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Qualitative features of a *NPZ-Model*

Yaya Youssouf Yaya[1], Diene Ngom[1], Mamadou Sy[2]
[1]Département de Mathématiques
Université Assane Seck de Ziguinchor, Sénégal
UMI 2019-IRD & UMMISCO-UGB
[2]Section de Mathématiques, UFR SAT
Université Gaston-Berger de Saint-Louis BP 234 Saint-Louis, Sénégal.

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***Abstract*— Qualitative study of higher order non linear dynamical systems is a rewarding experience and a great challenge. This reflective paper is an attempt to deeply analyze interaction features between nutrients, phytoplanktons and zooplanktons by building a so-called *NPZ-Model*. We used classical methods (of Lyapunov, Hopf, etc.) to examine existence, positivity, boundedness and stability of solutions. Our main contribution is the implementation of a meaningful space parameter that simultaneously guarantees instability of equilibria at the border and stability of the internal equilibrium. In the case of internal equilibrium instability, we observed the emergence of limit cycle which means the existence of periodical solutions.**

***Keywords*-Planktons ; Upwelling ; Dynamical System ; Limit-Cycle ; Stability.**

I. Introduction

Experiments and sporadic observations of front zones (intense upwelling) show significant primary production (i.e., phytoplankton and zoo-plankton) in these zones. This overproduction due to nutrients influx from ocean floor to the Ekman layer (surface layer) promotes the growth of animal populations living in this layer, sardines for example.

Dynamics of living species in aquatic environments involve biological phenomena such as predation or interspecies competition. There are also physical phenomena such as flowing water, temperatures changes and range of salinity. These phenomena are closely linked and are subject to important multidisciplinary scientific investigations-that is, oceanography, ecology, mathematics and physics.

Several deterministic models governing species dynamics in the food chain have emerged recently. In particular the interaction between nutrients, phytoplankton and zooplankton ([1], [2], [3], [4], [5], [6]) .

These studies can be roughly broken down into two categories. The first is dynamical systems where observables are densities (or number) of living species. In continuous case, the temporal evolution is described by an ODE [1]. The sec-

[1]System of Ordinary Differential Equations

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ond category is that of reaction-diffusion systems where evolution of observables is spatio-temporal, one uses PDEs [2] in the continuous case. Sometimes one can add transport effect to take into account water velocity. Note that algebraic systems are handled in discrete cases.

Among these systems there is a relevant model governing dynamics of three trophic chain species mentioned above. It was initiated by Steele and Henderson in 1981 ([7], [8]) and then fleshed out by Baretta and Ebenhöh in 1997 [9]). Although they have given a perfect description of numerical modeling and simulations,their studies failed to grasp the description of space parameters and properties of solutions. We suppose that this is due to a plethora of parameters and the strong non-linearity of equations. This is why we derive a model which will be called *NPZ-Model*, It's a 3-D dynamical system. Our study is first articulated on the space of admissible parameters. It's a set of conditions guaranteeing existence, positivity and boundedness of solutions. Then we rigorously analyzed the equilibrium stability by applying Lyapunov method and LaSalle principle of invariance. In the case of instability, we examined bifurcation in which a supercritical Hopf bifurcation has been discovered, this gives a stable limit cycle.

II. *NPZ-Model* & NOTATIONS

To describe dynamic of phytoplanktons [3], nutrients [4] and zooplanktons [5], we are going to adjust a model developed by Steele and Henderson in 1992 (cf. [8]) and modified by Edwards and Brindley in 1996 (cf. [10]) then Oschlies and Garçon in 1999 (cf. [11]).

The model describes interaction of three species in food chain: Nutrients $n(t)$, Phytoplankton $p(t)$ and Zooplanktons $z(t)$. Molecular concentration can be affected over time in an aquatic environment (ocean, lake, etc.). We have the following system of equations:

$$\begin{cases} \dfrac{dn}{dt} = \xi_n - \dfrac{\beta np}{k_n+n} \\ \qquad +\mu_n\Big(\dfrac{\alpha(1-\gamma)\eta p^2}{\alpha+\eta p^2}z+\mu_p p+\mu_z z^2\Big), \\ \dfrac{dp}{dt} = \dfrac{\beta np}{k_n+n} - \dfrac{\alpha\eta p^2}{\alpha+\eta p^2}z - \mu_p p\,, \\ \dfrac{dz}{dt} = \gamma\dfrac{\alpha\eta p^2}{\alpha+\eta p^2}z - \mu_z z^2\,. \end{cases} \tag{1}$$

The first equation of system (1) expresses nutrients evolution. The combined and vertical mixture results from an optimized and recycled nutrients supply for bacteria and phytoplanktons.
Vertical mixing transports nutrients from the deep layer of water to the mixing layer (Ekman layer), this transport is expressed by the flux

$$\xi_n = S(x,y,\vec{v}).(n_0-n), \tag{2}$$

where the function S designates design the front zone intensity. It depends essentially on horizontal position (x, y) and water velocity $\vec{v}$ from the upwelling phenomenon. In this paper, we consider $S(x,y,\vec{v})$ constant. This simplification eliminates the spatial aspect and does not take into account water velocity.

Nutrients are consumed by phytoplankton with a characteristic saturation described by a Holling type II functional response [6] $\left(-\frac{\beta np}{k_n+n}\right)$. Their recycling by bacteria is modeled by the last three terms in brackets of the first equation in system (1). A part of all organic waste and exudation of zoo-plankton are recycled by bacteria. However, bacteria dynamics is not included in the model.

Phytoplankton's dynamics is considered in the second equation of system (1). Their concentration depends on nutrients which constitute a food source $\left(\dfrac{\beta np}{k_n+n}\right)$. It is also reduced by natural mortality $(-\mu_p p)$ and by zoo-plankton's grazing (predation) $\left(-\dfrac{\alpha\eta p^2}{\alpha+\eta p^2}z\right)$ which is Holling type III functional response.

[2]System of Partial Differential Equation

[3]All chlorophyllian aquatic organisms from plankton, some microscopic, others large

[4]as nitrate, phosphate or silicate

[5]All animal species that are part of plankton

[6]Which takes into account nutrient consumption time. Therefore, catch rate decreases with increasing nutrient density.

TABLE I: Parameters description of *NPZ-Model*

Parameters	***Description***
S	Upwelling Intensity
β	Rate of grazing conversion (predation)
γ	Grazing Coefficient
α	Zoo-plankton attack rate
$h = \dfrac{\eta}{\alpha}$	Average Manipulation Time
k_n	Mid-saturation Constant for nutrient recruitment
μ_n	Nutrient regeneration efficiency
μ_p	Natural phytoplankton mortality rate
μ_z	Natural zoo-plankton mortality rate
n_0	Constant concentration of nutrients under the mixing layer

Grazing is also considered as zooplankton growth term with the factor $\gamma\frac{\alpha\eta p^2}{\alpha+\eta p^2}z-\mu_z z^2$ (third equation of (1) . This factor is there to take into account that only a part of nutrients is converted into zoo-plankton biomass. The Other part $(1-\gamma)$ is recycled. Mortality of zoo-plankton is assumed to be quadratic.This hypothesis implies the existence of a super predator acting on zoo-plankton whose dynamics are not explicitly considered [12]. It may also be an interspecies competition. Parameters (Table I) are described as in the work of Pasquero & al [13]. Their numerical values will be discussed in the paper through the space of admissible parameters (III.1).

As the Holling type-II functional response is one of the most realistic forms to represent predation rate of predators on their preys [14], we change the Holling type-III functional to a Holling type-II like $\frac{\alpha p}{1+\alpha hp}$.

We then assume that there is neither implicit predation on the zoo-plankton nor interspecies competition. We assumed that the steady constancy of nutrient recruitment mid saturation k_n is greater than the constant concentration of nutrients under the mixing layer n_0 (i.e., $k_n > n_0$). Then system (1) becomes what we will call *NPZ-Model*:

$$\begin{cases} \dfrac{dn}{dt} = \xi_n - \dfrac{\beta np}{k_n+n} \\ \qquad + \mu_n\Big(\dfrac{\alpha(1-\gamma)pz}{1+\alpha hp} + \mu_p p + \mu_z z\Big), \\ \dfrac{dp}{dt} = \dfrac{\beta np}{k_n+n} - \dfrac{\alpha p}{1+\alpha hp}z - \mu_p p\,, \\ \dfrac{dz}{dt} = \dfrac{\alpha\gamma pz}{1+\alpha hp} - \mu_z z\,. \end{cases} \tag{3}$$

To reduce occurrences of α in the *NPZ-Model*, we denote $\eta \equiv \alpha.h$. Then we set $\epsilon_n = \mu_n - 1$, $\bar{\gamma} = 1-\gamma$, therefore *NPZ-Model* (3) becomes

$$\begin{cases} \dfrac{dn}{dt} = S(n_0-n) - \dfrac{\beta np}{k_n+n} \\ \qquad + \mu_n\left(\dfrac{\alpha\bar{\gamma}pz}{1+\eta p} + \mu_p p + \mu_z z\right), \\ \dfrac{dp}{dt} = \dfrac{\beta np}{k_n+n} - \dfrac{\alpha p}{1+\eta p}z - \mu_p p\,, \\ \dfrac{dz}{dt} = \dfrac{\alpha\gamma pz}{1+\eta p} - \mu_z z\,. \end{cases} \tag{4}$$

