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Stability and Bifurcations in a Nutrient–Phytoplankton–Zooplankton Model with Delayed Nutrient Recycling with Gamma Distribution

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Abstract: Two nutrient–phytoplankton–zooplankton (NZP) models for a closed ecosystem that incorporates a delay in nutrient recycling, obtained using the gamma distribution function with one or two degrees of freedom, are analysed. The models are described by systems of ordinary differential equations of four and five dimensions. The purpose of this study is to investigate how the mean delay of the distribution and the total nutrients affect the stability of the equilibrium solutions. Local stability theory and bifurcation theory are used to determine the long-time dynamics of the models. It is found that both models exhibit comparable qualitative dynamics. There are a maximum of three equilibrium points in each of the two models, and at most one of them is locally asymptotically stable. The change of stability from one equilibrium to another takes place through a transcritical bifurcation. In some hypotheses on the functional response, the nutrient–phytoplankton–zooplankton equilibrium loses stability via a supercritical Hopf bifurcation, causing the apparition of a stable limit cycle. The way in which the results are consistent with prior research and how they extend them is discussed. Finally, various application-related consequences of the results of the theoretical study are deduced.

Keywords: plankton; nutrient recycling; delay; gamma distribution; closed ecosystem; dynamics; bifurcation

MSC: 37N25; 35G10; 34D20



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1. Introduction

Plankton are floating organisms that provide a food source for other organisms ranging from shellfish to whales. As such, they play a crucial role in aquatic foodwebs [1]. Phytoplankton are organisms, such as algae, which carry out photosynthesis and are an important means of carbon storage in the ocean [2]. Zooplankton feed on phytoplankton or other zooplankton and include insect larvae and jellyfish. Due to their fundamental role in aquatic ecosystems and their influence on the global carbon cycle, it is important to understand the temporal dynamics of plankton ecosystems.

A variety of different models have been proposed for plankton ecosystems, emphasizing different aspects of these complex systems [3–11]. Here, we study a model due to Kloosterman et al. [12], which focussed on two aspects. The chemical nutrients in the system are recycled, thus the system is closed—the total amount of nutrient remains constant. This recycling takes time (e.g., due to decomposition of dead organisms) and thus the model should include a time delay. Both are important features of plankton ecosystems that lead to interesting mathematics.

The model of Kloosterman et al. [12] is called an NPZ model as it is a system with three compartments, representing the dissolved nutrient (N), the amount of phytoplankton (P), and the amount of zooplankton (Z). It is described by the following equations:

$$\begin{cases} \frac{dN}{dt}(t) &= \lambda \int_0^\infty P(t-u)\eta(u)du + \delta \int_0^\infty Z(t-u)\eta(u)du \\ &\quad + (1-\gamma)g \int_0^\infty Z(t-u)h(P(t-u))\eta(u)du - \mu P(t)f(N(t)) \\ \frac{dP}{dt}(t) &= \mu P(t)f(N(t)) - gZh(P(t)) - \lambda P(t) \\ \frac{dZ}{dt}(t) &= \gamma gZ(t)h(P(t)) - \delta Z(t) \end{cases} \quad (1)$$

Here, $\lambda, \mu, \gamma, \delta$ and g are positive parameters representing biological properties while η is an appropriate distribution representing the time delay in nutrient recycling.

The function f stands for the phytoplankton nutrient uptake as a function of the available nutrient and it has the following properties [4]:

$$f(0) = 0, f'(N) > 0, f''(N) < 0, \lim_{N \rightarrow \infty} f(N) = 1. \quad (2)$$

Similarly, the function h stands for the available phytoplankton and it must satisfy conditions [13,14]:

$$h(0) = 0, h'(P) > 0, \lim_{P \rightarrow \infty} h(P) = 1. \quad (3)$$

Kloosterman et al. [12] investigated how this model for a planktonic ecosystem is affected by the quantity of biomass it contains and by the delay distribution. They described the existence of the equilibrium points and gave some stability results for a general distribution function, using methods as in [15]. Other stability results considered particular cases of the distribution function and relied primarily on numerical work.

In this study, we assume that the delay follows a gamma distribution function, with either one or two degrees of freedom, as these numbers of freedom degrees correspond to the biological data. We derive two models, described by systems of ordinary differential equations (ODEs), and analyse how the local stability and local bifurcation of the equilibrium points depend on the amount of total nutrients and on the mean delay of the distribution.

For the numerical simulations we have used a Holling type II functional response for f ,

$$f(N) = \frac{N}{N + k_N},$$

with $k_N > 0$. For function h , we used either a Holling Type II functional response

$$h(P) = \frac{P}{P + k_P},$$

or a Holling Type III response

$$h(P) = \frac{P^2}{P^2 + k_P^2},$$

with $k_P > 0$.

Using this delay, we have extended the results obtained in [12].

2. The Models

Consider η the gamma distribution of mean τ , with k degrees of freedom:

$$\eta(u) = \begin{cases} \frac{k^k}{\tau^k(k-1)!} u^{k-1} e^{-\frac{k}{\tau}u}, & u \geq 0 \\ 0, & u < 0 \end{cases} \quad (4)$$

Starting from system (1) and using the gamma distribution function for the cases $k = 1$ and $k = 2$, and some appropriate new variables, we derive two models, described by

systems of ordinary differential equations (ODEs), without explicit delay. This reduction is often called the linear chain trick [16–18].

For the case $k = 1$, we obtain a 4-dimensional system of ODEs, which is then reduced to a three-dimensional one. This will be called the weak model.

For $k = 2$, we obtain a five-dimensional system of ODEs that can be reduced to a four-dimensional system, which will be called the strong model.

2.1. The Weak Model

If $k = 1$, we have $\eta(u) = \frac{1}{\tau}e^{-\frac{u}{\tau}}$, for $u \geq 0$. Denoting

$$Q(t) = \int_0^{\infty} [\lambda P(t-u) + \delta Z(t-u) + (1-\gamma)gZ(t-u)h(P(t-u))]e^{-\frac{u}{\tau}} du, \quad (5)$$

the equation describing the evolution of the dissolved nutrient N can be written as:

$$\frac{dN}{dt}(t) = \frac{1}{\tau}Q(t) - \mu P(t)f(N(t)).$$

In addition, using the change of variable $t - u = \theta$, we have:

$$\begin{aligned} Q(t) &= - \int_t^{-\infty} [\lambda P(\theta) + \delta Z(\theta) + (1-\gamma)gZ(\theta)h(P(\theta))]e^{-\frac{t-\theta}{\tau}} d\theta \\ &= \int_{-\infty}^t [\lambda P(\theta) + \delta Z(\theta) + (1-\gamma)gZ(\theta)h(P(\theta))]e^{-\frac{t-\theta}{\tau}} d\theta. \end{aligned}$$

It follows:

$$\begin{aligned} \frac{dQ}{dt}(t) &= \lambda P(t) + \delta Z(t) + (1-\gamma)gZ(t)h(P(t)) \\ &\quad + \int_{-\infty}^t [\lambda P(\theta) + \delta Z(\theta) + (1-\gamma)gZ(\theta)h(P(\theta))]e^{-\frac{t-\theta}{\tau}} \left(-\frac{1}{\tau}\right) d\theta. \end{aligned}$$

With the change of variable $t - u = \theta$, we have

$$\frac{dQ}{dt}(t) = \lambda P(t) + \delta Z(t) + (1-\gamma)gZ(t)h(P(t)) - \frac{1}{\tau}Q(t)$$

Thus, we obtain a 4D model (NPZQ), called “the weak model” in the following, described by

$$\begin{cases} \frac{dN(t)}{dt} = \frac{1}{\tau}Q(t) - \mu P(t)f(N(t)), \\ \frac{dP(t)}{dt} = \mu P(t)f(N(t)) - gZh(P(t)) - \lambda P(t), \\ \frac{dZ(t)}{dt} = \gamma gZ(t)h(P(t)) - \delta Z(t), \\ \frac{dQ(t)}{dt} = \lambda P(t) + \delta Z(t) + (1-\gamma)gZ(t)h(P(t)) - \frac{1}{\tau}Q(t). \end{cases} \quad (6)$$

Since the conservation law $\frac{d}{dt}(N + P + Z + Q) = 0$ is fulfilled, we obtain $N(t) + P(t) + Z(t) + Q(t) = N_T^1 = \text{constant}$. The substitution $Q(t) = N_T^1 - N(t) - P(t) - Z(t)$, leads to the following reduced 3D system:

$$\begin{cases} \frac{dN(t)}{dt} = \frac{1}{\tau}(N_T^1 - N(t) - P(t) - Z(t)) - \mu P(t)f(N(t)) \\ \frac{dP(t)}{dt} = \mu P(t)f(N(t)) - gZh(P(t)) - \lambda P(t), \\ \frac{dZ(t)}{dt} = \gamma gZ(t)h(P(t)) - \delta Z(t). \end{cases} \quad (7)$$

with the phase space

$$D_1 = \{(N, P, Z), N \geq 0, P \geq 0, Z \geq 0, N + P + Z \leq N_T^1\}. \quad (8)$$

2.2. The Strong Model

If the number of freedom degrees is $k = 2$, we have $\eta(u) = \frac{4}{\tau^2} u e^{-\frac{2}{\tau} u}$, for $u \geq 0$. Denoting

$$Q_1(t) = \int_0^\infty [\lambda P(t-u) + \delta Z(t-u) + (1-\gamma)gZ(t-u)h(P(t-u))] \frac{2}{\tau} u e^{-\frac{2}{\tau} u} du, \quad (9)$$

the equation describing the evolution of the dissolved phytoplankton nutrient from (1) reads:

$$\frac{dN}{dt}(t) = \frac{2}{\tau} Q_1(t) - \mu P(t) f(N(t)). \quad (10)$$

In addition, using the change of variable $t - u = \theta$, we have

$$\begin{aligned} Q_1(t) &= -\frac{2}{\tau} \int_t^\infty [\lambda P(\theta) + \delta Z(\theta) + (1-\gamma)gZ(\theta)h(P(\theta))](t-\theta) e^{-\frac{2}{\tau}(t-\theta)} d\theta \\ &= \frac{2}{\tau} \int_{-\infty}^t [\lambda P(\theta) + \delta Z(\theta) + (1-\gamma)gZ(\theta)h(P(\theta))](t-\theta) e^{-\frac{2}{\tau}(t-\theta)} d\theta. \end{aligned}$$

Denoting by

$$Q_2(t) = \int_{-\infty}^t [\lambda P(\theta) + \delta Z(\theta) + (1-\gamma)gZ(\theta)h(P(\theta))] e^{-\frac{2}{\tau}(t-\theta)} d\theta, \quad (11)$$

it follows:

$$\frac{dQ_1}{dt}(t) = \frac{2}{\tau} (Q_2(t) - Q_1(t)), \quad (12)$$

$$\begin{aligned} \frac{dQ_2}{dt}(t) &= \lambda P(t) + \delta Z(t) + (1-\gamma)gZ(t)h(P(t)) \\ &\quad + \int_{-\infty}^t [\lambda P(\theta) + \delta Z(\theta) + (1-\gamma)gZ(\theta)h(P(\theta))] e^{-\frac{2}{\tau}(t-\theta)} \left(-\frac{2}{\tau}\right) d\theta \\ &= \lambda P(t) + \delta Z(t) + (1-\gamma)gZ(t)h(P(t)) - \frac{2}{\tau} Q_2(t). \end{aligned}$$

