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Effects of zooplancton grazing on phytoplankton viral infection

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1 Abstract

By studying a model including healthy phytoplankton, infected phytoplankton, and zooplankton, we observe that the maximum phytoplankton biomass is reached when zooplankton grazing pressure is high. Zooplankton regulate viral infection by consuming infected cells, which allows the phytoplankton population to be maintained. A phenomenon known as the healthy herd hypothesis. However, if zooplankton consume too much phytoplankton, their effect becomes detrimental, as they reduce the overall phytoplankton population.

2 Introduction

Photosynthetic planktonic organisms, known as phytoplankton, are responsible for approximately 50% of global oxygen production. As such, they play a crucial role in numerous biological and abiotic cycles. However, phytoplankton face intense viral infections, which can kill up to 20% of the population every day. In addition, they are consumed by zooplankton, the heterotrophic plankton. This raises a key question : how does phytoplankton maintain a stable population despite such strong pressure from both viruses and zooplankton ? One possible explanation is that zooplankton, while preying on phytoplankton, may help regulate viral infection by consuming infected cells — thus enabling the phytoplankton population to persist. This mechanism is known as the healthy herd hypothesis.

3 Materials and methods

3.1 Model

To address this question, it is necessary to study the dynamics of the phytoplankton–virus–zooplankton system. We propose the following model :

$$\begin{cases} \frac{dP}{dt} = aP - \frac{c}{L}PF - bPZ \\ \frac{dF}{dt} = \frac{c}{L}PF - \frac{1}{L}F - bFZ \\ \frac{dZ}{dt} = b(P+F)Z - mZ^2 \end{cases}$$

It is a continuous-time system with three state variables : P for healthy phytoplankton, F for infected phytoplankton, Z for zooplankton.
Healthy phytoplankton grows at a rate aP, becomes infected by viruses at a rate -$\frac{c}{L}PF$, and is grazed by zooplankton at a rate -bPZ.
Infected phytoplankton dies due to infection at rate -$\frac{1}{L}F$, and is also grazed by zooplankton at rate -bFZ.
Zooplankton feeds on both healthy and infected phytoplankton without distinction at rate $bZ(P+F)$, and experiences quadratic mortality at rate -mZ^2.
The parameters are as follows :

a : intrinsic growth rate of healthy phytoplankton ($days^{-1}$),
b : grazing rate of phytoplankton by zooplankton ($(mmolC.m^{-3})^{-1}.days^{-1}$),
c : infection rate of phytoplankton ($(mmolC.m^{-3})^{-1}.days^{-1}$),
L : latency time before infected phytoplankton dies ($days$),
m : zooplankton mortality rate ($(mmolC.m^{-3})^{-1}.days^{-1}$).

3.2 Equilibrium analysis

To solve this model, we start by looking for the equilibria of the system. Since it is a continuous system, equilibria are given by the solutions of :

$$\frac{dX}{dt} = 0 \quad \text{with} \quad \begin{cases} \frac{dP}{dt} = aP - \frac{c}{L}PF - bPZ = 0 \\ \frac{dF}{dt} = \frac{c}{L}PF - \frac{1}{L}F - bFZ = 0 \\ \frac{dZ}{dt} = bZ(P+F) - mZ^2 = 0 \end{cases}$$

This gives us :

$$\begin{cases} P = 0 \quad \text{or} \quad a - \frac{C}{L}F - bZ \\ F = 0 \quad \text{or} \quad \frac{c}{L}P - \frac{1}{L} - bZ = 0 \\ Z = 0 \quad \text{or} \quad b(P+F) - mZ = 0 \end{cases}$$

We begin by defining all mathematically and biologically realistic combinations for this system. Four equilibria can be defined :
1. All populations extinct (Equilibrium 1)
2. No infected phytoplankton (Equilibrium 2)
3. No zooplankton (Equilibrium 3)
4. Coexistence of all three populations (Equilibrium 4)