Let's define

$$\begin{aligned} F_1(n,p,z) &= S(n_0-n) - \frac{\beta np}{k_n+n} \\ &\quad + \mu_n\left(\frac{\alpha\bar{\gamma}pz}{1+\eta p} + \mu_p p + \mu_z z\right), \\ F_2(n,p,z) &= \frac{\beta np}{k_n+n} - \frac{\alpha p}{1+\eta p}z - \mu_p p\,, \\ F_3(n,p,z) &= \frac{\alpha\gamma pz}{1+\eta p} - \mu_z z\,. \end{aligned} \tag{5}$$

Then *NPZ-Model* (4) is written as:

$$\begin{cases} \dfrac{dn}{dt} = F_1(n,p,z)\,, \\ \dfrac{dp}{dt} = F_2(n,p,z)\,, \\ \dfrac{dz}{dt} = F_3(n,p,z)\,. \end{cases} \tag{6}$$

or, equivalently,

$$\frac{d\Phi}{dt}(t) = F(\Phi(t))$$

where

$$\Phi(t) = (n(t), p(t), z(t))^T,$$

and

$$\begin{array}{rccc} F: & \left(\mathbb{R}_+^*\right)^3 & \longrightarrow & \left(\mathbb{R}_+^*\right)^3 \\ & \Phi & \longmapsto & (F_1(\Phi), F_2(\Phi), F_3(\Phi))^T. \end{array}$$

Denoting by $F_{i,x}$ the partial derivative of F_i with respect to x, we have:

$$\begin{aligned} F_{1,n} &= -S - \frac{\beta k_n p}{(k_n+n)^2}, \\ F_{1,p} &= -\frac{\beta n}{k_n+n} + \frac{\alpha \mu_n \bar{\gamma} z}{(1+\eta p)^2} + \mu_n \mu_p, \\ F_{1,z} &= \frac{\alpha \mu_n \bar{\gamma} p}{1+\eta p} + \mu_n \mu_z, \\ F_{2,n} &= \frac{\beta k_n p}{(k_n+n)^2}, \\ F_{2,p} &= -\frac{\alpha z}{(1+\eta p)^2} + \frac{\beta n}{k_n+n} - \mu_p, \\ F_{2,z} &= -\frac{\alpha p}{1+\eta p}, \\ F_{3,n} &= 0, \\ F_{3,p} &= \frac{\alpha \gamma z}{(1+\eta p)^2}, \\ F_{3,z} &= \frac{\alpha \gamma p}{1+\eta p} - \mu_z. \end{aligned} \tag{7}$$

Thus, Jacobian matrix of field F is written:

$$J_{F(n,p,z)} = \begin{pmatrix} F_{1,n} & F_{1,p} & F_{1,z} \\ F_{2,n} & F_{2,p} & F_{2,z} \\ F_{3,n} & F_{3,p} & F_{3,z} \end{pmatrix}. \tag{8}$$

Thus, we have the main notations that we will use for qualitative study of *NPZ-Model*. Note that intermediate ratings will be defined as needed.

III. Qualitative features of *NPZ-Model*

A. Solutions Properties

Proposition III.1. *(**Existence, uniqueness, positivity & boundedness**)*
System (4) associated with initial condition has a unique positive and bounded solution.

Proof: (Proposition III.1)
Elements of Jacobian matrix of field F (8) are all continuous, then the function F is locally Lipschitzian. Thus by Cauchy-Lipschitz theorem [15], system (4) has a unique local solution.

To show the positively invariance of $\mathbb{R}_+^3$, let's consider these elements of boundaries: $\Gamma_1 \equiv \{0\} \times \mathbb{R}_+ \times \mathbb{R}_+$, $\Gamma_2 \equiv \mathbb{R}_+ \times \{0\} \times \mathbb{R}_+$ and $\Gamma_3 \equiv \mathbb{R}_+ \times \mathbb{R}_+ \times \{0\}$. Note that $\mathbb{R}_+^3 = \{(n,p,z) \in \mathbb{R}^3 : -n \leq 0; -p \leq 0 \text{ and } -z \leq 0\}$. We have also

$$\begin{aligned} F_{1/\Gamma_1} &= Sn_0 + (\epsilon_n + 1)\Big((1-\gamma)\frac{\alpha p}{1+\eta p} z \\ &\qquad + \mu_p p + \mu_z z\Big) \geq 0, \\ F_{2/\Gamma_2} &= 0\,, \\ F_{3/\Gamma_3} &= 0. \end{aligned}$$

Thus, by choosing a function $L(n,p,z) = -n$, we see that $\langle F, \nabla L \rangle \leq 0$. From the foregoing, we can deduce by the barrier theorem (theorem 16.9 in [16]) that the vector field point into the domain along Γ_1 and by analogy along Γ_2 and Γ_3. Hence, $\mathbb{R}_+^3$ is a positively invariant domain, i.e., for any positive initial condition, solutions remain positive.

To prove boundedness, let's define

$$\Theta(t) = an(t) + ap(t) + z(t) \quad ,$$

$$\text{with} \quad a > 0 \text{ such that } \frac{\gamma}{1-\mu_n\bar{\gamma}} < a < \frac{1}{\mu_n}.$$

Thus

$$\begin{aligned} \dot{\Theta}(t) &= a\dot{n}(t) + a\dot{p}(t) + \dot{z}(t) \\ &= aSn_0 - aSn - a\frac{\beta np}{k_n+n} + a\frac{\mu_n \bar{\gamma} \alpha pz}{1+\eta p} \\ &\quad + a\mu_n\mu_p p + a\mu_n\mu_z z + a\frac{\beta np}{k_n+n} - a\frac{\alpha pz}{1+\eta p} \\ &\quad - a\mu_p p + \frac{\alpha\gamma pz}{1+\eta p} - \mu_z z \end{aligned}$$

$$= aSn_0 - aSn + (a\alpha\mu_n\bar{\gamma} - a\alpha + \alpha\gamma)\frac{pz}{1+\eta p} - a\mu_p(1-\mu_n)p - \mu_z(1-a\mu_n)z.$$

We have

$$a\alpha\mu_n\bar{\gamma} - a\alpha + \alpha\gamma \leq 0 \quad \text{because} \quad \frac{\gamma}{1-\mu_n\bar{\gamma}} < a.$$

Thus

$$\dot{\Theta}(t) \leq -aSn - a\mu_p(1-\mu_n)p - \mu_z(1-a\mu_n)z + aSn_0.$$

Let us set

$$\tau = \min\{S;\ \mu_p(1-\mu_n);\ \mu_z(1-a\mu_n)\}.$$

Therefore

$$\dot{\Theta}(t) \leq -\tau\Theta(t) + aSn_0.$$

By applying Gronwall's inequality, we obtain:

$$\Theta(t) \leq e^{-\tau t}e^{t_0}\Theta(t_0) + aSn_0e^{-t_0}.$$

Accordingly, for a large t , $\Theta(t) < e^{t_0}\Theta(t_0) + aSn_0e^{-t_0}$, and the solutions are bounded. ■

B. Equilibria of System and Stability

Proposition III.2 (**Existence and positivity of equilibria**)**.** *System (4) has four stationary (equilibrium) points which will be called* e_1, e_2, e_3, e_4 *(equations (11) & (12)).* e_1 *is unconditionally positive. If we denote*

$$R_1 = \frac{\mu_p(k_n+n_0)}{\beta n_0},$$
$$R_2 = \frac{\eta\mu_z}{\alpha\gamma},$$
$$R_3 = \frac{\beta\epsilon_n\mu_z}{S(k_n-n_0)A} = \frac{\beta\epsilon_n\mu_z}{\alpha\gamma S(k_n-n_0)(1-R_2)},$$
$$R_4 = \frac{S\alpha\gamma k_n\mu_p + S\alpha\gamma\mu_p n_0 + S\beta\eta\mu_z n_0 + \beta\mu_p\mu_z + \mu_n\mu_p^2\mu_z}{S\alpha\beta\gamma n_0 + S\eta k_n\mu_p\mu_z + S\eta\mu_p\mu_z n_0 + \beta\mu_n\mu_p\mu_z + \mu_p^2\mu_z}, \quad (9)$$

and assume that

$$(R_1, R_2, R_3, R_4) \in]-\infty, 1[^4,$$

Then we have

$$e_2,\ e_3 \in \mathbb{R}^3_+ \ \text{and}\ e_4 \notin \mathbb{R}^3_+,$$

that is, the second and third equilibrium points are in the positive octant (i.e., $\mathbb{R}^3_+$*) and the fourth is not.*

Proof: (Proposition III.2)
To calculate equilibrium points, we replace the first equation by the sum of three others and we obtain the following system :

$$\begin{cases} S(n_0-n)+\epsilon_n\left(\dfrac{\alpha pz\,(1-\gamma)}{\eta p+1}+\mu_p p+\mu_z z\right) = 0, \\ p\left(-\dfrac{\alpha z}{\eta p+1}+\dfrac{\beta n}{k_n+n}-\mu_p\right) = 0, \\ z\left(\dfrac{\alpha\gamma p}{\eta p+1}-\mu_z\right) = 0. \end{cases} \quad (10)$$