Thus, we obtain the following 5D model $(NPZQ_1Q_2)$, also called “the strong model”:

$$\begin{cases} \frac{dN(t)}{dt} = \frac{2}{\tau} Q_1(t) - \mu P(t) f(N(t)), \\ \frac{dP(t)}{dt} = \mu P(t) f(N(t)) - gZ h(P(t)) - \lambda P(t), \\ \frac{dZ(t)}{dt} = \gamma gZ(t) h(P(t)) - \delta Z(t), \\ \frac{dQ_1(t)}{dt} = \frac{2}{\tau} (Q_2(t) - Q_1(t)), \\ \frac{dQ_2(t)}{dt} = \lambda P(t) + \delta Z(t) + (1-\gamma)gZ(t)h(P(t)) - \frac{2}{\tau} Q_2(t). \end{cases} \quad (13)$$

Obviously, the conservation law

$$\frac{d}{dt}(N + P + Z + Q_1 + Q_2) = 0 \quad (14)$$

is fulfilled, so we can substitute $Q_2(t) = N_T^2 - N(t) - P(t) - Z(t) - Q_1(t)$, leading to the following reduced 4D system of ordinary differential equations (ODE):

$$\begin{cases} \frac{dN(t)}{dt} = \frac{2}{\tau} Q_1(t) - \mu P(t)f(N(t)), \\ \frac{dP(t)}{dt} = \mu P(t)f(N(t)) - gZh(P(t)) - \lambda P(t), \\ \frac{dZ(t)}{dt} = \gamma gZ(t)h(P(t)) - \delta Z(t), \\ \frac{dQ_1(t)}{dt} = \frac{2}{\tau} (N_T^2 - N(t) - P(t) - Z(t) - 2Q_1(t)), \end{cases} \quad (15)$$

with the phase space

$$D_2 = \left\{ (N, P, Z, Q_1) \in \mathbb{R}^4, N \geq 0, P \geq 0, Z \geq 0, Q_1 > 0, N + P + Z + Q_1 \leq N_T^2 \right\}. \quad (16)$$

Also, for consistency, the initial conditions of the ODE model must satisfy

$$Q_1(0) = -\frac{2}{\tau} \int_{-\infty}^0 [\lambda P(\theta) + \delta Z(\theta) + (1 - \gamma)gZ(\theta)h(P(\theta))] \theta e^{\frac{2}{\tau}\theta} d\theta$$

2.3. The Model without Delay

In the absence of delay, the model (1) is described by the following equations:

$$\begin{cases} \frac{dN(t)}{dt} = \lambda P(t) + \delta Z(t) + (1 - \gamma)gZ(t)h(P(t)) - \mu P(t)f(N(t)) \\ \frac{dP(t)}{dt} = \mu P(t)f(N(t)) - gZh(P(t)) - \lambda P(t) \\ \frac{dZ(t)}{dt} = \gamma gZ(t)h(P(t)) - \delta Z(t) \end{cases}. \quad (17)$$

Using conservation law $N_T^0 = N(t) + P(t) + Z(t)$, this system can be reduced to the following 2D system:

$$\begin{cases} \frac{dP}{dt} = \mu P f(N_T^0 - P - Z) - gZh(P) - \lambda P \\ \frac{dZ}{dt} = \gamma gZh(P) - \delta Z \end{cases}, \quad (18)$$

with the phase space

$$D_0 = \left\{ (P, Z) \in \mathbb{R}^2, P \geq 0, Z \geq 0, P + Z \leq N_T^0 \right\}. \quad (19)$$

In the following, N_T shall denote the biomass of the model. Thus, when referring to the model without delay $N_T = N_T^0$, for the weak model $N_T = N_T^1$, while for the strong model $N_T = N_T^2$.

3. Equilibrium Solutions

In this section, we determine the stationary solutions of the two reduced systems (7) and (15), for the NPZ model with delayed gamma distribution, with one or two degrees of freedom. These solutions correspond to the equilibrium points of the corresponding dynamical systems.

Each of the three systems has at most three equilibrium points in the region of interest, namely:

- A trivial equilibrium E_1 , with no phytoplankton and no zooplankton;
- An equilibrium with phytoplankton and no zooplankton, denoted E_2 ;
- An equilibrium with both phytoplankton and zooplankton, denoted E_3 .

These equilibria may coexist for certain values of the total nutrients. The same property is valid for the reduced 2D system (18) for the NPZ model without delay.

3.1. Equilibrium Points for the System without Delay

In [12], it is shown that under the assumptions

$$\lambda < \mu, \quad \delta < g\gamma \quad (20)$$

system (18) has at most three equilibrium points in D_0 , depending on the value of the total nutrient N_T . Denoting as

$$N_{T_1} = f^{-1}\left(\frac{\lambda}{\mu}\right), \quad N_{T_2} = f^{-1}\left(\frac{\lambda}{\mu}\right) + h^{-1}\left(\frac{\delta}{g\gamma}\right), \quad (21)$$

the equilibrium points of system (18) are $E_1 = (0, 0)$, for all N_T , $E_2 = (\hat{P}, 0)$, with $\hat{P} = N_T - N_{T_1}$, for all $N_T \geq N_{T_1}$, and $E_3 = (P^*, Z^*)$, with $P^* = h^{-1}\left(\frac{\delta}{g\gamma}\right)$, and Z^* unique solution of the equation

$$Z^* = \frac{\mu\gamma}{\delta}P^* \left(f(N_T - P^* - Z^*) - \frac{\lambda}{\mu} \right), \quad (22)$$

for all N_T , with $N_T \geq N_{T_2}$.

3.2. Equilibrium Points for the Reduced Weak System (7)

The system (7) possesses at most three equilibria with the first three coordinates non-negative, solutions of the system

$$\begin{cases} \frac{1}{\tau}(N_T - N - P - Z) - \mu Pf(N) = 0 \\ \mu Pf(N) - gZh(P) - \lambda P = 0 \\ \gamma gZh(P) - \delta Z = 0 \end{cases} \quad (23)$$

It follows that the trivial equilibrium is $E_1 = (N_T, 0, 0)$.

The equilibrium with only phytoplankton is $E_2 = (\hat{N}, \hat{P}, 0)$, with $f(\hat{N}) = \frac{\lambda}{\mu}$. Taking into account the properties of f , if the condition

$$\lambda < \mu \quad (24)$$

is satisfied (that is the growth rate of the plankton must be greater than the death rate), then there exists a unique $\hat{N}$, namely $\hat{N} = f^{-1}\left(\frac{\lambda}{\mu}\right)$, satisfying this condition. From the first equation we obtain

$$\hat{P} = \frac{1}{1 + \lambda\tau}(N_T - \hat{N}). \quad (25)$$

while from the conservation law we obtain

$$\hat{Q} = \lambda\tau\hat{P}. \quad (26)$$

This equilibrium is in the domain of interest D_1 if and only if $N_T \geq \hat{N}$. Note that if $N_T = f^{-1}\left(\frac{\lambda}{\mu}\right)$, then $E_1 = E_2$.

The equilibrium with both phyto- and zooplankton is $E_3 = (N^*, P^*, Z^*)$, with $h(P^*) = \frac{\delta}{\gamma g}$ from the third equation in (23). If condition

$$\delta < \gamma g \quad (27)$$

is satisfied, then there exists a unique $P^* > 0$ such that $h(P^*) = \frac{\delta}{\gamma g}$, namely

$$P^* = h^{-1}\left(\frac{\delta}{\gamma g}\right). \quad (28)$$

and

$$Z^* = \frac{\gamma\mu}{\delta} \left(f(N^*) - \frac{\lambda}{\mu} \right) h^{-1}\left(\frac{\delta}{\gamma g}\right). \quad (29)$$

The condition $f(N^*) \geq \frac{\lambda}{\mu}$ must be satisfied in order to have $Z^* \geq 0$. As f is an increasing function, it follows that $N^* \geq f^{-1}(\frac{\lambda}{\mu})$ and using the first equation of system (23) we have

$$\begin{aligned} N_T &= N^* + P^* + Z^* + \tau\mu P^* f(N^*) \\ &\geq f^{-1}\left(\frac{\lambda}{\mu}\right) + (1 + \lambda\tau)h^{-1}\left(\frac{\delta}{\gamma g}\right). \end{aligned}$$

To show that there exists an N^* such that

$$N_T = N^* + P^* \left(1 - \frac{\gamma\lambda}{\delta} + \mu\left(\tau + \frac{\gamma}{\delta}\right)f(N^*)\right) \quad (30)$$

is satisfied, consider the function

$$F(N) = N + \left(1 - \frac{\gamma\lambda}{\delta} + \mu\left(\tau + \frac{\gamma}{\delta}\right)f(N)\right)h^{-1}\left(\frac{\delta}{\gamma g}\right) - N_T.$$

It follows that $F\left(f^{-1}\left(\frac{\lambda}{\mu}\right)\right) < 0$ and $\lim_{N \rightarrow \infty} F(N) = \infty$. As F is an increasing function, there exists a unique value N^* such that $F(N^*) = 0$.

Denote, as in [12], $N_{T_2}(\tau) = f^{-1}\left(\frac{\lambda}{\mu}\right) + (1 + \lambda\tau)h^{-1}\left(\frac{\delta}{\gamma g}\right)$. Remark that $N_{T_2}(0) = N_{T_2}$. As a consequence, the third equilibrium point (N^*, P^*, Z^*) exists in D_1 and is uniquely determined by (30) if the conditions $N_T \geq N_{T_2}(\tau)$ and (20) are satisfied. Note that if $N_T = N_{T_2}(\tau)$, then $E_3 = E_2$. The transitions between the equilibrium points will be discussed further in Section 5.

Finally, we note that if (N_0, P_0, Z_0) is an equilibrium of system (7), then (N_0, P_0, Z_0, Q_0) , with $Q_0 = \tau\mu P_0 f(N_0)$ is an equilibrium point for system solution of system (6) and conversely.

In Figure 1, the coordinates N, P, Z, Q of the three equilibrium points are represented as functions of the total nutrient N_T , for a fixed $\tau = 5$. As function h , a type II functional response was considered. The values of the parameters used for simulations are $\mu = 5.9$, $g = 7$, $\lambda = 0.017$, $\gamma = 0.7$, $\delta = 0.17$, $k_N = 1$, $k_P = 1$, as in [12]. For these values of the parameters, the following values were obtained for thresholds: $N_{T_1} = 0.0028$, $N_{T_2}(\tau) = 0.0418$.

