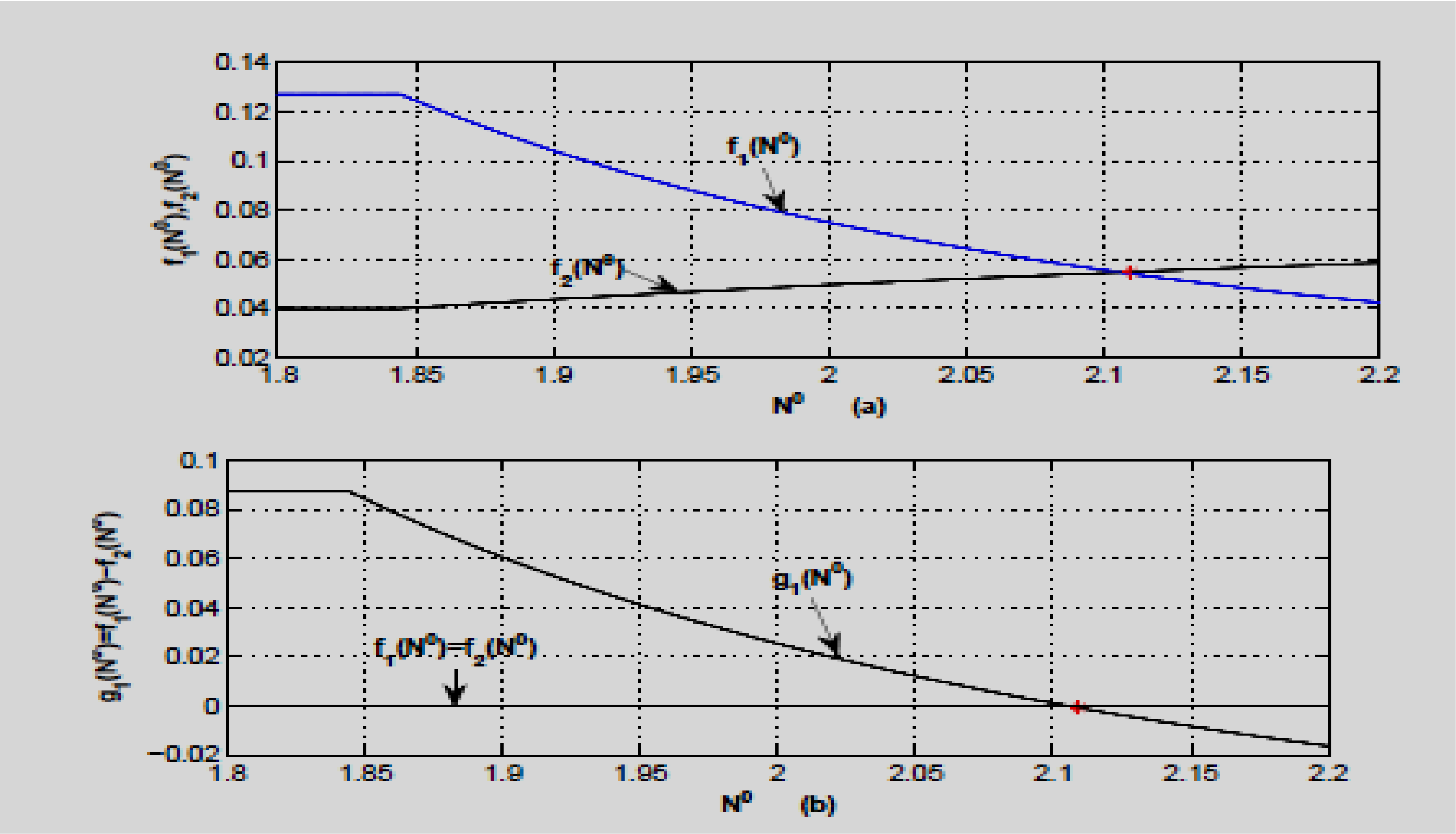
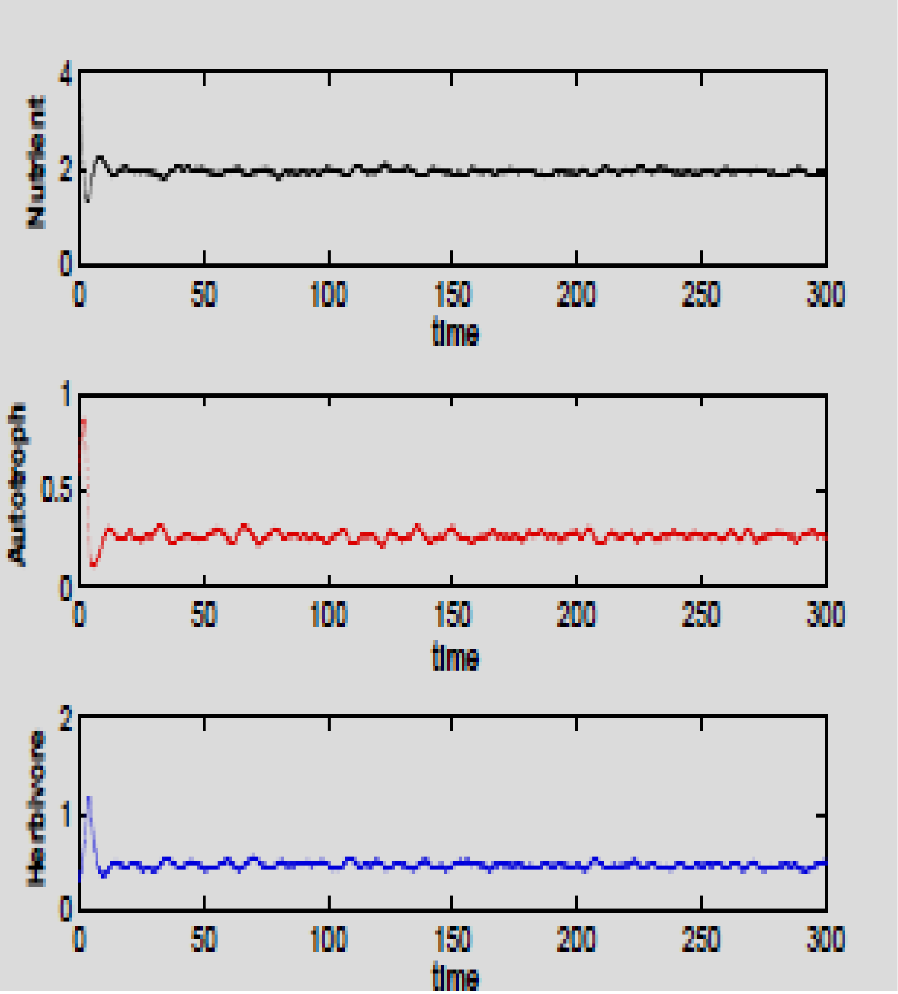
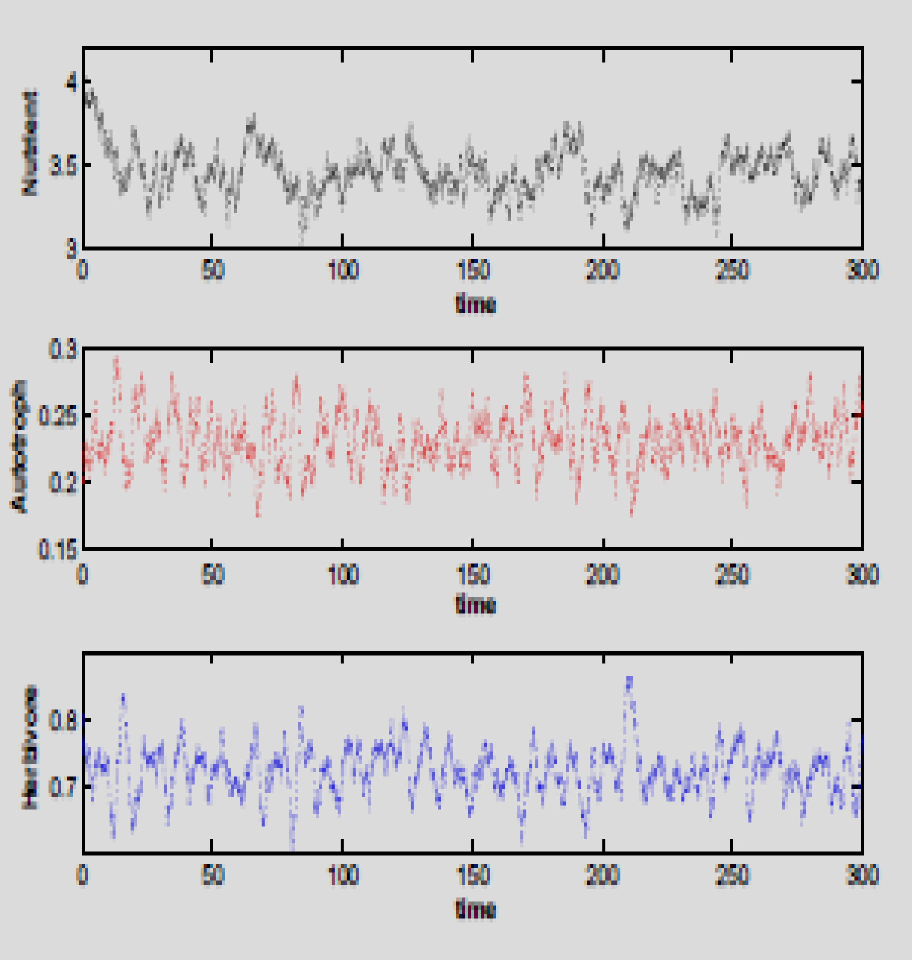


Figure 7: Effects of environmental fluctuations. Left: $\sigma_1 = 0.09$, $\sigma_2 = 0.08$, $\sigma_3 = 0.09$; Right: $\sigma_1 = 0.25$, $\sigma_2 = 0.15$, $\sigma_3 = 0.12$.





Conclusions

- The system exhibits dynamics instability (plankton bloom) due to high nutrient input rate and low value of harvesting rate of herbivores population separately.

- In presence of high dilution rate of nutrient the system exhibits recurrence bloom.

- Low value of harvesting rate of herbivores may lead to extinction of herbivores population.

Conclusions

- The additional food source of autotroph biomass maintains stability.

- Discussed stochastic stability in presence of environmental disturbances and compared with deterministic model.

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Thank You