From the third equation of system (10), we have $z=0$ where $p = \frac{\mu_z}{\alpha\gamma-\eta\mu_z}$.
By treating the case where $z = 0$, we have two equilibrium points :

$$\begin{aligned} e_1 &= (\overset{*}{n}_1, \overset{*}{p}_1, \overset{*}{z}_1) = (n_0, 0, 0), \\ e_2 &= (\overset{*}{n}_2, \overset{*}{p}_2, \overset{*}{z}_2) \\ &= \left(\frac{k_n\mu_p}{\beta-\mu_p}, \frac{S\,(k_n\mu_p - n_0(\beta-\mu_p))}{\mu_p\,(\beta-\mu_p)\,\epsilon_n}, 0\right). \end{aligned} \quad (11)$$

By treating the case where $p = \frac{\mu_z}{\alpha\gamma-\eta\mu_z}$, two other equilibrium points are determined $e_3 = (\overset{*}{n}_3, \overset{*}{p}_3, \overset{*}{z}_3)$ and
$e_4 = (\overset{*}{n}_4, \overset{*}{p}_4, \overset{*}{z}_4)$ (after substitution of p in the first two equations of system (10)), where

$$\begin{aligned} \overset{*}{n}_3 &= \frac{-B_1+\sqrt{\Delta}}{2S(\alpha\gamma-\eta\mu_z)}, \\ \overset{*}{p}_3 &= \frac{\mu_z}{\alpha\gamma-\eta\mu_z}, \\ \overset{*}{z}_3 &= \frac{-B_2+\sqrt{\Delta}}{\frac{2\epsilon_n\mu_z}{\gamma}(\alpha\gamma-\eta\mu_z)}, \\ \overset{*}{n}_4 &= \frac{-B_1-\sqrt{\Delta}}{2S(\alpha\gamma-\eta\mu_z)}, \\ \overset{*}{p}_4 &= \frac{\mu_z}{\alpha\gamma-\eta\mu_z}, \\ \overset{*}{z}_4 &= \frac{-B_2-\sqrt{\Delta}}{\frac{2\epsilon_n\mu_z}{\gamma}(\alpha\gamma-\eta\mu_z)}, \end{aligned} \quad (12)$$

with relations:

$$\begin{aligned} A &= S(\alpha\gamma - \eta\mu_z), \\ B_1 &= S\alpha\gamma k_n - S\alpha\gamma n_0 - S\eta k_n\mu_z \\ &\quad +S\eta\mu_z n_0 - \beta\epsilon_n\mu_z, \\ B_2 &= S\alpha\gamma k_n + S\alpha\gamma n_0 - S\eta k_n\mu_z - S\eta\mu_z n_0 \\ &\quad -\beta\epsilon_n\mu_z + 2\epsilon_n\mu_p\mu_z \\ &= S(k_n - n_0)A - \beta\epsilon_n\mu_z, \\ C &= -S\alpha\gamma k_n n_0 + S\eta k_n\mu_z n_0 = -k_n n_0 A \\ &= 2(An_0 + \epsilon_n\mu_p\mu_z) + B_1, \\ \Delta &= B_1^2 - 4AC = B_1^2 + 4k_n n_0 A^2 > 0. \end{aligned} \tag{13}$$

Note that $0 < \mu_n < 1$, thus $\epsilon_n = \mu_n - 1 < 0$. According to hypothesis $R_1 < 1$, we have $\beta > \mu_p$, which implies

$$\overset{*}{n}_2 = \frac{k_n\mu_p}{\beta - \mu_p} > 0 \text{ and } k_n\mu_p < n_0(\beta - \mu_p).$$

Thus $\overset{*}{p}_2 > 0$. Consequently, $R_1 < 1$ implies $e_2 = (\overset{*}{n}_2, \overset{*}{p}_2, \overset{*}{z}_2) \in \mathbb{R}^3_+$. From $R_2 = \dfrac{\eta\mu_z}{\alpha\gamma} < 1$, we deduce $\overset{*}{p}_3 = \dfrac{\mu_z}{\alpha\gamma - \eta\mu_z} > 0$. Considering hypothesis

$$R_3 = \frac{\beta\epsilon_n\mu_z}{S(k_n - n_0)A} < 1$$

and the fact that $A > 0$ because $R_2 < 1$, we have :

$$B_1 = S(k_n - n_0)A - \beta\epsilon_n\mu_z > 0$$

$$C = -k_n n_0 A < 0.$$

Thus $B_1^2 < \Delta = B_1^2 - 4AC$, so $-B_1 + \sqrt{\Delta} > 0$. Thereby

$$\frac{-B_1 + \sqrt{\Delta}}{2S(\alpha\gamma - \eta\mu_z)} > 0.$$

Hence

$$R_3 < 1 \quad \text{implies that} \quad \overset{*}{n}_3 > 0.$$

We have also

$$R_4 < 1,$$

from where

$$\begin{aligned} &4\epsilon_n\mu_z(S\alpha\beta\gamma n_0 - S\alpha\gamma k_n\mu_p - S\alpha\gamma\mu_p n_0 \\ &-S\beta\eta\mu_z n_0 + S\eta k_n\mu_p\mu_z \\ &+S\eta\mu_p\mu_z n_0 + \beta\epsilon_n\mu_p\mu_z - \epsilon_n\mu_p^2\mu_z) < 0 \end{aligned}.$$

Then

$$-B_2 + \sqrt{\Delta} > 0.$$

Therefore

$$R_4 < 1 \quad \Longrightarrow \quad \overset{*}{z}_3 > 0.$$

Ultimately

$$e_4 \notin \mathbb{R}^3_+ \quad \text{because} \quad \overset{*}{n}_4 < 0$$

Indeed

$$\overset{*}{n}_4 = \frac{-B_1 - \sqrt{\Delta}}{2S(\alpha\gamma - \eta\mu_z)}$$

and

$$2S(\alpha\gamma - \eta\mu_z) > 0 - B_1 - \sqrt{\Delta} < 0,$$

because

$$B_1 > 0.$$

■

Definition III.1 (**Space of admissible parameters**).
We define the space of admissible parameters $\mathcal{P}_{ad}$ by

$$\mathcal{P}_{ad} = \Big\{(\alpha,\beta,\eta,\mu_p,\mu_z,k_n,n_0,S,\mu_n,\gamma) \in (\mathbb{R}^*_+)^7 \times]0,1[^2 \\ : n_0 < k_n;\ R_1, R_2, R_3, R_4 < 1\Big\}. \tag{14}$$

Remark III.1. *The space of admissible parameters defined above (III.1) $\mathcal{P}_{ad}$ is not empty . Table II gives examples of admissible parameters.*

Proposition III.3 (**Stability of e_1 and e_2**). *Equilibrium points e_1 (11) is always unstable, and if $\sqrt{\Delta_0} > b_0$, e_2 is unstable also.*

Proof: (Proposition III.3)
By substituting e_1 into the Jacobian matrix (8), we have:

$$J_{F(n_0,0,0)} = \begin{pmatrix} -S & -\frac{\beta n_0}{k_n + n_0} + \mu_n\mu_p & \mu_n\mu_z \\ 0 & \frac{\beta n_0}{k_n + n_0} - \mu_p & 0 \\ 0 & 0 & -\mu_z \end{pmatrix}. \tag{15}$$

The eigenvalues are

$$-S, \quad -\mu_z, \quad \text{and} \quad \frac{\beta n_0}{k_n + n_0} - \mu_p.$$

TABLE II: Some admissible parameters with conditions R_1, R_2, R_3, R_4.

α	0.33	0.94	0.52
β	0.84	0.89	0.47
γ	0.85	0.88	0.30
η	0.15	0.24	0.13
μ_n	0.66	0.88	0.71
μ_p	0.19	0.38	0.07
μ_z	0.82	0.41	0.43
k_n	0.55	0.23	0.95
n_0	0.82	0.69	0.98
S	0.92	0.78	0.40
R_1	0.38	0.57	0.34
R_2	0.46	0.11	0.35
R_3	0.01	0.01	$-6.8e^{-4}$
R_4	0.92	0.77	0.82

One of the eigenvalues is strictly positive, it is $\frac{\beta n_0}{k_n+n_0} - \mu_p = \mu_p \left(\frac{1-R_1}{R_1}\right) > 0$. Then, according to Lyapunov's indirect theorem, the equilibrium point e_1 is unstable.