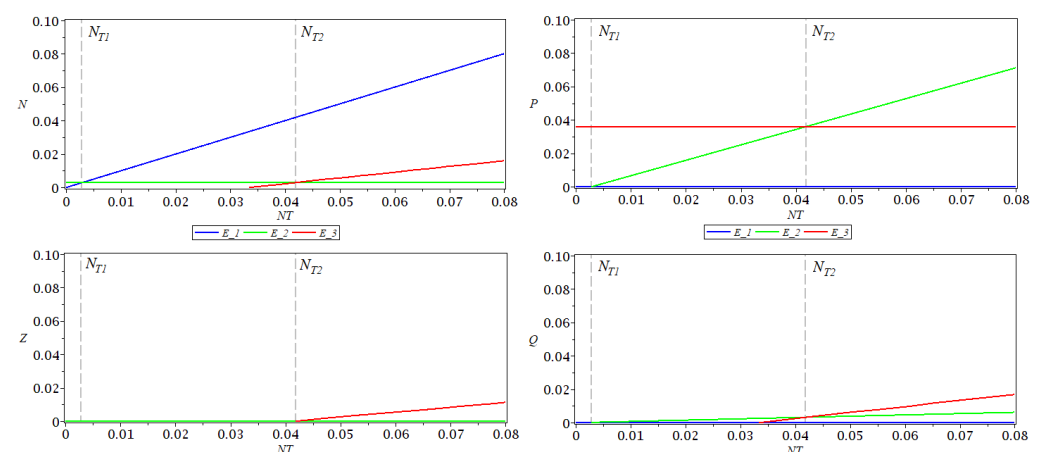


Figure 1. N, P, Z, Q as functions of N_T , for fixed $\tau = 5$, for the equilibrium points E_1 (blue line), E_2 (green line), E_3 (red line), using a type II response.

3.3. Equilibria for the Reduced Strong Model (15)

The equilibria of system (15) correspond to the solutions of the system

$$\begin{cases} \frac{2}{\tau}Q_1 - \mu Pf(N) = 0 \\ \mu Pf(N) - gZh(P) - \lambda P = 0 \\ \gamma gZh(P) - \delta Z = 0 \\ \frac{2}{\tau}(N_T - N - P - Z - 2Q_1) = 0 \end{cases} \quad (31)$$

Substituting

$$Q_1 = \frac{\tau}{2}\mu Pf(N), \quad (32)$$

from the first equation into the last equation in (31), the remaining three equations coincide with system (23). Consequently, we obtain the same expressions for N, P , and Z as for system (23). Taking into account (32), we obtain the following equilibrium points for system (15):

- (1) The trivial equilibrium $E_1 = (N_T, 0, 0, 0)$, for all $N_T \geq 0$;
- (2) The equilibrium with no zooplankton $E_2 = (\hat{N}, \hat{P}, 0, \hat{Q}_1)$, with $Q_1 = \frac{\tau\lambda}{2}\hat{P}$, for all N_T , with $N_T \geq N_{T_1}$, if $\lambda < \mu$;
- (3) The equilibrium $E_3 = (N^*, P^*, Z^*, Q_1^*)$, with $Q_1^* = \frac{\mu\tau}{2}f(N^*)h^{-1}\left(\frac{\delta}{\gamma g}\right)$, for all N_T , with $N_T \geq N_{T_2}(\tau)$, if $\lambda < \mu$ and $\delta < \gamma g$.

Note that if (N_0, P_0, Z_0, Q_0) is an equilibrium of system (15), then $(N_0, P_0, Z_0, Q_0, Q_0)$ is an equilibrium point for system solution of system (13) and conversely.

In Figure 2, there are represented the coordinates N, P, Z, Q_1 of the three equilibrium points as functions of the total nutrient N_T , for a fixed $\tau = 5$. As function h , a type III functional response was considered. The values of the parameters used for simulations are $\mu = 5.9, g = 7, \lambda = 0.017, \gamma = 0.7, \delta = 0.17, k_N = 1, k_P = 1$, as in [12]. For these values of the parameters, the following values were obtained for stability thresholds: $N_{T_1} = 0.0028, N_{T_2(\tau)} = 0.2085, N_{T_3(\tau)} = 1.0967$. Remark that $E_1 = E_2$ at $N_T = N_{T_1}$ and $E_2 = E_3$ at $N_T = N_{T_2}(\tau)$.

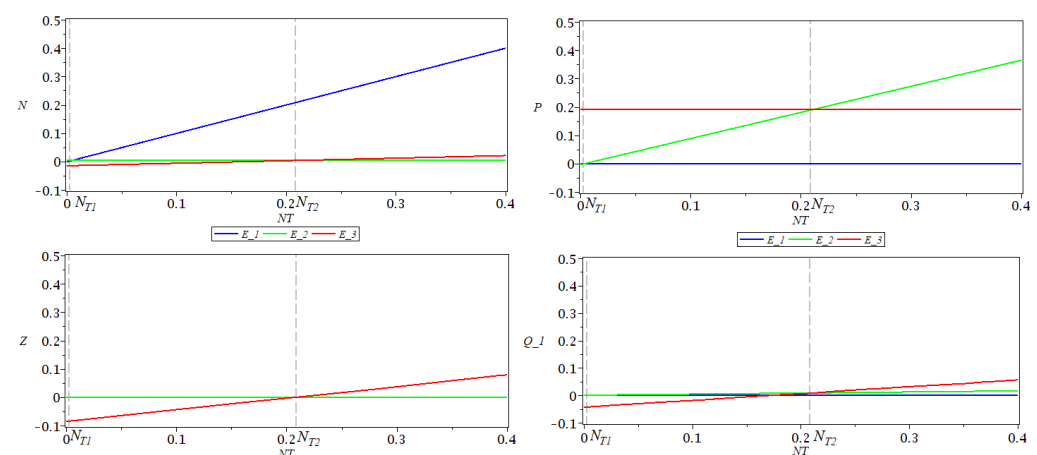


Figure 2. N, P, Z, Q_1 as functions of N_T , for fixed $\tau = 5$, for the equilibrium points E_1 (blue line), E_2 (green line), E_3 (red line), using a type III response.

Comparing the systems with and without delay, we see the following.

- The equilibrium point E_1 is unaffected by the delay.
- For the equilibrium point E_2 , the value of P is reduced by the delay.
- For the equilibrium point E_3 , the values of N and Z are reduced by the delay.
- The first transition point is unaffected by the delay, $N_{T_1} = N_{T_1}(\tau)$, while the second transition point is increased by the delay, $N_{T_2} < N_{T_2}(\tau)$, if $\tau > 0$.

4. Local Stability

For all three systems (7), (15) and (18), we find that at each value of the total nutrient at most one of the equilibrium points is locally asymptotically stable. More precisely,

- for $N_T < N_{T_1}$, the only equilibrium point is E_1 , and it is asymptotically stable,
- for $N_{T_1} < N_T < N_{T_2}(\tau)$ the equilibrium E_2 is asymptotically stable, while E_1 is unstable,
- and, finally, as $N_T > N_{T_2}(\tau)$, the equilibrium E_3 is asymptotically stable either for all $N_T > N_{T_2}(\tau)$ or there exists an $N_{T_3}(\tau)$ such that E_3 is asymptotically stable for $N_{T_2}(\tau) < N_T < N_{T_3}(\tau)$, and unstable for $N_T > N_{T_3}(\tau)$, depending on the response function h , while the other two equilibria are unstable.

Note that for the system without delay (18), N_{T_2} is equal to $N_{T_2}(0)$. Our results for E_1 and E_2 reproduce the results of [12] for the system with general delay (1), while our results for E_3 improve those of [12].

Note that, for the two-dimensional reduced system without delay (18), the local stability of the equilibria on the boundary of the domain can be extended to global stability [12]. Those arguments cannot apply for systems (7) and (15). Results on the global stability could be obtained using Lyapunov functions, if they can be constructed.

4.1. The System without Delay

In [12], it is shown that the equilibrium E_1 is globally asymptotically stable on D_0 if $N_T < N_{T_1}$, the equilibrium E_2 is globally asymptotically stable on D_0 , except for the z axis, if $N_{T_1} < N_T < N_{T_2}$, while the stability of the equilibrium point E_3 depends on the sign of the quantity T , denoting the trace of the Jacobi matrix J_0 at (P^*, Z^*) ,

$$J_0(N_T) = \begin{pmatrix} \frac{\delta Z^*}{\gamma P^*} - \mu P^* a - g Z^* b & -\mu P^* a - \frac{\delta}{\gamma} \\ \gamma g b Z^* & 0 \end{pmatrix}.$$

Here, to simplify the expression, we denoted $a = f'(N_T - P^* - Z^*)$, $b = h'(P^*)$.

They proved that if $h'(P^*) \geq h(P^*)/P^*$, then the equilibrium point E_3 is stable for all $N_T > N_{T_2}$. This is valid for a type III zooplankton grazing response function h . While if $h'(P^*) < h(P^*)/P^*$, then there exists a unique value N_{T_3} of the total nutrient, such that the equilibrium point E_3 is asymptotically stable for all $N_{T_2} < N_T < N_{T_3}$ and unstable if $N_T > N_{T_3}$. The value N_{T_3} is found as the unique solution of the equation $T(N_T) = 0$, with

$$T(N_T) = g Z^* \left(\frac{h(P^*)}{P^*} - h'(P^*) \right) - \mu P^* f'(N_T - P^* - Z^*). \quad (33)$$

For $N_T = N_{T_3}$, the Jacobi matrix J_0 has the purely imaginary eigenvalues $\lambda_{1,2}(N_T) = \pm i\omega_0$, with $\omega_0 > 0$, $\omega_0^2 = \gamma g b Z^* \left(\mu P^* a + \frac{\delta}{\gamma} \right)$. Close to N_{T_3} , we have $\text{Re}\lambda_{1,2}(N_T) = \frac{1}{2}T(N_T)$. Consequently,

$$\frac{d}{dN_T} \text{Re}\lambda_{1,2}(N_T) = \frac{1}{2} \frac{d}{dN_T} T(N_T) > 0, \quad (34)$$

and thus the transversality condition in the Hopf bifurcation theorem is satisfied. A Hopf bifurcation takes place for $N_T = N_{T_3}$ if the Lyapunov coefficient $L_1(N_{T_3})$ is non-zero.

4.2. The Weak Model Case

We analyse here the stability of the equilibrium points for the system (7) corresponding to the gamma distribution delay, with one degree of freedom.

Proposition 1. For the equilibrium point E_1 of system (7), the following statements hold:

- If $N_T < N_{T_1}$, then E_1 is locally asymptotically stable in D_1 ;
- If $N_T > N_{T_1}$, then E_1 is a (2,1) type saddle point;
- If $N_T = N_{T_1}$, then E_1 is a fold singularity.

Proof. The Jacobian matrix J_1 associated to system (7) at $E_1 = (N_T, 0, 0)$,

$$J_1 = \begin{pmatrix} -\frac{1}{\tau} & -\frac{1}{\tau} - \mu f(N_T) & -\frac{1}{\tau} \\ 0 & \mu f(N_T) - \lambda & 0 \\ 0 & 0 & -\delta \end{pmatrix}$$

has the eigenvalues

$$\lambda_1^1 = -\frac{1}{\tau} < 0, \lambda_2^1 = \mu \left(f(N_T) - \frac{\lambda}{\mu} \right), \lambda_3^1 = -\delta < 0.$$

As two eigenvalues are negative, the topological type of E_1 is determined by the sign of λ_2^1 . Thus, the equilibrium point E_1 is an attractor if $\lambda_2^1 < 0$, i.e., $f(N_T) < \frac{\lambda}{\mu}$. As f is an increasing function, we have $\lambda_2^1 < 0$ if $N_T < f^{-1}\left(\frac{\lambda}{\mu}\right) = N_{T_1}$. $\square$

Proposition 2. The equilibrium point $E_2 = (\hat{N}, \hat{P}, 0)$ of system (7) is locally asymptotically stable in D_1 if and only if

$$N_{T_1} < N_T < N_{T_2}(\tau).$$

In addition,

- (i) if $N_T = N_{T_1}$ or $N_T = N_{T_2}(\tau)$ then E_2 is a fold singularity;
- (ii) if $N_T > N_{T_2}(\tau)$ then E_2 is a saddle point of type (2,1);
- (iii) if $N_T < N_{T_1}$ then E_2 is not in D_1 .