We discard the case where healthy phytoplankton equals zero, since as the base of the trophic network, the equilibrium would tend toward case 1 by definition.
For each of these, we simplify the system and obtain the following equilibria :

Equilibrium 1 :

$$\begin{cases} P_1 = 0 \\ F_1 = 0 \\ Z_1 = 0 \end{cases}$$

Equilibrium 2 :

$$\begin{cases} P_2 = \frac{ma}{b^2} \\ F_2 = 0 \\ Z_2 = \frac{a}{b} \end{cases}$$

Equilibrium 3 :

$$\begin{cases} P_2 = \frac{1}{c} \\ F_2 = \frac{aL}{c} \\ Z_2 = 0 \end{cases}$$

Equilibrium 4 :

$$\begin{cases} P = \frac{b^2L(aL+1)}{mc^2} + \frac{1}{c} \\ F = -\frac{b^2L(aL+1)}{mc^2} + \frac{aL}{c} \\ Z = \frac{b(aL+1)}{mc} \end{cases}$$

Note : Equilibrium 4 only exists if the following condition is satisfied :

$$cma > b^2(aL + 1)$$

(see Appendix 1, pages 3 and 4 for details).

3.3 Stability Analysis of the Equilibria

We now investigate the stability of each of these equilibria. To do so, we compute the Jacobian matrix J defined as :

$$J = \begin{pmatrix} \frac{d}{dP}\left(\frac{dP}{dt}\right) & \frac{d}{dF}\left(\frac{dP}{dt}\right) & \frac{d}{dZ}\left(\frac{dP}{dt}\right) \\ \frac{d}{dP}\left(\frac{dF}{dt}\right) & \frac{d}{dF}\left(\frac{dF}{dt}\right) & \frac{d}{dZ}\left(\frac{dF}{dt}\right) \\ \frac{d}{dP}\left(\frac{dZ}{dt}\right) & \frac{d}{dF}\left(\frac{dZ}{dt}\right) & \frac{d}{dZ}\left(\frac{dZ}{dt}\right) \end{pmatrix} = \begin{pmatrix} a - \frac{c}{L}F - bZ & -\frac{c}{L}P & -bP \\ \frac{c}{L}F & \frac{c}{L}P - \frac{1}{L} - bZ & -bF \\ -bZ & -bZ & bP + bF - 2mZ \end{pmatrix}$$

The values of P, F and Z at equilibrium are substituted into matrix J, and we then study the sign of the real parts of its eigenvalues. This procedure is repeated for each of the four equilibria.
For a 3×3 matrix, finding the eigenvalues analytically can be complex. We therefore use **Sarrus' rule** (see Appendix 1, page 5) to compute the characteristic polynomial of each matrix as :

$$P(\lambda) = \lambda^3 + a\lambda^2 + b\lambda + c$$

An equilibrium is stable if all the following conditions are met :

$$a > 0, \quad b > 0, \quad 0 < c < ab$$

4 Results

The stability analysis shows that the coexistence equilibrium is locally stable under the appropriate conditions. This implies that such an equilibrium is biologically plausible. The analytical expressions reveal that increasing the grazing rate b leads to an increase in the healthy phytoplankton population (P) and a decrease in the infected phytoplankton population (F). Conversely, decreasing the zooplankton mortality rate m results in a higher zooplankton biomass, which in turn produces the same qualitative effect : an increase in P and a reduction in F.

To better assess the influence of zooplancton grazing on the model, the biomass of healthy phytoplankton was computed for all possible values of b (the grazing rate of phytoplankton by zooplankton) and m (the mortality rate of zooplankton).