On the other hand, characteristic polynomial of the linearized system around e_2 is :

$$P_{e_2}(\lambda) = (\lambda - \lambda_0) Q_{e_2}(\lambda), \tag{16}$$

where $Q_{e_2}(\lambda)$ is the quadratic form given by (17)

$$a_0\lambda^2 + b_0\lambda + c_0, \tag{17}$$

with

$$\begin{aligned}
a_0 &= k_n\mu_p,\\
b_0 &= R_1 S\beta^3\epsilon_n n_0 - 3R_1 S\beta^2\epsilon_n\mu_p n_0\\
&\quad +3R_1 S\beta\epsilon_n\mu_p^2 n_0 - R_1 S\epsilon_n\mu_p^3 n_0 n\\
&\quad -S\beta^3\epsilon_n n_0 + 3S\beta^2\epsilon_n\mu_p n_0\\
&\quad -3S\beta\epsilon_n\mu_p^2 n_0 + S\epsilon_n\mu_p^3 n_0 + Sk_n\mu_p,\\
c_0 &= -R_1 S\beta^3\epsilon_n^2\mu_p n_0 + 3R_1 S\beta^2\epsilon_n^2\mu_p^2 n_0\\
&\quad -3R_1 S\beta\epsilon_n^2\mu_p^3 n_0 + R_1 S\epsilon_n^2\mu_p^4 n_0\\
&\quad +S\beta^3\epsilon_n^2\mu_p n_0 - 3S\beta^2\epsilon_n^2\mu_p^2 n_0\\
&\quad +3S\beta\epsilon_n^2\mu_p^3 n_0 - S\epsilon_n^2\mu_p^4 n_0.
\end{aligned}$$

After simplification

$$\begin{aligned}
a_0 &= k_n\mu_p\,,\\
b_0 &= S\epsilon_n n_0(R_1-1)\left(\beta-\mu_p\right)^3 + Sk_n\mu_p\,,\\
c_0 &= \epsilon_n\mu_p(Sa_0 - b_0).
\end{aligned}$$

We observe that $a_0 > 0, \quad c_0 < 0$ because $R_1 < 1$. So the discriminant of the quadratic form $Q_{e_2}(\lambda)$ is

$$\Delta_0 = b_0^2 - 4a_0c_0 > 0.$$

Then, the two real roots of $Q_{e_2}(\lambda)$ are

$$\lambda_1 = \frac{-b_0 + \sqrt{\Delta_0}}{2a_0} > 0 \text{ and } \quad \lambda_2 = \frac{-b_0 - \sqrt{\Delta_0}}{2a_0}. \tag{18}$$

As λ_1 is positive because $\sqrt{\Delta_0} > b_0$, we conclude from Lyapunov's indirect theorem [15] that the equilibrium point e_2 is unstable. □ ■

Theorem III.1. *(**Stability of** e_3) Let's define*

$$\begin{aligned}
H_{11} &= \frac{S}{n} + \frac{\beta k_n \overset{*}{p}}{n(k_n+n)(k_n+\overset{*}{n})},\\
H_{22} &= \frac{\alpha\omega_0}{(1+\eta p)(1+\eta\overset{*}{p})},\\
\Pi &= \frac{\mu_p\mu_n}{-2n} + \frac{\beta\overset{*}{n}}{-2(k_n+n)(k_n+\overset{*}{n})}\\
&\quad + \frac{\mu_n\bar{\gamma}\alpha\overset{*}{z}}{-2n(1+\eta p)(1+\eta\overset{*}{p})},\\
\Gamma &= \frac{\mu_n}{-2n}\left(\mu_z + \bar{\gamma}\alpha(1+\eta\overset{*}{p})p\right),\\
\Psi &= \frac{\delta\gamma - \alpha}{(1+\eta p)(1+\eta\overset{*}{p})},\\
f(n,p,z) &= H_{11}H_{22} - \Pi^2,\\
g(n,p,z) &= -\Psi^2 H_{11} - \Gamma^2 H_{22} + 2\Pi\Psi\Gamma,\\
\zeta(n,p,z) &= \alpha\frac{(\omega_0+\eta\overset{*}{z})p - \eta\overset{*}{p}z - \omega_0\overset{*}{p}}{(1+\eta p)(1+\eta\overset{*}{p})},\\
\mathbb{G} &= \big\{(n,p,z)\in\mathbb{R}^3_+ \quad / \quad f(n,p,z) > 0,\\
&\quad g(n,p,z) > 0,\ \zeta(n,p,z) < 0\big\},
\end{aligned}$$

where $\omega_0 > 0$ and $\delta \in \mathbb{R}^*$, A, B, C are auxiliary constants defined precisely in the proof (See equations (22) & (23)).
If $\Delta = B^2 - AC > 0$, then we have:

(i) *$\mathbb{G}$ is an open set containing the inner equilibrium e_3 ,*
(ii) *the equilibrium e_3 is asymptotically stable in $\mathbb{G}$.*

Proof: (Theorem III.1)
We will directly show the global stability before checking condition (i) .

Let $e_3 = (\overset{*}{n}_3, \overset{*}{p}_3, \overset{*}{z}_3) \triangleq (\overset{*}{n}, \overset{*}{p}, \overset{*}{z})$ be the inner equilibrium point. We denote $X^T = (n-\overset{*}{n}, p-\overset{*}{p}, z-\overset{*}{z})$ and $V : \mathbb{G} \longrightarrow \mathbb{R}$ defined by

$$V(n,p,z)=\int_{\overset{*}{n}}^{n} \frac{\sigma-\overset{*}{n}}{\sigma} d\sigma+\int_{\overset{*}{p}}^{p} \frac{\sigma-\overset{*}{p}}{\sigma} d\sigma+\delta\int_{\overset{*}{z}}^{z} \frac{\sigma-\overset{*}{z}}{\sigma} d\sigma,$$

where $\delta > 0$. Then, V is a positive function of class $\mathcal{C}^1$ and radially unbounded. In addition to that $V(\overset{*}{n}, \overset{*}{p}, \overset{*}{z}) = 0$. We will investigate the sign of $\dot{V}$. We have

$$\begin{aligned} \dot{V} &= \frac{dV}{dt} = \frac{n-\overset{*}{n}}{n}\frac{dn}{dt} + \frac{p-\overset{*}{p}}{p}\frac{dp}{dt} + \delta\frac{z-\overset{*}{z}}{z}\frac{dz}{dt} \\ &\triangleq \dot{V}_1 + \dot{V}_2 + \dot{V}_3 \\ \dot{V}_1 &= \frac{n-\overset{*}{n}}{n}\big(Sn_0 - Sn - \frac{\beta np}{k_n+n} + \frac{\alpha\mu_n\bar{\gamma}pz}{1+\eta p} \\ &\qquad +\mu_n\mu_p p + \mu_n\mu_p z\big). \end{aligned}$$

As $(\overset{*}{n}, \overset{*}{p}, \overset{*}{z})$ is an equilibrium, then from the first equation of system (4) we have :

$$Sn_0 = S\overset{*}{n} + \frac{\beta\overset{*}{n}\overset{*}{p}}{k_n+\overset{*}{n}} - \frac{\alpha\mu_n\bar{\gamma}\overset{*}{p}\overset{*}{z}}{1+\eta p} - \mu_n\mu_p\overset{*}{p} - \mu_n\mu_z\overset{*}{z}.$$

By substituting this equality into $\dot{V}_1$, we get:

$$\begin{aligned} \dot{V}_1 = \frac{n-\overset{*}{n}}{n}\Bigg[&- S(n-\overset{*}{n}) - \beta\left(\frac{np}{k_n+n} - \frac{\overset{*}{n}\overset{*}{p}}{k_n+\overset{*}{n}}\right) \\ &+\mu_n\bar{\gamma}\alpha\left(\frac{pz}{1+\eta p} - \frac{\overset{*}{p}\overset{*}{z}}{1+\eta\overset{*}{p}}\right) \\ &+\mu_n\mu_p(p-\overset{*}{p}) + \mu_n\mu_z(z-\overset{*}{z})\Bigg] \end{aligned}$$

Let's consider : $\dot{V}_1 = M_1 + M_2 + M_3 + M_4 + M_5$ with

$$\begin{aligned} M_1 &= -\frac{S}{n}(n-\overset{*}{n})^2, \\ M_2 &= -\frac{\beta}{n}(n-\overset{*}{n})\left(\frac{np}{k_n+n} - \frac{\overset{*}{n}\overset{*}{p}}{k_n+\overset{*}{n}}\right), \\ M_3 &= \frac{\alpha\mu_n\bar{\gamma}}{n}(n-\overset{*}{n})\left(\frac{pz}{1+\eta p} - \frac{\overset{*}{p}\overset{*}{z}}{1+\eta\overset{*}{p}}\right), \\ M_4 &= \frac{\mu_n\mu_p}{n}(n-\overset{*}{n})(p-\overset{*}{p}), \\ M_5 &= \frac{\mu_n\mu_z}{n}(n-\overset{*}{n})(z-\overset{*}{z}). \end{aligned}$$

Thus,

$$\begin{aligned} M_2 &= -\frac{\beta}{n}(n-\overset{*}{n})\frac{\left[k_n(np-\overset{*}{n}\overset{*}{p}) - n\overset{*}{n}(p-\overset{*}{p})\right]}{(k_n+n)(k_n+\overset{*}{n})} \\ &= \beta\overset{*}{n}\frac{(n-\overset{*}{n})(p-\overset{*}{p})}{(k_n+n)(k_n+\overset{*}{n})} \\ &\quad -\frac{\beta k_n}{n}\frac{(n-\overset{*}{n})(np-\overset{*}{n}\overset{*}{p})}{(k_n+n)(k_n+\overset{*}{n})} \end{aligned}.$$