Proof. For the equilibrium $E_2 = (\hat{N}, \hat{P}, 0)$, we obtain the Jacobi matrix

$$J_2 = \begin{pmatrix} -\frac{1}{\tau} - \mu \hat{P} f'(\hat{N}) & -\frac{1}{\tau} - \lambda & -\frac{1}{\tau} \\ \mu \hat{P} f'(\hat{N}) & 0 & -g h(\hat{P}) \\ 0 & 0 & \gamma g h(\hat{P}) - \delta \end{pmatrix}$$

and the characteristic equation

$$(X^2 + p_1 X + p_2)(X - \gamma g h(\hat{P}) + \delta) = 0$$

with

$$\begin{aligned} p_1 &= \frac{1}{\tau} + \mu \hat{P} f'(\hat{N}), \\ p_2 &= \frac{\mu(1 + \lambda\tau)}{\tau} \hat{P} f'(\hat{N}). \end{aligned}$$

Thus, one eigenvalue is $\lambda_3^2 = \gamma g \left(h(\hat{P}) - \frac{\delta}{\gamma g} \right)$ and we have $\lambda_3^2 < 0$ if $h(\hat{P}) < \frac{\delta}{\gamma g}$ (that is $\hat{P} < P^*$, as h is an increasing function). Consequently, $\lambda_3^2 < 0$ iff

$$N_T < f^{-1}\left(\frac{\lambda}{\mu}\right) + (1 + \lambda\tau)h^{-1}\left(\frac{\delta}{\gamma g}\right) = N_{T_2}(\tau)$$

and $\lambda_3^2 = 0$ if $N_T = N_{T_2}(\tau)$.

The other two eigenvalues λ_1^2, λ_2^2 , are solutions of the equation $X^2 + p_1 X + p_2 = 0$. Further, if $N_T > N_{T_1}$, it follows that $p_1 > 0, p_2 > 0$, both solutions of this equation have negative real parts. As a consequence, if $N_{T_1} < N_T < N_{T_2}(\tau)$, all eigenvalues have negative real parts, hence the equilibrium point E_2 is an attractor.

Note that if $N_T = N_{T_1}$, then $p_2 = 0, p_1 > 0$, thus $\lambda_2^2 = 0$ and $\text{Re}(\lambda_1^2) < 0$. The equilibrium point E_2 is a fold singularity both at $N_T = N_{T_1}$ and $N_T = N_{T_2}(\tau)$. $\square$

For the equilibrium point $E_3 = (N^*, P^*, Z^*)$ of system (7), the Jacobi matrix reads

$$J_3 = \begin{pmatrix} -\frac{1}{\tau} - \mu Pa & -\frac{1}{\tau} - \mu c & -\frac{1}{\tau} \\ \mu Pa & \mu c - gZ^*b - \lambda & -\frac{\delta}{\gamma} \\ 0 & \gamma gZ^*b & 0 \end{pmatrix},$$

where, to simplify computation, we denoted:

$$a = f'(N^*) > 0, b = h'(P^*) > 0, c = f(N^*) > 0, d = h(P^*) > 0, \quad (35)$$

Thus, the characteristic polynomial of J_3 reads

$$X^3 + a_1X^2 + a_2X + a_3, \quad (36)$$

with

$$\begin{aligned} a_1 &= \frac{1}{\tau} + \lambda - c\mu + \mu P^*a + Z^*bg \\ a_2 &= \frac{1}{\tau}(\lambda - c\mu + \mu P^*a + Z^*bg) + g\delta Z^*b + \lambda\mu P^*a + g\mu P^*Z^*ab \\ a_3 &= \frac{g}{\tau}Z^*b(\delta + P^*a\gamma\mu + \tau\mu\delta P^*a) \end{aligned} \quad (37)$$

Using the Routh–Hurwitz criterion [19], all the roots of the characteristic polynomial have negative real parts if and only if the following conditions are satisfied:

$$(i) \quad a_1 > 0, (ii) \quad a_3 > 0, (iii) \quad a_1a_2 - a_3 > 0. \quad (38)$$

Thus, the equilibrium point E_3 is asymptotically stable if all these conditions are fulfilled. In [12], one result on the stability of E_3 with the weak gamma distributed delay was obtained. For completeness and for comparison with the strong gamma distribution case, we repeat that result here with proof.

Proposition 3. *If*

$$P^*h'(P^*) - h(P^*) \geq 0, \quad (39)$$

then the equilibrium E_3 of system (7) is locally asymptotically stable for all $N_T > N_{T_2}(\tau)$.

Proof. The equilibrium point E_3 is stable if all conditions in (38) are fulfilled. To simplify computation, denote

$$A = \mu P^*a > 0, B = \mu c - \lambda > 0, C = \frac{\gamma g b P^*}{\delta} > 0, D = \frac{\delta}{\gamma} > 0, T = A + B(C - 1)$$

Note that, $C - 1 = \frac{\gamma g}{\delta}(P^*h'(P^*) - h(P^*)) > 0$. With these notations, we can write

$$\begin{aligned} a_1 &= T + \frac{1}{\tau}, \\ a_2 &= BCD\gamma + ABC + A\lambda + \frac{1}{\tau}T, \end{aligned}$$

As all parameters are positive, it follows that $a_3 > 0$. As $T > 0$, conditions $a_1 > 0$ and $a_2 > 0$ are satisfied. As

$$a_1a_2 - a_3 = AT(BC + \lambda) + B^2CD\gamma(C - 1) + \frac{1 - \gamma}{\tau}ABC + \frac{\lambda}{\tau}A + \frac{1}{\tau^2}T(T\tau + 1) > 0, \quad (40)$$

condition (iii) in (38) is satisfied. Consequently, all eigenvalues have negative real parts, and E_3 is an attractor for all $N_T > N_{T_2}(\tau)$. $\square$

Proposition 4. *If*

$$P^*h'(P^*) - h(P^*) < 0, \quad (41)$$

the following assertions hold for the equilibrium point E_3 of system (7).

- (i) *For $N_T > N_{T_2}(\tau)$, close to $N_{T_2}(\tau)$, the equilibrium point E_3 is an attractor.*
- (ii) *If $a_1a_2 - a_3 > 0$, then E_3 is locally asymptotically stable.*
- (iii) *If $a_1a_2 - a_3 = 0$ then E_3 is a Hopf singularity.*
- (iv) *If $a_1a_2 - a_3 < 0$ then E_3 is a (1,2) saddle point. In addition, for each τ there exists a value $N_{T_3}(\tau)$, given by*

$$N_{T_3}(\tau) = \min\{N_T, \quad N_T > N_{T_2}(\tau), \quad a_1a_2 - a_3 = 0\},$$

such that $E_3(N_T)$ is locally asymptotically stable for all $N_{T_2}(\tau) < N_T < N_{T_3}(\tau)$ and unstable for $N_T > N_{T_3}(\tau)$, close to $N_{T_3}(\tau)$.

Proof. (i) The coefficient a_3 is equal to 0 if and only $Z^* = 0$, which occurs when $f(N^*) = \frac{\lambda}{\mu}$. The discussion following (29) then shows that $a_3 = 0$ at $N_T = N_{T_2}(\tau)$, and $a_3 > 0$ for $N_T > N_{T_2}(\tau)$.

For $N_T = N_{T_2}(\tau)$, the other two coefficients of the characteristic equation associated to E_3 ,

$$\begin{aligned} a_1 &= \frac{1}{\tau} + \mu P^* a > 0, \\ a_2 &= \frac{1}{\tau} \mu P^* a + \lambda \mu P^* a > 0, \end{aligned}$$

have positive values, and also $a_1a_2 - a_3 = a_1a_3 > 0$. As the expressions $a_1, a_2, a_1a_2 - a_3$ are continuous functions of N_T , they remain positive for $N_T > N_{T_2}(\tau)$, in a neighbourhood of $N_{T_2}(\tau)$. Hence (i).

(ii) Considering a_1 as a function of N_T , we obtain

$$\lim_{N_T \rightarrow \infty} a_1(N_T) = \frac{1}{\tau} + \lambda + \frac{\gamma}{\delta}(\mu - \lambda)P^* > \frac{1}{\tau} + \lambda > 0.$$

Also,

$$\frac{da_1}{dN_T} = \mu \left(P^* f''(N^*) + f'(N^*) \left(\frac{P^* h'(P^*)}{h(P^*)} - 1 \right) \right) \frac{dN^*}{dN_T}$$

Differentiating with respect to N_T in (30), we obtain

$$1 = \frac{dN^*}{dN_T} \left(1 + \frac{\mu(\gamma + \tau\delta)}{\delta} P^* f'(N^*) \right),$$

hence $\frac{dN^*}{dN_T} > 0$. As $f'' < 0$ and $\frac{P^* h'(P^*)}{h(P^*)} - 1 < 0$, it follows that $\frac{da_1}{dN_T} < 0$, thus a_1 is a decreasing function of N_T . Consequently, $a_1 > \frac{1}{\tau} + \lambda > 0$. The result follows by applying the Routh–Hurwitz criterion [19].

(iii) The characteristic polynomial (36) has a pair of purely imaginary roots $\lambda_{1,2} = \pm \omega i$ if conditions

$$a_2 = \omega^2 > 0, \quad a_1a_2 - a_3 = 0.$$

As $a_1 > 0, a_3 > 0$ for all $N_T > N_{T_2}(\tau)$, if $a_1a_2 - a_3 = 0$ then $a_2 > 0$. Thus, E_3 is a Hopf singularity.

(iv) As $a_1 > 0, a_3 > 0$ for all $N_T > N_{T_2}(\tau)$, and $(a_1a_2 - a_3)(N_{T_2}(\tau)) > 0$, it follows that $N_{T_3}(\tau)$ is the minimum value of $N_T > N_{T_2}(\tau)$ for which condition $a_1a_2 - a_3 > 0$ is not satisfied. $\square$

For the type II response function h , we have

$$Ph'(P) - h(P) = -\frac{P^2}{(P + k_P)^2} < 0, \forall P \geq 0.$$

In this case, Proposition 4 applies for the stability of the equilibrium point E_3 . See Figure 3.

For the type III response function h , we obtain

$$Ph'(P) - h(P) = \frac{(k_P^2 - P^2)P^2}{(P^2 + k_P^2)^2}.$$

In this case, if $P^* \leq k_P$ (i.e., $\frac{\delta}{g\gamma} \leq h(k_P)$), then $P^*h'(P^*) - h(P^*) \geq 0$ and the equilibrium point E_3 is stable for all $N_T > N_{T_2}(\tau)$. If $h(k_P) < \frac{\delta}{g\gamma} < 1$, then Proposition 4 applies for the stability of the equilibrium point E_3 .

4.3. The Strong Model Case

Proposition 5. The following assertions hold for the equilibrium point E_1 of system (15).