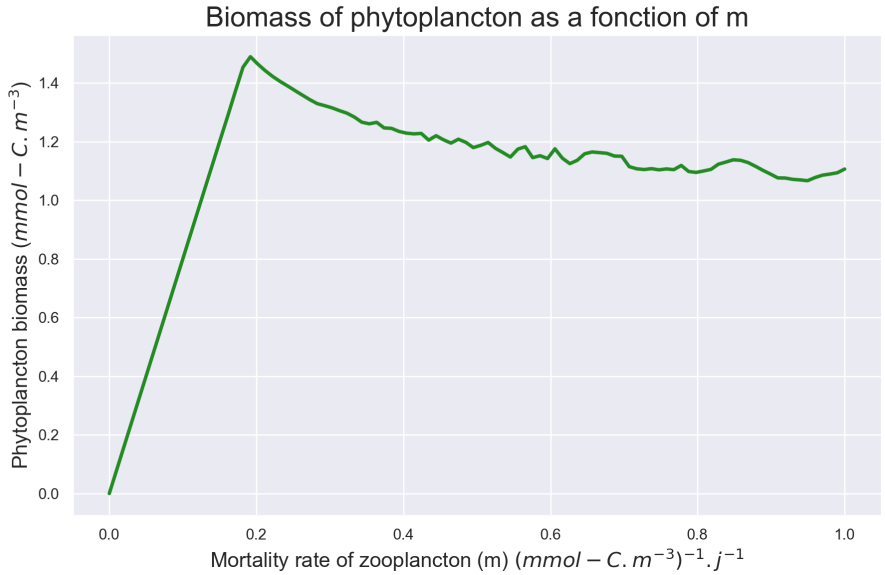

FIGURE 1 – Phytoplankton biomass as a function of zooplankton mortality rate m

Figure 1 shows the evolution of phytoplankton biomass P as a function of zooplankton mortality rate m. We observe that the biomass reaches its maximum under normal conditions at $P = 1.5\ mmol \cdot C \cdot m^{-3}$ when zooplankton mortality is low. Around $m = 0.19$, when zooplankton pressure is high, a shift is observed : a sudden change in dynamics leads to a decrease in phytoplankton biomass until it reaches a plateau around $P = 1\ mmol \cdot C \cdot m^{-3}$.

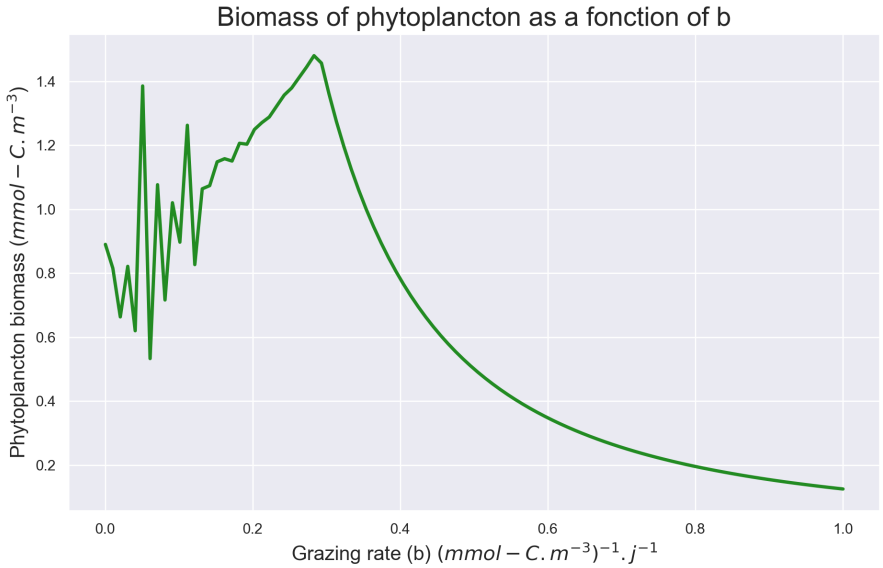

FIGURE 2 – Phytoplankton biomass as a function of phytoplankton grazing rate b

Figure 2 shows the evolution of phytoplankton biomass P as a function of the grazing rate b. The biomass increases between $b = 0$ and $b = 0.3$, where it reaches its maximum at $P = 1.5\ mmol \cdot C \cdot m^{-3}$ under normal conditions. Then, a shift similar to Figure 4 occurs, with a decrease in phytoplankton biomass down to $P = 0.1\ mmol \cdot C \cdot m^{-3}$ for high values of b.