We have :

$$np-\overset{*}{n}\overset{*}{p} = np-n\overset{*}{p}+n\overset{*}{p}-\overset{*}{n}\overset{*}{p} = n(p-\overset{*}{p})+\overset{*}{p}(n-\overset{*}{n})$$

$$\begin{aligned} M_2 &= \beta\overset{*}{n}\frac{(n-\overset{*}{n})(p-\overset{*}{p})}{(k_n+n)(k_n+\overset{*}{n})} \\ &\quad -\frac{\beta k_n\overset{*}{p}}{n}\frac{(n-\overset{*}{n})^2}{(k_n+n)(k_n+\overset{*}{n})} \\ &\quad -\beta k_n\frac{(n-\overset{*}{n})(p-\overset{*}{p})}{(k_n+n)(k_n+\overset{*}{n})}, \end{aligned}$$

$$\begin{aligned} M_2 &= \beta(\overset{*}{n}-k_n)\frac{(n-\overset{*}{n})(p-\overset{*}{p})}{(k_n+n)(k_n+\overset{*}{n})} \\ &\quad -\frac{\beta k_n\overset{*}{p}}{n}\frac{(n-\overset{*}{n})^2}{(k_n+n)(k_n+\overset{*}{n})}, \end{aligned}$$

$$M_3 = \frac{\mu_n\bar{\gamma}\alpha}{n}(n-\overset{*}{n})\frac{\left[pz+\eta p\overset{*}{p}z - \overset{*}{p}\overset{*}{z} - \eta p\overset{*}{p}\overset{*}{z}\right]}{(1+\eta p)(1+\eta\overset{*}{p})}.$$

We have also

$$\begin{aligned} &pz+\eta p\overset{*}{p}z - \overset{*}{p}\overset{*}{z} - \eta p\overset{*}{p}\overset{*}{z} \\ &\quad = \eta\overset{*}{p}p(z-\overset{*}{z}) + pz - p\overset{*}{z} \\ &\quad = \eta\overset{*}{p}p(z-\overset{*}{z}) + pz - p\overset{*}{z} + p\overset{*}{z} - p\overset{*}{z} \\ &\quad = \eta\overset{*}{p}p(z-\overset{*}{z}) + p(z-\overset{*}{z}) + \overset{*}{z}(p-\overset{*}{p}) \\ &\quad = (1+\eta\overset{*}{p})p(z-\overset{*}{z}) + \overset{*}{z}(p-\overset{*}{p}). \end{aligned}$$

$$\begin{aligned} M_3 &= \mu_n\bar{\gamma}\alpha(1+\eta\overset{*}{p})\frac{p}{n}\frac{(n-\overset{*}{n})(z-\overset{*}{z})}{(1+\eta p)(1+\eta\overset{*}{p})} \\ &\quad +\mu_n\bar{\gamma}\alpha\frac{\overset{*}{z}}{n}\frac{(n-\overset{*}{n})(p-\overset{*}{p})}{(1+\eta p)(1+\eta\overset{*}{p})} \end{aligned}$$

So, we can rewrite $\dot{V}_1$ like :

$$\dot{V}_1 = -\frac{1}{n}\left(S+\frac{\beta k_n\overset{*}{p}}{(k_n+n)(k_n+\overset{*}{n})}\right)(n-\overset{*}{n})^2+ \left(\frac{\mu_p\mu_n}{n}+\frac{\beta(\overset{*}{n}-k_n)}{(k_n+n)(k_n+\overset{*}{n})}+\frac{\mu_n\bar{\gamma}\alpha\overset{*}{z}}{n(1+\eta p)(1+\eta\overset{*}{p})}\right) \times(n-\overset{*}{n})(p-\overset{*}{p}) + \left(\frac{\mu_n\mu_z}{n}+\frac{\mu_n\bar{\gamma}\alpha(1+\eta\overset{*}{p})p}{n}\right)(n-\overset{*}{n})(z-\overset{*}{z}).$$

Let's look at

$$\dot{V}_2 = (p-\overset{*}{p})\left(\beta\frac{n}{k_n+n}-\frac{\alpha}{1+\eta p}z-\mu_p\right).$$

From the second equation of system (4) we have:

$$-\mu_p = -\frac{\beta\overset{*}{n}}{k_n+\overset{*}{n}}+\frac{\alpha\overset{*}{z}}{1+\eta\overset{*}{p}}.$$

By substituting μ_p in $\dot{V}_2$ we obtain:

$$\begin{aligned}\dot{V}_2 &= (p-\overset{*}{p})\left(\frac{\beta n}{k_n+n}-\frac{\beta\overset{*}{n}}{k_n+\overset{*}{n}} -\frac{\alpha z}{1+\eta p}+\frac{\alpha\overset{*}{z}}{1+\eta\overset{*}{p}}\right)\\ &= (p-\overset{*}{p})\left(\frac{\beta k_n(n-\overset{*}{n})}{(k_n+n)(k_n+\overset{*}{n})} -\alpha\frac{z(1+\eta\overset{*}{p})-\overset{*}{z}(1+\eta p)}{(1+\eta p)(1+\eta\overset{*}{p})}\right).\end{aligned}$$

Let's denote $\dot{V}_2 = N_1 + N_2$ with

$$\begin{aligned}N_1 &= \frac{\beta k_n(p-\overset{*}{p})(n-\overset{*}{n})}{(k_n+n)(k_n+\overset{*}{n})},\\ N_2 &= -\alpha(p-\overset{*}{p})\frac{z+\eta\overset{*}{p}z-\overset{*}{z}-\eta p\overset{*}{z}}{(1+\eta p)(1+\eta\overset{*}{p})}\end{aligned}$$

Then, N_2 can be expressed like

$$N_2 = \frac{-\alpha(p-\overset{*}{p})(z-\overset{*}{z})}{(1+\eta p)(1+\eta\overset{*}{p})}-\frac{\alpha\omega_0(p-\overset{*}{p})^2}{(1+\eta p)(1+\eta\overset{*}{p})} +\alpha\frac{(\omega_0+\eta\overset{*}{z})p-\eta\overset{*}{p}z-\omega_0\overset{*}{p}}{(1+\eta p)(1+\eta\overset{*}{p})},$$

with $\omega_0 > 0$. Likewise $\dot{V}_1$ and $\dot{V}_2$, $\dot{V}_3$ can be written as

$$\dot{V}_3 = \delta(z-\overset{*}{z})\left(\frac{\gamma p}{1+\eta p}-\mu_z\right).$$

From the third equation of system (4) we have: $\mu_z = \frac{\gamma\overset{*}{p}}{1+\eta\overset{*}{p}}$, thereby:

$$\dot{V}_3 = \frac{\delta\gamma(z-\overset{*}{z})(p-\overset{*}{p})}{(1+\eta p)(1+\eta\overset{*}{p})},$$

thus

$$\begin{aligned}\dot{V}_2+\dot{V}_3 =& -\frac{\alpha\omega_0}{(1+\eta p)(1+\eta\overset{*}{p})}(p-\overset{*}{p})^2\\ &+\frac{\beta k_n}{(k_n+n)(k_n+\overset{*}{n})}(n-\overset{*}{n})(p-\overset{*}{p})\\ &+\frac{\delta\gamma-\alpha}{(1+\eta p)(1+\eta\overset{*}{p})}(p-\overset{*}{p})(z-\overset{*}{z})\\ &+\alpha\frac{(\omega_0+\eta\overset{*}{z})p-\eta\overset{*}{p}z-\omega_0\overset{*}{p}}{(1+\eta p)(1+\eta\overset{*}{p})}.\end{aligned}$$

Then, $\dot{V}$ can be written as $\dot{V} = -X^THX + \zeta(n,p,z)$ where :

$$H = \begin{pmatrix} H_{11} & \Pi & \Gamma\\ \Pi & H_{22} & \Psi\\ \Gamma & \Psi & 0\end{pmatrix}. \tag{19}$$

As $(n,p,z) \in \mathbb{G}$, Sylvester's criterion [17] is satisfied and we have H positive defined. Then

$$\dot{V} = -X^THX+\zeta(n,p,z) < 0,\ \forall(n,p,z)\in\mathbb{G}\backslash\{e_3\}.$$

Thus, V satisfy conditions of Lyapunov stability theorem, [15, page 194], then e_3 is asymptotically stable in $\mathbb{G}$. Now let's show condition (i):

$$\begin{aligned}p_0 &= 1+\eta\overset{*}{p}\\ k_0 &= k_n+\overset{*}{n}\end{aligned}$$

Then elements of H are written at point e_3 like

$$\begin{aligned}H_{11} &= \frac{Sk_0^2+\beta k_n\overset{*}{p}\overset{*}{n}}{\overset{*}{n}k_o^2},\\ H_{22} &= \frac{\alpha\omega_0}{p_o^2},\end{aligned} \tag{20}$$