- (i) If $N_T < N_{T_1}$, then E_1 is locally asymptotically stable in D_2 .
- (ii) If $N_T > N_{T_1}$, then E_1 is a (3,1) type saddle point.
- (iii) If $N_T = N_{T_1}$, then E_1 is a fold singularity.

Proof. For the equilibrium $E_1 = (N_T, 0, 0, 0)$, we obtain the Jacobi matrix

$$J_1 = \begin{pmatrix} 0 & -\mu f(N_T) & 0 & \frac{2}{\tau} \\ 0 & \mu f(N_T) - \lambda & 0 & 0 \\ 0 & 0 & -\delta & 0 \\ -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{4}{\tau} \end{pmatrix},$$

and the characteristic polynomial $(X + \frac{2}{\tau})^2(X + \delta)(X + \lambda - \mu f(N_T))$. Thus, J_1 has the eigenvalues

$$\lambda_1^1 = \lambda_2^1 = -\frac{2}{\tau} < 0, \lambda_3^1 = -\delta < 0, \lambda_4^1 = \mu \left(f(N_T) - \frac{\lambda}{\mu} \right).$$

As three eigenvalues are negative, the topological type of E_1 is determined by the sign of λ_4^1 . Thus, the equilibrium point E_1 is an attractor if $\lambda_4^1 < 0$, i.e., $f(N_T) < \frac{\lambda}{\mu}$. As f is an increasing function, we obtain $\lambda_4^1 < 0$ if $N_T < f^{-1}(\frac{\lambda}{\mu}) = N_{T_1}$. $\square$

Proposition 6. The equilibrium $E_2 = (\hat{N}, \hat{P}, 0, \hat{Q}_1)$ of system (15) is locally asymptotically stable in D_2 if and only if

$$N_{T_1} < N_T < N_{T_2}(\tau).$$

In addition,

- (i) If $N_T = N_{T_1}$ or $N_T = N_{T_2}(\tau)$, then the equilibrium E_2 is a fold singularity;
- (ii) If $N_T > N_{T_2}(\tau)$, then the equilibrium E_2 is a saddle point of type (3,1);
- (iii) If $N_T < N_{T_1}$, then the equilibrium E_2 is not in D_2 .

Proof. For the equilibrium $E_2 = (\hat{N}, \hat{P}, 0, \hat{Q}_1)$, we obtain the Jacobi matrix

$$J_2 = \begin{pmatrix} -\mu \hat{P} f'(\hat{N}) & -\lambda & 0 & \frac{2}{\tau} \\ \mu \hat{P} f'(\hat{N}) & 0 & -g h(\hat{P}) & 0 \\ 0 & 0 & \gamma g h(\hat{P}) - \delta & 0 \\ -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{4}{\tau} \end{pmatrix}$$

and the characteristic equation

$$(X^3 + p_1X^2 + p_2X + p_3)(X - \gamma gh(\hat{P}) + \delta) = 0$$

with

$$\begin{aligned} p_1 &= \frac{4}{\tau} + \mu \hat{P} f'(\hat{N}), \\ p_2 &= \frac{4}{\tau^2} + \frac{\mu(4 + \lambda\tau)}{\tau} \hat{P} f'(\hat{N}), \\ p_3 &= \frac{4\mu(1 + \tau\lambda)}{\tau^2} \hat{P} f'(\hat{N}). \end{aligned}$$

Thus, one eigenvalue is $\lambda_4^2 = \gamma g(h(\hat{P}) - \frac{\delta}{\gamma g})$ and we have $\lambda_4^2 < 0$ if $h(\hat{P}) < \frac{\delta}{\gamma g}$ (that is $\hat{P} < P^*$, as h is an increasing function). Consequently, $\lambda_4^2 < 0$ if

$$N_T < f^{-1}\left(\frac{\lambda}{\mu}\right) + (1 + \lambda\tau)h^{-1}\left(\frac{\delta}{\gamma g}\right) = N_{T_2}(\tau)$$

and $\lambda_4^2 = 0$ as $N_T = N_{T_2}(\tau)$. The other three eigenvalues $\lambda_1^2, \lambda_2^2, \lambda_3^2$ are solutions of the equation $X^3 + p_1X^2 + p_2X + p_3 = 0$. According to the Routh–Hurwitz criterion, all solutions of this equation have negative real parts if conditions

$$p_1 > 0, p_3 > 0, p_1p_2 > p_3$$

are fulfilled. As all parameters μ, λ, τ are positive, if $N_T > N_{T_1}$ the first two conditions $p_1 > 0, p_3 > 0$ are satisfied. A simple computation shows that the third condition is also satisfied if $N_T > N_{T_1}$. As a consequence, if $N_{T_1} < N_T < N_{T_2}(\tau)$ all eigenvalues have negative real part, hence the equilibrium point E_2 is an attractor.

Note that if $N_T = N_{T_1}$, then $p_3 = 0, p_1 > 0, p_2 > 0$, thus $\lambda_3^2 = 0$ and $\text{Re}(\lambda_{1,2}^2) < 0$. The equilibrium point E_2 is a fold singularity both at $N_T = N_{T_1}$ and $N_T = N_{T_2}(\tau)$. $\square$

For the equilibrium $E_3 = (N^*, P^*, Z^*, Q_1^*)$ of system (15), the Jacobi matrix reads

$$J_3 = \begin{pmatrix} -\mu P^* f'(N^*) & -\mu f(N^*) & 0 & \frac{2}{\tau} \\ \mu P^* f'(N^*) & \mu f(N^*) - gZ^* h'(P^*) - \lambda & -gh(P^*) & 0 \\ 0 & \gamma gZ^* h'(P^*) & \gamma gh(P^*) - \delta & 0 \\ -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{4}{\tau} \end{pmatrix}$$

and the characteristic polynomial is

$$X^4 + b_1X^3 + b_2X^2 + b_3X + b_4, \quad (42)$$

with

$$\begin{aligned} b_1 &= \frac{4}{\tau} + \mu P^* f'(N^*) + \frac{\gamma g}{\delta} (\mu f(N^*) - \lambda) (P^* h'(P^*) - h(P^*)), \\ b_2 &= \frac{4}{\tau^2} + \frac{4}{\tau} (\lambda - f(N^*)\mu + \mu P^* f'(N^*) + gZ^* h'(P^*)) + g\delta Z^* h'(P^*) + \lambda \mu P^* f'(N^*) + g\mu P^* Z^* f'(N^*) h'(P^*) \\ b_3 &= \frac{4}{\tau} (g\delta Z^* h'(P^*) + c\mu^2 P^* f'(N^*) + \mu P^* f'(N^*) (\lambda - c\mu + gZ^* h'(P^*))) + \frac{4}{\tau^2} (\lambda - c\mu + \mu P^* f'(N^*) + gZ^* h'(P^*)) \\ &\quad + g\delta Z^* h'(P^*) (\lambda - c\mu + \mu P^* f'(N^*) + gZ^* h'(P^*)) - g\delta Z h'(P^*) (\lambda - c\mu + gZ h'(P^*)), \\ b_4 &= \frac{4g}{\tau^2} (\delta + \mu(\gamma + \delta\tau) P^* f'(N^*)) \frac{\mu\gamma}{\delta} \left(f(N^*) - \frac{\lambda}{\mu} \right) P^* h'(P^*). \end{aligned} \quad (43)$$

Using the Routh–Hurwitz criterion [19], all the roots of the characteristic polynomial have negative real parts if and only if the following conditions are satisfied:

$$(i) \ b_1 > 0, b_2 > 0, b_3 > 0, b_4 > 0, (ii) \ b_5 = b_1 b_2 - b_3 > 0, (iii) \ b_6 = (b_1 b_2 - b_3) b_3 - b_1^2 b_4 > 0. \quad (44)$$

Thus, the equilibrium point E_3 is stable if all these conditions are fulfilled.

Proposition 7. For the equilibrium point E_3 of system (15), the following assertions hold.

- (i) For $N_T > N_{T_2}(\tau)$, close to $N_{T_2}(\tau)$, the equilibrium point E_3 is an attractor.
- (ii) If one of the conditions $b_j > 0$, $j = \overline{1, 6}$, in (44) is not satisfied, then E_3 is unstable. In addition, for each τ there exists a value $N_{T_3}(\tau)$, given by

$$N_{T_3}(\tau) = \min \left\{ N_T \mid N_T > N_{T_2}(\tau), \prod_{j=1}^6 b_j = 0 \right\},$$

such that E_3 is locally asymptotically stable for all $N_{T_2}(\tau) < N_T < N_{T_3}(\tau)$.

Proof. The coefficient b_4 is equal to 0 if and only if $f(N^*) = \frac{\lambda}{\mu}$. Thus, we have $b_4 = 0$ at $N_T = N_{T_2}(\tau)$, and $b_4 > 0$ for $N_T > N_{T_2}(\tau)$.

At $N_T = N_{T_2}(\tau)$, the other three coefficients of the characteristic equation associated with E_3 have the following values:

$$\begin{aligned} b_1 &= \frac{4}{\tau} + \mu P^* a > 0, \\ b_2 &= \frac{4}{\tau^2} + \frac{4}{\tau} \mu P^* a + \mu^2 P^* a c > 0, \\ b_3 &= \frac{4}{\tau} \mu^2 P^* a c + \frac{4}{\tau^2} \mu P^* a > 0. \end{aligned}$$

In addition, we have

$$\begin{aligned} b_5 &= \left(\mu^2 P^* a c + \frac{4}{\tau} \mu P^* a \tau + \frac{16}{\tau^2} \right) \mu P^* a + \frac{16}{\tau^3} > 0, \\ b_6 &= b_3 b_5 > 0. \end{aligned}$$

As the expressions $b_j, j = \overline{1, 6}$, are continuous functions of N_T , they remain positive for $N_T > N_{T_2}(\tau)$, in a neighbourhood of $N_{T_2}(\tau)$. Hence (i). Obviously, $N_{T_3}(\tau)$ is the minimum value of $N_T > N_{T_2}(\tau)$ for which one of the conditions (44) is not satisfied. $\square$

Remark 1. As for $N_T > N_{T_2}(\tau)$, we have $b_4 > 0$, none of the eigenvalues $\lambda_i^3, i = \overline{1, 4}$, can be 0. Thus, the topological type of E_3 could change only with the appearance of a pair of purely imaginary eigenvalues. Using the Viète relations, if conditions

$$b_1 b_3 > 0, (b_1 b_2 - b_3) b_3 - b_1^2 b_4 = 0, \quad (45)$$

are satisfied, then the equilibrium point E_3 is a Hopf singularity. If

$$b_1 = 0, b_2 > 0, b_3 = 0, b_4 > 0, b_2^2 - 4b_4 > 0, \quad (46)$$

then the equilibrium point E_3 has two pairs of purely imaginary eigenvalues and it is a double-Hopf singularity.

Proposition 8. Assume

$$P^* h'(P^*) - h(P^*) \geq 0, \quad (47)$$

- (i) If $(b_1 b_2 - b_3) b_3 - b_1^2 b_4 > 0$, then the equilibrium E_3 of system (15) is locally asymptotically stable for all $N_T > N_{T_2}(\tau)$.