Together, these results and the analytical equilibrium highlight that, within a certain range, higher grazing pressure

and lower zooplankton mortality can reduce viral infection and sustain phytoplankton populations. This counterintuitive effect, where predation helps maintain host populations by limiting disease spread, is a textbook example of the *healthy herd hypothesis*.

5 Discussion

This simple predator–prey–infection model provides theoretical insight into the potential role of zooplankton in modulating viral infections in phytoplankton populations. Our analysis suggests that grazing by zooplankton can have a paradoxical protective effect on phytoplankton by removing infected individuals, thereby reducing the viral load in the environment. This mechanism supports the so-called *healthy herd hypothesis*, typically observed in epidemiological contexts, where moderate predation helps reduce disease prevalence in a host population.

However, this positive effect only holds within a limited parameter range. Excessive grazing (high b) leads to phytoplankton collapse, while low zooplankton mortality (low m) can also destabilize the system. These results highlight the importance of balancing top-down control : predators can suppress infections, but too much pressure compromises the host population itself.

This model is a simplification of real ecological dynamics. It assumes a well-mixed environment, does not include explicit viral dynamics, and neglects spatial or evolutionary processes. Including virus concentration as an explicit state variable, or accounting for spatial heterogeneity, could help refine predictions and reveal new emergent behaviors.

Despite its simplicity, this framework opens perspectives for studying the indirect role of grazers in ecosystem resilience. It suggests that the impact of predators on ecosystem health may go beyond simple biomass consumption and includes epidemiological regulation mechanisms. Such considerations are particularly relevant in marine systems, where microbial interactions play a key role in biogeochemical cycles.

6 Conclusion

In conclusion, by consuming infected phytoplankton cells, zooplankton help regulate viral infections and allow the phytoplankton population to persist. However, this beneficial effect is only observed when the grazing pressure is within a suitable range : only when predation is strong enough zooplankton can effectively reduce infection rates. This mechanism aligns with the *healthy herd hypothesis*, where a predator indirectly protects a host population by limiting disease spread.

Nevertheless, excessive grazing becomes detrimental. When zooplankton consume too much phytoplankton, the overall population declines due to direct predation. There therefore exists a critical balance : zooplankton must graze enough to limit viral infections, but not to the extent that they collapse the phytoplankton population.

Future work could explore the evolution of phytoplankton biomass as a function of two parameters simultaneously, or modify the current model to test alternative assumptions — for example, using a linear mortality term for zooplankton instead of a quadratic one. Another extension would be to replace the infected phytoplankton compartment with a free virus pool, introduce preferenced grazing or to construct a five-variable model including two phytoplankton species, each infected by a specialist virus, and a generalist zooplankton. These refinements would help better understand the indirect effects of zooplankton on viral dynamics in planktonic ecosystems.

A Annexe 1 : Résolution du système et stabilité des équilibres

On considère le modèle PFZ, caractérisé par le système différentiel suivant :

$$\begin{cases} \frac{dP}{dt} = aP - \frac{c}{L}PF - bPZ \\ \frac{dF}{dt} = \frac{c}{L}PF - \frac{1}{L}F - bFZ \\ \frac{dZ}{dt} = b(P+F)Z - mZ^2 \end{cases}$$

Pour chercher les équilibres du modèle, on résout $\frac{dX}{dt} = 0$ avec $X = (P, F, Z)$:

$$\begin{cases} \frac{dP}{dt} = 0 \Rightarrow aP - \frac{c}{L}PF - bPZ = 0 \\ \frac{dF}{dt} = 0 \Rightarrow \frac{c}{L}PF - \frac{1}{L}F - bFZ = 0 \\ \frac{dZ}{dt} = 0 \Rightarrow b(P+F)Z - mZ^2 = 0 \end{cases}$$