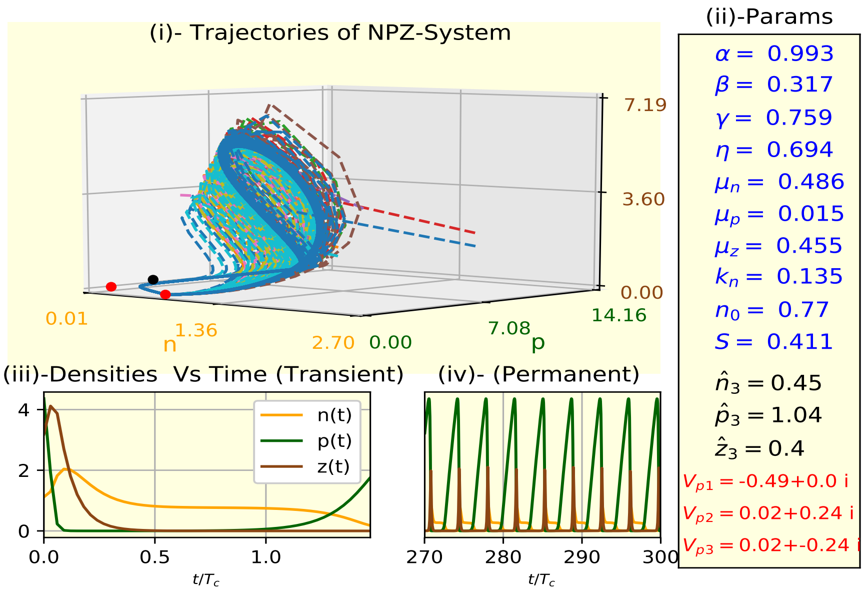

Fig. 1: (i)- Some orbits in the phase space. The point in black is the equilibrium e_3 and in red the two others .(ii)-System parameters (blue), coordinates of e_3 (black) and associated eigenvalues (red). (iii)- Density evolution vs time transient phase and (iv) permanent phase. $\omega_0 = 1.79$ et $\Delta = 0.0037$

$$\begin{aligned}
\Pi &= \frac{\Pi_1 - \Pi_2}{2\overset{*}{n} p_o^2 k_o^2} = \\
&\frac{\alpha\gamma\mu_n \overset{*}{z} k_o^2 - (\mu_n k_o^2 \mu_p p_o^2 + \mu_n k_o^2 \alpha \overset{*}{z} + \beta \overset{*}{n}^2 p_o^2)}{2\overset{*}{n} p_o^2 k_o^2}, \\
\Gamma &= \frac{\Gamma_1 - \Gamma_2}{2\overset{*}{n}} \\
&= \frac{\alpha\gamma\mu_n p_0 \overset{*}{p} - \mu_n(\mu_z + \alpha p_0 \overset{*}{p})}{2\overset{*}{n}}, \\
\Psi &= \frac{\Psi_1 - \Psi_2}{2p_o^2} = \frac{\alpha - \delta\gamma}{2p_o^2}.
\end{aligned} \tag{21}$$

We thus obtain

$$\begin{aligned}
f(\overset{*}{n}, \overset{*}{p}, \overset{*}{z}) &= \frac{4\omega_0 \alpha \overset{*}{n} k_o^2 p_o^2 (S k_o^2 + \beta k_n \overset{*}{p}\overset{*}{n})}{4\overset{*}{n}^2 k_0^4 p_0^4} \\
&\quad - \frac{(\Pi_1 - \Pi_2)^2}{4\overset{*}{n}^2 k_0^4 p_0^4}.
\end{aligned}$$

If we choose ω_0 such that

$$\omega_0 > \frac{(\Pi_1 - \Pi_2)^2}{4\alpha \overset{*}{n} k_o^2 p_o^2 (S k_o^2 + \beta k_n \overset{*}{p}\overset{*}{n})}, \tag{22}$$

then

$$f(\overset{*}{n}, \overset{*}{p}, \overset{*}{z}) > 0.$$

We have also

$$g(\overset{*}{n}, \overset{*}{p}, \overset{*}{z}) = -\Psi^2 H_{11} - \Gamma^2 H_{22} + 2\Pi\Psi\Gamma \quad \text{with}$$

$$\begin{aligned}
-\Psi^2 H_{11} &= \frac{-\delta^2 \overset{*}{n}^2 \gamma^2 (S k_0^2 + \beta k_n \overset{*}{p}\overset{*}{n})}{4\overset{*}{n}^2 p_0^4 k_0^2} \\
&+ \frac{\delta 2\alpha\gamma \overset{*}{n}^2 (S k_0^2 + \beta k_n \overset{*}{p}\overset{*}{n}) - \alpha^2 \overset{*}{n}^2 (S k_0^2 + \beta k_n \overset{*}{p}\overset{*}{n})}{4\overset{*}{n}^2 p_0^4 k_0^2}, \\
-\Gamma^2 H_{22} &= \frac{-2\omega_0 (\Gamma_1 - \Gamma_2)^2 p_o^2 k_o^2}{4\overset{*}{n}^2 p_0^4 k_0^2}, \\
2\Pi\Psi\Gamma &= \frac{\alpha(\Pi_1 - \Pi_2)(\Gamma_1 - \Gamma_2)}{4\overset{*}{n}^2 p_0^4 k_0^2} \\
&\quad - \frac{\delta\gamma(\Pi_1 - \Pi_2)(\Gamma_1 - \Gamma_2)}{4\overset{*}{n}^2 p_0^4 k_0^2}.
\end{aligned}$$

Thus

$$g(\overset{*}{n}, \overset{*}{p}, \overset{*}{z}) = \frac{A\delta^2 + B\delta + C}{4\overset{*}{n}^2 p_0^4 k_0^2} \quad \text{with :}$$

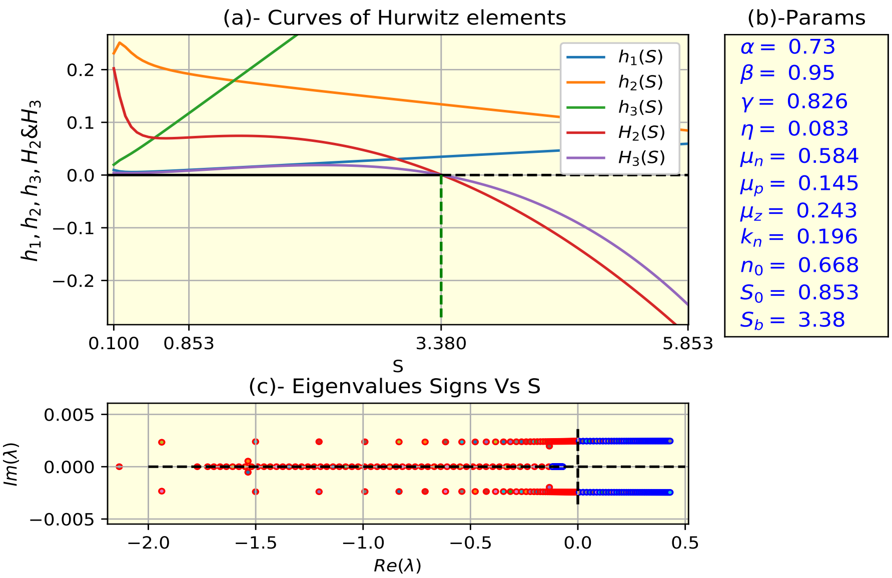

Fig. 2: (a) - Bifurcation diagram illustrating the bifurcation value S_b according to functions $H_2, \frac{dH_2}{dS}$, (b) -System's parameters , (c)- Eigenvalues in red for $S < S_b$ and in blue for $S > S_b$.

$$
\begin{aligned}
A &= -\overset{*}{n}\gamma^2(Sk_0^2 + \beta k_n \overset{*}{p}\overset{*}{n}),\\
B &= 2\alpha\overset{*}{n}\gamma(Sk_0^2 + \beta k_n \overset{*}{p}\overset{*}{n})\\
&\quad -\gamma(\Pi_1 - \Pi_2)(\Gamma_1 - \Gamma_2),\\
C &= -\alpha^2\overset{*}{n}(Sk_0^2 + \beta k_n \overset{*}{p}\overset{*}{n})\\
&\quad -2\omega_0(\Gamma_1 - \Gamma_2)^2 p_o^2 k_o^2\\
&\quad +\alpha(\Pi_1 - \Pi_2)(\Gamma_1 - \Gamma_2).
\end{aligned}
\tag{23}
$$

Let's set the condition

$$\Delta = B^2 - 4AC > 0 \tag{24}$$

And let δ_1 and δ_2 the two real roots of the polynomial $A\delta^2 + B\delta + C$ such that $\delta_1 < \delta_2$. Then, there exist admissible parameters ($\omega_0 = 1.79$ and $\Delta = 0.0077$, See Fig 1 for the rest of parameters) verifying the condition (24). So it's sufficient to choose $\delta < \delta_1$ or $\delta > \delta_2$ and we will have $A\delta^2 + B\delta + C > 0$, which implies :

$$g(\overset{*}{n}, \overset{*}{p}, \overset{*}{z}) > 0.$$

As we have obviously $\zeta(\overset{*}{n}, \overset{*}{p}, \overset{*}{z}) = 0 \leq 0$, we conclude that $e_3 \in \mathbb{G}$.