- (ii) If $(b_1b_2 - b_3)b_3 - b_1^2b_4 = 0$, then E_3 is a Hopf singularity.
 (iii) If $(b_1b_2 - b_3)b_3 - b_1^2b_4 < 0$, then E_3 is unstable. In addition, for each τ , there exists a value $N_{T_3}(\tau)$, given by

$$N_{T_3}(\tau) = \min \left\{ N_T \mid N_T > N_{T_2}(\tau), (b_1b_2 - b_3)b_3 - b_1^2b_4 = 0 \right\},$$

such that E_3 is locally asymptotically stable for all $N_{T_2}(\tau) < N_T < N_{T_3}(\tau)$.

Proof. The equilibrium point E_3 is stable if all conditions in (38) are fulfilled. To simplify computation, denote:

$$\begin{aligned} a &= f'(N^*) > 0, b = h'(P^*) > 0, c = f(N^*) > 0, d = h(P^*) > 0, \\ A &= \mu P^* a > 0, B = \mu c - \lambda > 0, C = \frac{\gamma g b P^*}{\delta} > 0, D = \frac{\delta}{\gamma} > 0, T = A + B(C - 1) \end{aligned}$$

Note that, $C - 1 = \frac{\gamma g}{\delta} (P^* h'(P^*) - h(P^*)) > 0$. With these notations, we can write:

$$\begin{aligned} b_1 &= T + \frac{4}{\tau}, \\ b_2 &= BCD\gamma + ABC + A\lambda + \frac{4}{\tau}T + \frac{4}{\tau^2}, \\ b_3 &= ABCD\gamma + \frac{4}{\tau}(BCD\gamma + ABC + A\lambda) + \frac{4}{\tau^2}T, \\ b_4 &= \frac{1}{\tau^2}ABC\gamma(AD\tau + A + D) \end{aligned}$$

As all parameters are positive, it follows that $b_4 > 0$. As $T > 0$, conditions $b_1 > 0$, $b_2 > 0$, $b_3 > 0$ are satisfied if the hypothesis (47) is true. As

$$b_1b_2 - b_3 = AT(BC + \lambda) + B^2CD\gamma(C - 1) + \frac{4}{\tau^3}(T\tau + 2)^2,$$

condition $b_1b_2 - b_3 > 0$ is satisfied if (47).

Consequently, if $(b_1b_2 - b_3)b_3 - b_1^2b_4 > 0$, then all eigenvalues have negative real parts, thus E_3 is an attractor.

If $(b_1b_2 - b_3)b_3 - b_1^2b_4 < 0$, at least two eigenvalues have negative real parts, thus E_3 is unstable. As for $N_T = N_{T_2}(\tau)$ we have

$$(b_1b_2 - b_3)b_3 - b_1^2b_4 = \left(\mu^2 P^* ac + \frac{4}{\tau} \mu P^* a + \frac{24}{\tau^2} \right) \mu P^* a + \frac{16}{\tau^3} > 0,$$

the expression continues to be positive for $N_T > N_{T_2}(\tau)$, close to $N_{T_2}(\tau)$. Obviously, $N_{T_3}(\tau)$ is the minimum value of $N_T > N_{T_2}(\tau)$ for which $(b_1b_2 - b_3)b_3 - b_1^2b_4 = 0$. $\square$

In Figure 3, there are represented the strata in the (τ, N_T) plane that exhibit different behaviours for the three equilibrium points, obtained in the case of a type II response $h(P) = \frac{P}{P+k_P}$. The curve denoted NT_1 (blue line) separates the strata where E_1 changes stability with E_2 . The equilibrium E_2 is stable for parameters in the stratum limited by the curves NT_1 (blue line) and NT_2 (green line). The equilibrium E_3 is stable for parameters in region 3, in the stratum limited by the curves NT_2 (green line) and NT_3 (red line), and loses stability in region 4. The other two equilibria are unstable in regions 3 and 4.

The values of the parameters used for simulations are $\mu = 5.9$, $g = 7$, $\lambda = 0.017$, $\gamma = 0.7$, $\delta = 0.17$, $k_N = 1$, $k_P = 1$. The results are consistent with the ones obtained in [12].

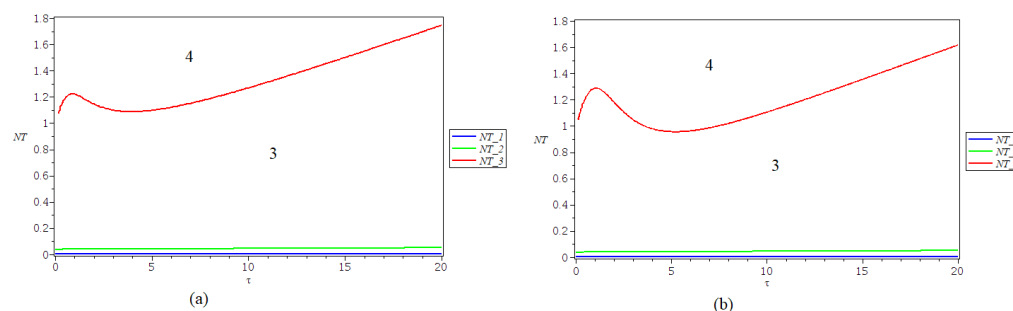


Figure 3. Regions in the (τ, N_T) plane that exhibit different behaviours for the equilibrium E_3 , using the Type II response for: (a) the weak model; (b) the strong model. Region 3 is where the E_3 is stable, but where E_1, E_2 are unstable. For parameters on the curve separating regions 3 and 4, E_3 is a Hopf singularity, while in region 4, E_3 is unstable. A Hopf bifurcation may take place when parameters cross from region 3 to region 4.

5. Local Bifurcations

In the previous section, we proved that at each value of the total nutrients at most one of the equilibrium points is locally asymptotically stable. In this section, we show that the change of stability is realized either through a transcritical bifurcation or a Hopf bifurcation that may occur at a fold singular point or at a Hopf singularity, respectively.

5.1. Transcritical Bifurcations

Two transcritical bifurcations undergo for both the weak and the strong models, namely:

- (i) at $N_T = N_{T_1}$, the equilibrium points E_1 and E_2 collide and interchange stability;
- (ii) at $N_T = N_{T_2}(\tau)$, the equilibrium points E_2 and E_3 collide and interchange stability.

We prove these results by using the Sotomayor theorem [20], ([21], p. 338).

5.1.1. Transcritical Bifurcations for the Weak Model

Proposition 9. A transcritical bifurcation takes place at the equilibrium E_1 of system (7) as $N_T = N_{T_1}$.

Proof. As $N_T = N_{T_1}$ we have $E_2 = E_1$ and the equilibrium E_1 is a fold singularity. We consider $\varepsilon = \mu f(N_T) - \lambda$ as the bifurcation parameter, and the bifurcation value is $\varepsilon_0 = 0$. It follows $\lambda = \mu f(N_T) - \varepsilon$, and at $\varepsilon = 0$ we have $\lambda = \mu f(N_{T_1})$. The normal form on the centre manifold is determined using Sotomayor theorem [20,21]. In order to carry this out, consider first two eigenvectors $v, w \in \mathbb{R}^4$, such that $J_1 v = 0$ and $w^T J_1 = 0$. As for $J_2 = J_1 = \begin{pmatrix} -\frac{1}{\tau} & -\frac{1}{\tau} - \lambda & -\frac{1}{\tau} \\ 0 & 0 & 0 \\ 0 & 0 & -\delta \end{pmatrix}$, we obtain that $w^T = (0, 1, 0)$ and $v^T = (-(\lambda\tau + 1), 1, 0)$. Then, we compute the quantities A, B, C in Sotomayor theorem, where

$$A = \frac{1}{\langle v, w \rangle} \left\langle w, \frac{\partial \Phi}{\partial \varepsilon}(E_2, \varepsilon_0) \right\rangle, B = \frac{1}{\langle v, w \rangle} \sum_{i,j,k=1}^3 w_i v_j v_k \frac{\partial^2 \Phi_i}{\partial x_j \partial x_k}(E_2, \varepsilon_0),$$

$$C = \frac{2}{\langle v, w \rangle} \sum_{i,j=1}^3 w_i v_j \frac{\partial^2 \Phi_i}{\partial x_j \partial \varepsilon}(E_2, \varepsilon_0),$$

with $\varepsilon_0 = 0$ and $(x_1, x_2, x_3) = (N, P, Z)$, and Φ is the vector field associated with system (7). As $\langle v, w \rangle = 1$ and vector w has only one non-zero component, we need only the second component of the vector field Φ , which can be written as

$$\Phi_2(N, P, Z) = \mu P(t) f(N(t)) - g Z h(P(t)) - (\mu f(N_T) - \varepsilon) P(t).$$

We obtain

$$\begin{aligned} A &= \frac{\partial \Phi_2}{\partial \varepsilon}(E_2, 0) = 0, \\ B &= \sum_{j,k=1}^4 v_j v_k \frac{\partial^2 \Phi_2}{\partial x_j \partial x_k}(E_2, 0) = -2(\lambda\tau + 1)\mu f'(N_{T_1}) \neq 0, \end{aligned}$$

and

$$C = 2 \sum_{j=1}^4 v_j \frac{\partial^2 \Phi_2}{\partial x_j \partial \varepsilon}(E_2, 0) = 2v_2 \frac{\partial^2 \Phi_2}{\partial P \partial \varepsilon}(E_2, 0) = -2 \neq 0.$$

Consequently, a transcritical bifurcation takes place as $\varepsilon = 0$, i.e., $f(N_T) = \frac{\lambda}{\mu}$. $\square$

In a similar way we prove that a transcritical bifurcation takes place when the equilibria E_2 and E_3 coincides, as $N_T = N_{T_2}(\tau)$.

Proposition 10. A transcritical bifurcation takes place at the equilibrium E_2 of system (7) as $N_T = N_{T_2}(\tau)$.