■

C. *Bifurcation around equilibrium* e_3

We are interested in system behavior according to upwelling intensity, the parameter S. We set a range of admissible parameters where equilibrium e_3 is stable. We denote S_0 the parameter resulting from this choice and we will call it *bifurcation parameter*. By varying S in $[S_{min}, S_{max}] = [0.1, 5.85]$, we look for the *bifurcation value* denoted by S_b , this will be the point where equilibrium e_3 loses its stability. Let $P(X)$ be the characteristic polynomial of system linearized around e_3,

$$P(X) = h_0 X^3 + h_1(S)X^2 + h_2(S)X + h_3(S),$$

where $h_0 = 1$, h_1, h_2, h_3 are functions of S given by :

$$
\begin{aligned}
h_1(S) &= -(F_{1,\overset{*}{n}} + F_{2,\overset{*}{p}} + F_{3,\overset{*}{z}}),\\
h_2(S) &= F_{1,\overset{*}{n}}(F_{2,\overset{*}{p}} + F_{3,\overset{*}{z}})\\
&\quad +F_{2,\overset{*}{p}}F_{3,\overset{*}{z}} - F_{3,\overset{*}{p}}F_{2,\overset{*}{z}} - F_{2,\overset{*}{n}}F_{1,\overset{*}{p}},\\
h_3(S) &= -F_{1,\overset{*}{n}}F_{2,\overset{*}{p}}F_{3,\overset{*}{z}} + F_{1,\overset{*}{n}}F_{3,\overset{*}{p}}F_{2,\overset{*}{z}}\\
&\quad +F_{2,\overset{*}{n}}F_{1,\overset{*}{p}}F_{3,\overset{*}{z}} - F_{1,\overset{*}{z}}F_{3,\overset{*}{p}}F_{2,\overset{*}{n}},
\end{aligned}
$$

where $F_{i,x}$ are the elements of the Jacobian matrix of field F (7) .

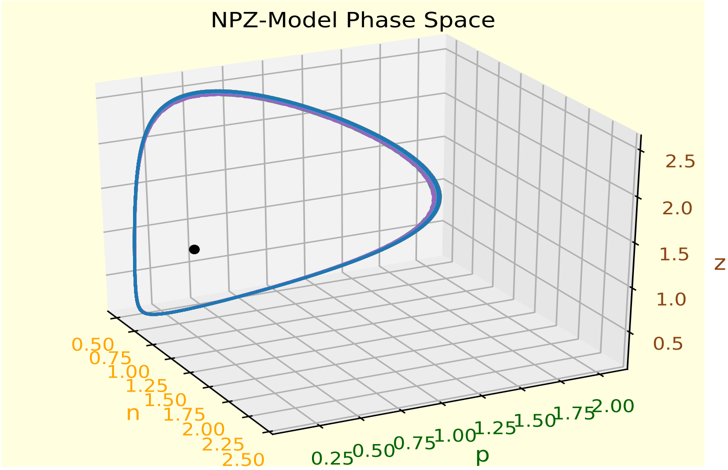

Fig. 3: Emerging limit-cycle after Hopf bifurcation ($S = 4$) . It is the convergence of 11 trajectories after a transient time of 8000. The black dot indicates the unstable equilibrium.

The 3×3 matrix given by

$$H = \begin{pmatrix} h_1 & h_3 & 0 \\ h_0 & h_2 & 0 \\ 0 & h_1 & h_3 \end{pmatrix}$$

is called *Hurwitz's matrix* associated to polynomial $P(X)$. Then P is stable (i.e., the real parts of the eigenvalues are strictly positive) if and only if all the principal minors of H (noted H_i) are positive i.e.,

$$H_1(S) = h_1(S) > 0,$$
$$H_2(S) = h_1(S)h_2(S) - h_3(S) > 0,$$
$$H_3(S) = h_3(S)H_2(S) > 0.$$

By fixing $S_0 = 0.85$, we observe numerically that $H_2(3.38) = H_3(3.38) = 0$ (Fig 2). Then $S_b = 3.38$ is a bifurcation value. It is a Hopf bifurcation according to the Liu criterion [18] (III.1).

Lemma III.1 (Liu criterion). *Suppose that the following conditions are satisfied*

(i) $h_0(S_b) > 0,\ H_1(S_b) > 0,\ H_2(S_b) = 0,$
(ii) $\frac{dH_2}{dS}(S_b) \neq 0.$

Then there is a simple Hopf bifurcation.

Looking at the typology of eigenvalues (Fig 2)[7], we have :

(i) For $S \in [S_{min}, S_b[$, a negative real eigenvalue, and two conjugate complexes of strictly negative real part. The equilibrium e_3 is therefore locally stable.
(ii) For $S \in]S_b, S_{max}]$, we have a negative real eigenvalue, and two conjugate complexes with a strictly positive real part. The equilibrium e_3 is therefore unstable.

We conclude from the Poincaré-Andronov-Hopf theorem [19], that there exists a limit cycle for $S \in]S_b, S_{max}] =]3.38; 5.85]$.

IV. Results & Discussion

After the definition of *NPZ-Model*, we are interested in qualitative study of system. We made sure of the existence, uniqueness, positivity and boundedness of solutions. Then, we calculated the stationary points and established sufficient conditions for their positivity. We have discovered that the two equilibria on the border of $\mathbb{R}^3_+$ are unconditionally unstable, which is interpreted as

[7]The eigenvalues are scaled for image visibility.

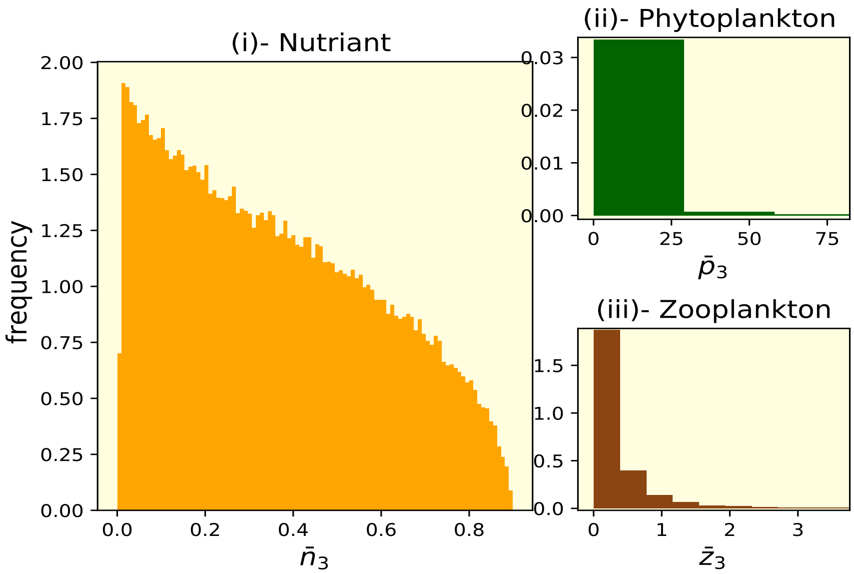

Fig. 4: Distribution of concentrations at equilibrium e_3 with 10^5 range from admissible parameters (dist-equ3(n) in NPZ-Prog.py)

a correlation of dependence between the three species. We have shown thanks to Lyapunov's theorem [15] , that the internal equilibrium is stable in a subset $\mathbb{G} \in \mathbb{R}^3_+$. This set is not unique and depends strongly on parameters of system.

We have written a python program (NPZ-Prog.py) [8] whose main task is to select a range of admissible parameters (i.e., checking proposition III.1). Then, we used these parameters to evaluate respectively equilibria and the associated eigenvalues.Thus, by drawing 10^5 ranges of admissible parameters, it was observed that $\overset{*}{p}_3$ is a uniform distribution in $[0.4, 5.85]$ on the other hand $\overset{*}{n}_3$ and $\overset{*}{z}_3$ are not at all uniform and are distributed respectively in $[0.01, 0.89]$ and $[0.30, 5.55]$(Fig 4).

Then comes the integration of the NPZ system with the *odein* function of python which is based on a Runge-Kutta method of order 4 with adaptive steps.

As shown in Theorem III.1, there is a range of parameters where the equilibrium e_3 is stable. In this case, simulations confirm that eigenvalues are of negative real part and two of them are complex conjugate. Orbits spiral and converge towards equilibrium e_3 (Figure 6). By varying upwelling intensity S, we have shown that a super-critic Hopf bifurcation occurs, that is to say, there is a value of S where the equilibrium e_3 loses its stability and a limit cycle appears. We have not rigorously studied stability of this cycle but the numerical simulations conjecture its stability. This phenomenon of periodic maintained oscillations was observed by Edwards & Bees [10] where they considered zooplankton predation of Holling type-III. This shows that our choice of Holling type-II does not remove this fundamental aspect of the original model (Fig 5).

In the case where we have these periodic solutions, we are interested in primary production which is defined as the growth term in phytoplankton's dynamics and defined by

$$PP = \frac{\beta np}{k_n + n} \tag{25}$$

The quantity PP is periodic because n and p are, looking at evolution of its average with respect to $S \in [3.4, 5.85]$ (after bifurcation), we see that the average primary production is constant ($\langle PP \rangle =$

[8] Attached with additional files

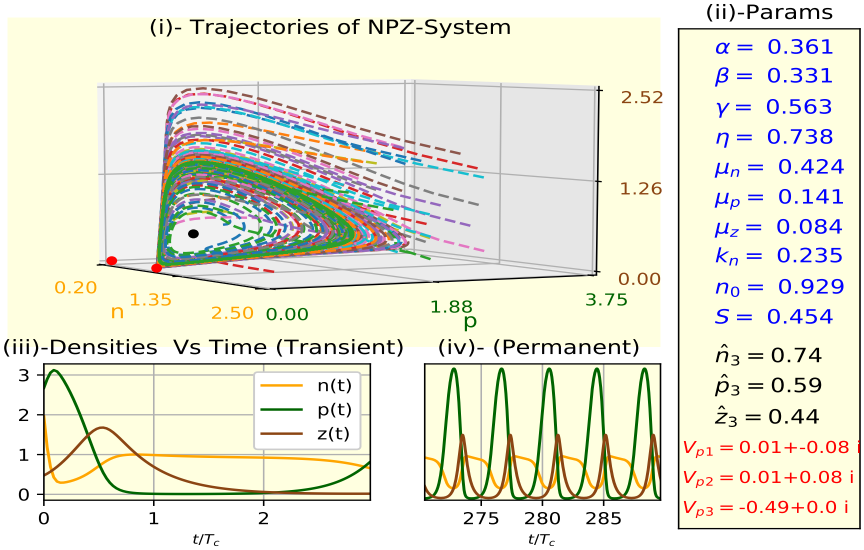

Fig. 5: e_3 Unstable: (i)-Some orbits in the phase space. The point in black is the equilibrium e_3 and in red the two others . (ii)- System parameters (blue), coordinates of e_3 (black) and associated eigenvalues (red). (iii)-Density evolution vs time transient phase and (iv) permanent phase.

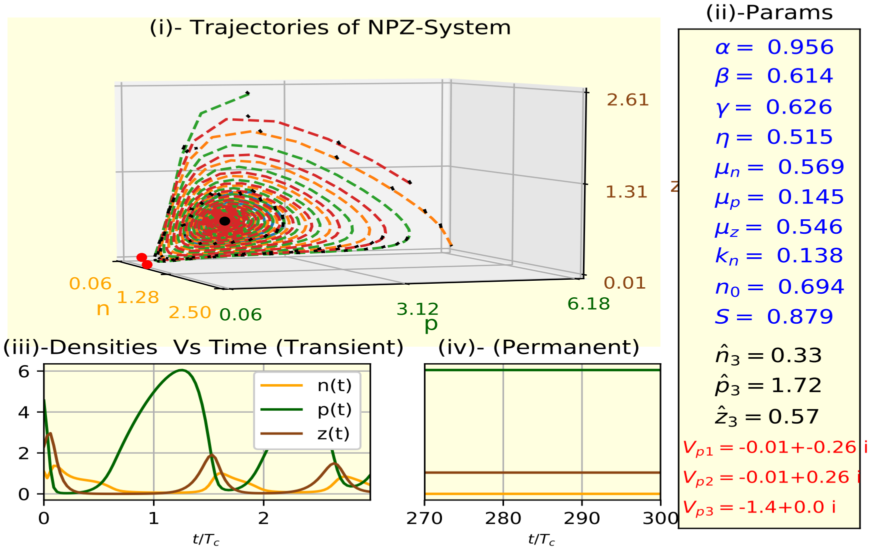

Fig. 6: Same as caption in Figure 5. Case where equilibrium e_3 is stable.

0.29) with a growing standard deviation through S (Figure 7).

V. Conclusion

To study the dynamics of nutrients, phytoplanktons and zoo-planktons, we focused on a system of ODE (4). There is a space of admissible parameters where solutions are well defined. We also have an interior equilibrium point. In the case where the equilibrium is unstable, there is a stable limit cycle which means periodical solutions. We had algebraically determined four equilibria, of which $e_4 \notin \mathbb{R}^3_+$. This is due to the sufficient conditions stated on positivity of three others (9). It would be interesting to look for positivity conditions for the

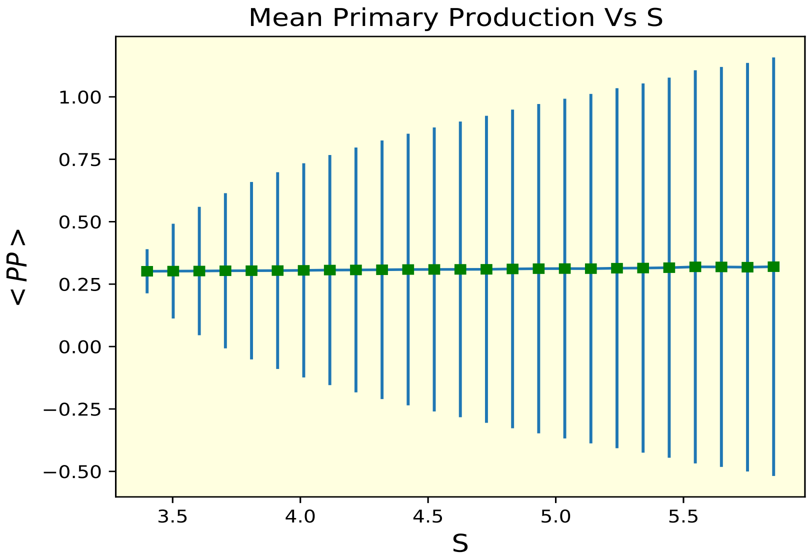

Fig. 7: Average primary production according to the upwelling intensity S.

four equilibria and to study if necessary, the bistability of e_3 and e_4. A biological interpretation of the parameter and time spaces would strengthen understanding of the model. Finally, it would be enriching to consider transport-diffusion effect and to couple the *NPZ-model* with an upwelling equation.

Appendix

Tables III, IV and V show a list of some functions used to perform this paper. There are three python codes [9] : NPZ _ Sympy_ Calcul.py , NPZ_ Prog.py, Hurwitz_ Prog.py . Tables below give functions and their outputs

TABLE III: NPZ _ Sympy_ Calcul.py

Function	Output
Coef_ Jacobienne()	Jacibian Matrix
SolveNZZero()	$\overset{*}{n}_1, \overset{*}{p}_1, \overset{*}{n}_2, \overset{*}{p}_2$
SolveNZOriginal()	$\overset{*}{n}_3, \overset{*}{p}_3, \overset{*}{n}_4, \overset{*}{p}_4$
Val _ Propres()	Eigenvalues
Coef_ Hurwitz()	Elements of Hurwitz Matrix

[9]File attached as support materials.

TABLE IV: NPZ _ Prog.py

Function	Output
Test_ param()	Range of admissible parameters
Condition _ Lasalle()	$\Delta = B^2 - 4AC$ 24
dist_ equ3(n)	Figure 4
plot _ snapshot()	Figures 1 , 5 , 6
plot _ orbit()	Figure 3

TABLE V: Hurwitz _ Prog.py

Function	Output
plot _ prim _ production ()	Figure 7
plot _ orbite _ projection ()	Figure 8
plot _ val _ pro _ color	Figure 2

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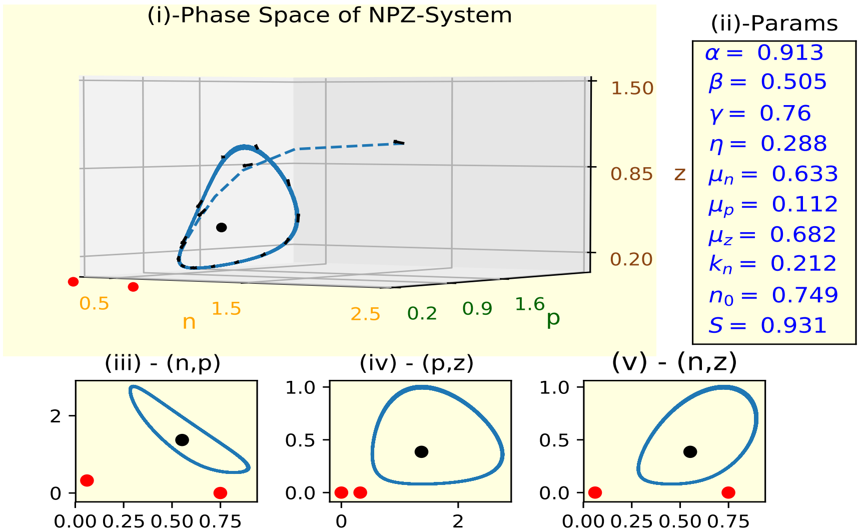

Fig. 8: (i)-Emerging limit cycle after the Hopf bifurcation. It is the convergence of 11 trajectories after a transient time of 8000. The black point indicates the unstable internal equilibrium.(ii)-System Parameters . (iii), (iv) and (v) are respectively the projections of cycle on planes (n,p), (p,z) and (n, z).

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