Proof. As $N_T = N_{T_2}(\tau)$ we have $E_2 = E_3 = (N_0, P_0, Z_0)$, with $N_0 = N_{T_1}$, $P_0 = \frac{1}{1+\lambda\tau}(N_{T_2}(\tau) - N_{T_1})$, $Z_0 = 0$, and the equilibrium is a fold singularity. We consider $\varepsilon = \delta - \gamma gh(\hat{P})$ as the bifurcation parameter, and the bifurcation value is $\varepsilon = 0$. Apply the Sotomayor theorem [21] as above. Consider two eigenvectors $v, w \in \mathbb{R}^4$, such that $J_2 v = 0$ and $w^T J_2 = 0$. As $J_2 = \begin{pmatrix} -\frac{1}{\tau} - \mu P_0 f'(N_0) & -\frac{1}{\tau} - \lambda & -\frac{1}{\tau} \\ \mu P_0 f'(N_0) & 0 & -\frac{\delta}{\gamma} \\ 0 & 0 & 0 \end{pmatrix}$, we obtain that $w^T = (0, 0, 1)$ and $v^T = (v_1, v_2, v_3)$, with $v_1 = \frac{\delta}{\gamma \mu P_0 f'(N_{T_1})}$, $v_2 = -\frac{1}{\lambda\tau+1} \left(\frac{\tau\delta}{\gamma} + 1 + \frac{\delta}{\gamma \mu P_0 f'(N_{T_1})} \right) \neq 0$, $v_3 = 1$. As $\langle v, w \rangle = 1$ and vector w has only one non-zero component, we need only the third component of the vector field Φ , which can be written as

$$\Phi_3(N, P, Z) = \gamma gZh(P(t)) - (\varepsilon + \gamma gh(\hat{P}))Z.$$

We obtain

$$\begin{aligned} A &= \frac{\partial \Phi_2}{\partial \varepsilon}(E_2, \varepsilon_0) = 0, \\ B &= \sum_{j,k=1}^4 v_j v_k \frac{\partial^2 \Phi_3}{\partial x_j \partial x_k}(E_2, \varepsilon_0) = 2v_2 v_3 \frac{\partial^2 \Phi_3}{\partial Z \partial P}(E_2, \varepsilon_0) = 2v_2 \gamma gh'(P_0) \neq 0, \end{aligned}$$

and

$$C = 2 \sum_{j=1}^4 v_j \frac{\partial^2 \Phi_3}{\partial x_j \partial \varepsilon}(E_2, \varepsilon_0) = 2v_3 \frac{\partial^2 \Phi_3}{\partial Z \partial \varepsilon}(E_2, \varepsilon_0) = -2 \neq 0.$$

Consequently, a transcritical bifurcation takes place as $\varepsilon = 0$, i.e., $N_T = N_{T_2}(\tau)$. $\square$

Remark 2. At the bifurcation, point the two equilibria E_2 and E_3 have the same eigenvalues, $\lambda_j^2 = \lambda_j^3$, $j = 1, 3$, with $\text{Re}\lambda_j^2 < 0$, for $j = 1, 2$, and $\lambda_3^2 = \lambda_3^3 = 0$. As a consequence of the transcritical bifurcation, the eigenvalues these two eigenvalues change signs when passing through the bifurcation values, while the real parts of the other three pairs of eigenvalues remain negative close to the bifurcation value, due to continuity. Thus, the two equilibria exchange stability. Consequently, close to $N_T = N_{T_2}(\tau)$, if $N_T < N_{T_2}(\tau)$ the equilibrium point E_2 is an attractor and E_3 is a saddle of type (2,1), while if $N_T > N_{T_2}(\tau)$ the equilibrium point E_2 is a saddle of type (2,1) and E_3 is an attractor.

5.1.2. Transcritical Bifurcations for the Strong Model

Proposition 11. A transcritical bifurcation takes place at the equilibrium E_1 of system (15) as $N_T = N_{T_1}$.

Proof. As $N_T = N_{T_1}$, we have $E_2 = E_1$ and the equilibrium is a fold singularity. We consider $\varepsilon = \mu f(N_T) - \lambda$ as the bifurcation parameter, and the bifurcation value is $\varepsilon = 0$. It follows $\lambda = \mu f(N_T) - \varepsilon$, and at $\varepsilon = 0$ we have $\lambda = \mu f(N_{T_1})$. Consider two eigenvectors

$v, w \in \mathbb{R}^4$, such that $J_2 v = 0$ and $w^T J_2 = 0$. As $J_2 = \begin{pmatrix} 0 & -\lambda & 0 & \frac{2}{\tau} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -\delta & 0 \\ -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{4}{\tau} \end{pmatrix}$, we obtain

that $w^T = (0, 1, 0, 0)$ and $v^T = (-(\lambda\tau + 1), 1, 0, \frac{\lambda\tau}{2})$. Then compute the quantities A, B, C in Sotomayor theorem. As $\langle v, w \rangle = 1$ and vector w has only one non-zero component, we need only the second component of the vector field Φ , associated with system (15), which can be written as

$$\Phi_2(N, P, Z, Q_1) = \mu P(t)f(N(t)) - gZh(P(t)) - (\mu f(N_T) - \varepsilon)P(t).$$

We obtain

$$\begin{aligned} A &= \frac{\partial \Phi_2}{\partial \varepsilon}(E_2, 0) = 0, \\ B &= \sum_{j,k=1}^4 v_j v_k \frac{\partial^2 \Phi_2}{\partial x_j \partial x_k}(E_2, 0) = -2(\mu f(N_{T_1})\tau + 1)\mu f'(N_{T_1}) \neq 0, \end{aligned}$$

and

$$C = 2 \sum_{j=1}^4 v_j \frac{\partial^2 \Phi_2}{\partial x_j \partial \varepsilon}(E_2, 0) = 2v_2 \frac{\partial^2 \Phi_2}{\partial P \partial \varepsilon}(E_2, 0) = -2 \neq 0.$$

Consequently, a transcritical bifurcation takes place as $\varepsilon = 0$, i.e., $f(N_T) = \frac{\lambda}{\mu}$. $\square$

In a similar way, we prove that a transcritical bifurcation takes place when the equilibria E_2 and E_3 of system (15) coincides, as $N_T = N_{T_2}(\tau)$.

Proposition 12. A transcritical bifurcation takes place at the equilibrium E_2 of system (15) as $N_T = N_{T_2}(\tau)$.

Proof. As $N_T = N_{T_2}(\tau)$, we have $E_2 = E_3 = (N_0, P_0, Z_0, Q_{10})$, with $N_0 = N_{T_1}$, $P_0 = \frac{1}{1+\lambda\tau}(N_{T_2}(\tau) - N_{T_1})$, $Z_0 = 0$, $Q_{10} = \frac{\lambda\tau}{2}P_0$, and the equilibrium is a fold singularity. We consider $\varepsilon = \delta - \gamma gh(\hat{P})$ as the bifurcation parameter, and the bifurcation value is $\varepsilon = 0$. Apply the Sotomayor theorem [21] as above. Consider two eigenvectors

$v, w \in \mathbb{R}^4$, such that $J_2 v = 0$ and $w^T J_2 = 0$. As $J_2 = \begin{pmatrix} -\mu Pa & -\lambda & 0 & \frac{2}{\tau} \\ \mu Pa & 0 & -\frac{\delta}{\gamma} & 0 \\ 0 & 0 & 0 & 0 \\ -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{2}{\tau} & -\frac{4}{\tau} \end{pmatrix}$,

we obtain that $w^T = (0, 0, 1, 0)$ and $v^T = (v_1, v_2, v_3, v_4)$, with $v_1 = \frac{\delta}{\gamma\mu P_0 f'(N_{T_1})}$, $v_2 = -\frac{1}{\lambda\tau+1} \left(\frac{\tau\delta}{\gamma} + 1 + \frac{\delta}{\gamma\mu P_0 f'(N_{T_1})} \right) \neq 0$, $v_3 = 1$, $v_4 = \frac{\tau}{2(\lambda\tau+1)} \left(\frac{\delta}{\gamma} - \left(1 + \frac{\delta}{\gamma\mu P_0 f'(N_{T_1})} \right) \right)$. As $\langle v, w \rangle = 1$ and vector w has only one non-zero component, we need only the third component of the vector field Φ , which can be written as

$$\Phi_3(N, P, Z, Q_1) = \gamma gZh(P(t)) - (\varepsilon + \gamma gh(\hat{P}))Z.$$

We obtain

$$\begin{aligned} A &= \frac{\partial \Phi_3}{\partial \varepsilon}(E_2, \varepsilon_0) = 0, \\ B &= \sum_{j,k=1}^4 v_j v_k \frac{\partial^2 \Phi_3}{\partial x_j \partial x_k}(E_2, \varepsilon_0) = 2v_2 v_3 \frac{\partial^2 \Phi_3}{\partial Z \partial P}(E_2, \varepsilon_0) = 2v_2 \gamma g h'(P_0) \neq 0, \end{aligned}$$

and

$$C = 2 \sum_{j=1}^4 v_j \frac{\partial^2 \Phi_3}{\partial x_j \partial \varepsilon}(E_2, \varepsilon_0) = 2v_3 \frac{\partial^2 \Phi_3}{\partial Z \partial \delta}(E_2, \varepsilon_0) = -2 \neq 0.$$

Consequently, a transcritical bifurcation takes place as $\varepsilon_0 = 0$, i.e., $N_T = N_{T_2}(\tau)$. $\square$

Remark 3. At the bifurcation point the two equilibria E_2 and E_3 have the same eigenvalues, $\lambda_j^2 = \lambda_j^3$, $j = 1, 4$, with $\operatorname{Re} \lambda_j^2 < 0$, for $j = 1, 2, 3$, and $\lambda_4^2 = \lambda_4^3 = 0$. As a consequence of the transcritical bifurcation, the eigenvalues these two eigenvalues change signs when passing through the bifurcation values, while the real parts of the other three pairs of eigenvalues remain negative close to the bifurcation value, due to continuity. Thus, the two equilibria exchange stability. Consequently, close to $N_T = N_{T_2}(\tau)$, if $N_T < N_{T_2}(\tau)$ the equilibrium point E_2 is an attractor and E_3 is a saddle of type (3,1), while if $N_T > N_{T_2}(\tau)$ the equilibrium point E_2 is a saddle of type (3,1) and E_3 is an attractor.

5.2. Hopf Bifurcations

A Hopf bifurcation may occur at a Hopf singularity. As we proved in Section 4, only the equilibrium point E_3 is a Hopf non-hyperbolic point, in certain conditions (see Propositions 4, 7 and 8). At such a singular point, a Hopf bifurcation takes place if the conditions of the Hopf bifurcation theorem [22] are fulfilled.

5.2.1. Hopf Bifurcations for the Weak Model

As a consequence of Proposition 3, if $P^* h'(P^*) - h(P^*) \geq 0$, then the equilibrium point $E_3 = (N^*, P^*, Z^*)$ of system (7) is locally asymptotically stable for all $N_T > N_{T_2}(\tau)$, so there can be no Hopf bifurcation in this case.

If $P^* h'(P^*) - h(P^*) < 0$, then equilibrium point E_3 is a Hopf singularity for parameters in the bifurcation stratum defined by the equation

$$a_1 a_2 - a_3 = 0, \quad (48)$$

with a_1, a_2, a_3 given by (37). Consequently, for each $N_T > N_{T_2}(\tau)$ such that (48), a Hopf bifurcation may occur, and a branch of periodic solutions may emerge around E_3 .

Note that the eigenvalues of the Jacobi matrix associated with E_3 are $\lambda_{1,2}^1 = \pm i\omega$, $\lambda_3^1 = -a_1$, with $\omega^2 = a_2$. Thus, as $a_1 > 0$, the centre manifold of E_3 is attractive. As a consequence, if the conditions of the Andronov–Hopf bifurcation theorem [22] are satisfied and a supercritical Hopf bifurcation takes place (i.e., the first Lyapunov coefficient is negative), then the stable limit cycle born through this bifurcation on the extended centre manifold is locally asymptotically stable.

For the type II response function h , in the hypotheses of Proposition 4, a Hopf bifurcation may take place for each τ , at the bifurcation value $N_T = N_{T_3}(\tau)$.

The numerical simulations in Figure 4 show the existence of a stable limit cycle for values of $N_T > N_{T_3}(\tau)$. The values of the parameters used for simulations are $\mu = 5.9$, $g = 7$, $\lambda = 0.017$, $\gamma = 0.7$, $\delta = 0.17$, $k_N = 1$, $k_P = 1$. The results are consistent with the ones obtained in [12]. For $\tau = 5$, the approximate value of N_T for the Hopf bifurcation is $N_{T_3}(\tau) = 1.096$. The simulations show time series for an initial point closed to the equilibrium E_3 , proving an evolution towards the steady state E_3 for $N_T = 1.05 < N_{T_3}(5)$ and to a limit cycle for $N_T = 1.2 > N_{T_3}(5)$.

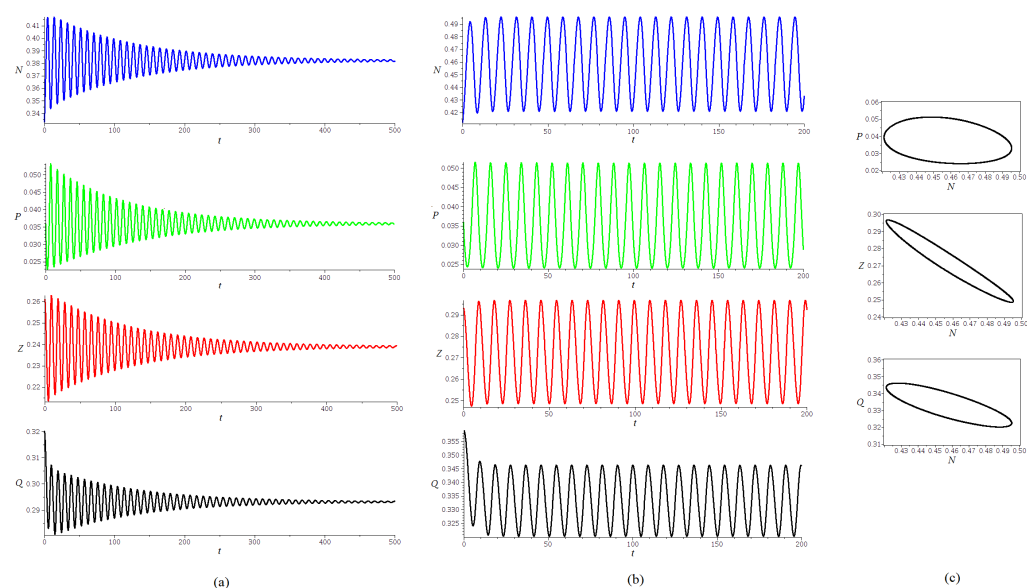


Figure 4. Simulations for the weak model, using a type II response $h(P) = \frac{P}{P+k_P}$: (a) $\tau = 5$, $N_T = 1.05$, showing an evolution towards E_3 ; (b) $\tau = 5$, $N_T = 1.2$, showing a periodic behavior; (c) projections of the attractor, for $\tau = 5$, $N_T = 1.2$, $t \in [400, 500]$. The stable limit cycle may appear through a supercritical Hopf bifurcation at $N_{T_3}(\tau) = 1.096$.

For the type III response function h , for the values of the parameters considered for simulations we have $\frac{\delta}{g\gamma} \leq h(k_P)$, so there are no Hopf bifurcations at E_3 , as $N_T > N_{T_2}(\tau)$.

5.2.2. Hopf Bifurcation for the Strong Model

According to Proposition 8, if $P^*h'(P^*) - h(P^*) \geq 0$ the equilibrium point $E_3 = (N^*, P^*, Z^*, Q_1^*)$ of system (15) is a Hopf singularity if condition

$$(b_1b_2 - b_3)b_3 - b_1^2b_4 = 0, \quad (49)$$

with $b_j, j = \overline{1, 4}$ given by (43), is satisfied.

If $P^*h'(P^*) - h(P^*) < 0$, the equilibrium point E_3 is a Hopf singularity for parameters in the bifurcation stratum defined by the conditions (45). Consequently, for each $N_T > N_{T_2}(\tau)$ such that (45), a Hopf bifurcation may occur.

For the type II response function h , Proposition 8 does not apply. For the considered values of the parameters, $\mu = 5.9$, $g = 7$, $\lambda = 0.017$, $\gamma = 0.7$, $\delta = 0.17$, $k_N = 1$, $k_P = 1$, we have found that, for (τ, N_T) on the curve defined by (49) in the (τ, N_T) parameter plane, the equilibrium P^* is a Hopf singularity. This curve separates regions 3 and 4 in Figure 3b, and a Hopf bifurcation may take place when the parameters cross this curve.

For $\tau = 5$, the approximate value of N_T for the Hopf bifurcation is $N_{T_3}(\tau) = 0.955$. The simulations in Figure 5, show the projections of parts of the trajectories for an initial point near the equilibrium E_3 , proving an evolution towards a stable limit cycle, for (a) $N_T = 1.05 > N_{T_3}(5)$, (b) $N_T = 1.096 > N_{T_3}(5)$ and (c) $N_T = 1.2 > N_{T_3}(5)$.

The trajectories in Figures 4 and 5 were obtained using the DETools package in MAPLE 18, applying the fourth-order Runge–Kutta method, with a stepsize 0.01.

Remark 4. As the parameters vary away from the Hopf bifurcation curve, the limit cycle born through the Hopf bifurcation may disappear, may double the period, etc. Since the dimensions of both the weak and the strong models are greater than three, strange attractors may also exist. Nevertheless, as the domains for each of the two models are bounded, the ω -limit set for each model is also bounded, and so are their attractors.

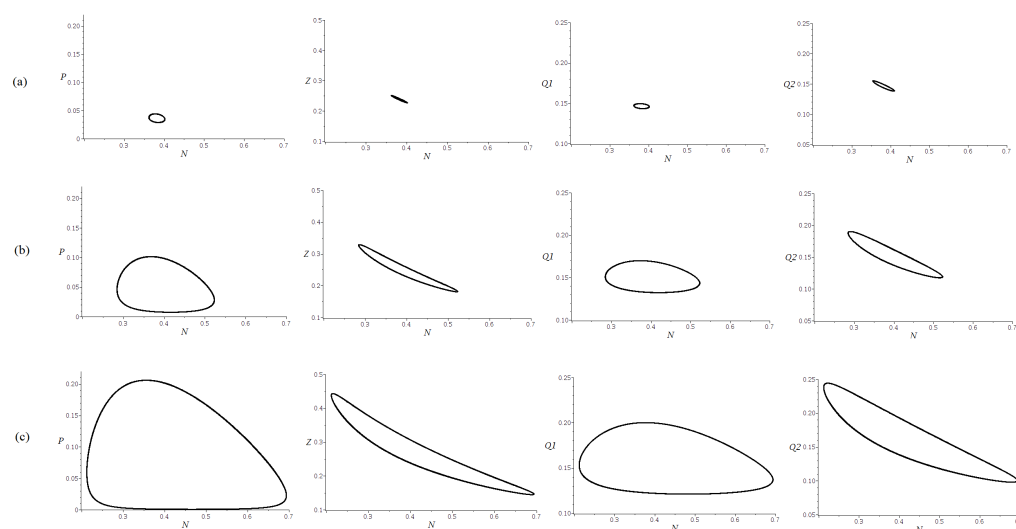


Figure 5. Simulations for the strong model, using a type II response $h(P) = \frac{P}{P+k_P}$. Projections of the attractor for $\tau = 5$ and (a) $N_T = 1.05$; (b) $N_T = 1.096$; (c) $N_T = 1.2$; $t \in [700, 800]$. The stable limit cycle may appear through a supercritical Hopf bifurcation at $N_{T_3}(\tau) = 0.955$.

6. Discussion

In this study, we have analysed two NPZ models for a closed ecosystem with three compartments, dissolved nutrient, phytoplankton and zooplankton, incorporating a delay in nutrient recycling. The models were obtained starting from a NPZ model introduced in [12], by using the gamma distribution function with one or two degrees of freedom. The aim of the paper was to study how the stability and bifurcation of the equilibrium solutions depend on the total amount of nutrient and the delay.

We have shown that each of the two models have at most three equilibrium points in the region of interest, and that at most one of the equilibrium points is locally asymptotically stable at each value of the total nutrients. More precisely,

- (1) For $N_T < N_{T_1}$, there is only one equilibrium point with no phytoplankton and no zooplankton (E_1), which is asymptotically stable;
- (2) For $N_{T_1} < N_T < N_{T_2}(\tau)$ the equilibrium E_2 with phytoplankton and no zooplankton is asymptotically stable, while E_1 is unstable;
- (3) As $N_T > N_{T_2}(\tau)$, the first two equilibria are unstable, while the equilibrium E_3 with both phytoplankton and zooplankton is asymptotically stable either for all $N_T > N_{T_2}(\tau)$ or there exists an $N_{T_3}(\tau)$ such that E_3 is stable for $N_{T_2}(\tau) < N_T < N_{T_3}(\tau)$, and unstable for $N_T > N_{T_3}(\tau)$, close to $N_{T_3}(\tau)$, depending on the response function h .

Further, we have proven that the changes of stability at N_{T_1} and $N_{T_2}(\tau)$ occur through transcritical bifurcations. Finally, we have shown that the change of stability at N_{T_3} is a Hopf singularity and the associated bifurcation will lead to stable limit cycles if it is supercritical. Numerical simulations show the existence of stable limit cycles for each delay τ , close to the bifurcation value $N_T = N_{T_3}(\tau)$.

Thus, for each of the two considered models, the ω -limit sets contains at most one equilibrium point. In specific hypotheses on the response function h , the ω -limit sets may contain a limit cycle for certain values of the parameters N_T and τ . However, as the dimension of both models is greater than 2, the ω -limit sets may also contain strange attractors.

Our results on the existence of equilibria are consistent with those of [12] for the system with a general distribution (1), who showed the equilibrium values of N, P, Z are only affected by the mean delay and not the form of the distribution. The stability result (1) above reproduces that of [12] for the general distribution case. The stability result (2) is stronger than that of [12] for a general distribution, and thus is likely a consequence of our choice of distributions. In fact, [12] showed that if the system has a discrete delay (Dirac

distribution), then the equilibrium E_2 may undergo a Hopf bifurcation; however, we show that it is not possible for the distributions we consider. Our results extend those of [12] by proving the stability result (3) for the two systems studied and by proving the types of bifurcations that occur as the stability of the equilibrium points changes. Further, we showed the possibility of a codimension-two double Hopf bifurcation in the system with the two-degrees of freedom gamma distribution.

To conclude, we discuss the implications of our work for application. The general trend of bifurcations of the equilibrium points as the total amount of nutrients is increased is as follows: first, the phytoplankton only equilibrium point, E_2 , appears and then the coexistence equilibrium point, E_3 . This is biologically plausible: as more nutrients are available, the system can support more organisms. Our work highlights the fact that a delay in the recycling can be stabilizing: the amount of nutrients needed for the transcritical bifurcation leading to the emergence of E_3 to occur increases with the size of the mean delay. We also showed, for a given amount of total nutrients, the delay decreases the equilibrium size of at least one of N, P, Z . This is because some of the nutrients are stored in the other compartments of the system, which represent the nutrients that are being recycled. Both these results were identical for the weak and strong models. Where these models differ was in the effect of the delay on the Hopf bifurcation of the E_3 equilibrium point. For both models, as the delay is increased we observe the same qualitative effect: the Hopf bifurcation value N_{T3} increases, then decreases, then increases. However, the variation is larger for the strong model than for the weak model. Thus, the N_{T3} for the weak model is less than that for the strong model for small enough delay, with the reverse for large enough delay.

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