On factorise chaque équation :

$$\begin{cases} P\left(a - \frac{c}{L}F - bZ\right) = 0 \\ F\left(\frac{c}{L}P - \frac{1}{L} - bZ\right) = 0 \\ Z\left(b(P+F) - mZ\right) = 0 \end{cases}$$

On identifie alors les solutions possibles comme :

$$\begin{cases} P = 0 \quad \text{ou} \quad a - \frac{c}{L}F - bZ = 0 \\ F = 0 \quad \text{ou} \quad \frac{c}{L}P - \frac{1}{L} - bZ = 0 \\ Z = 0 \quad \text{ou} \quad b(P+F) - mZ = 0 \end{cases}$$

We distinguish four biologically meaningful equilibria :

Equilibrium 1 : No organisms present

$$X_1 = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$$

We do not consider the case where the healthy phytoplankton population is zero, as it constitutes the base of the trophic network and would naturally drive the system toward extinction (equilibrium 1).

Equilibrium 2 : No infected phytoplankton We assume $F = 0$, i.e., no infected phytoplankton. The system becomes :

$$\begin{cases} aP - bPZ = 0 \\ Z(bP - mZ) = 0 \\ F = 0 \end{cases}$$

Solving the first equation :

$$aP - bPZ = 0 \quad \Rightarrow \quad P(a - bZ) = 0 \quad \Rightarrow \quad Z = \frac{a}{b}$$

Solving the second :

$$Z(bP - mZ) = 0$$

Assuming $Z \neq 0$ (otherwise we are back to equilibrium 1), we get :

$$bP = mZ \quad \Rightarrow \quad P = \frac{mZ}{b} = \frac{m}{b} \cdot \frac{a}{b} = \frac{ma}{b^2}$$

Thus :

$$X_2 = \begin{pmatrix} \frac{ma}{b^2} \\ 0 \\ \frac{a}{b} \end{pmatrix}$$

Equilibrium 3 : No zooplankton

We now assume $Z = 0$, meaning the zooplankton has disappeared. The system becomes :

$$\begin{cases} aP - \frac{c}{L}PF = 0 \\ \frac{c}{L}PF - \frac{1}{L}F = 0 \\ Z = 0 \end{cases}$$

From the first equation :

$$aP - \frac{c}{L}PF = 0 \quad \Rightarrow \quad P\left(a - \frac{c}{L}F\right) = 0 \quad \Rightarrow \quad F = \frac{aL}{c}$$

From the second :

$$\frac{c}{L}PF = \frac{1}{L}F \quad \Rightarrow \quad P = \frac{1}{c}$$

So :

$$X_3 = \begin{pmatrix} \frac{1}{c} \\ \frac{aL}{c} \\ 0 \end{pmatrix}$$

Equilibrium 4 : Coexistence

We solve the entire system with all the components

$$\begin{cases} a - \frac{c}{L}F - bZ = 0 \\ \frac{c}{L}P - \frac{1}{L} - bZ = 0 \quad (1) \Rightarrow Z = \frac{1}{b}\left(\frac{c}{L}P - \frac{1}{L}\right) \\ b(P + F) - mZ = 0 \end{cases}$$

Injecting Z in the two other equations :

$$\begin{cases} a - \frac{c}{L}F - \frac{c}{L}P + \frac{1}{L} = 0 \quad \Rightarrow \quad P = \frac{aL}{c} - F + \frac{1}{c} \\ Z = \frac{1}{b}\left(\frac{c}{L}P - \frac{1}{L}\right) \\ bP + bF - \frac{m}{b}\left(\frac{c}{L}P - \frac{1}{L}\right) = 0 \end{cases}$$

Injecting P in the two others :

$$\begin{cases} P = \dfrac{aL}{c} - F + \dfrac{1}{c} \\ Z = \dfrac{1}{b}\left(\dfrac{c}{L}P - \dfrac{1}{L}\right) \\ \dfrac{baL}{c} - bF + bF - \dfrac{m}{b}\left(\dfrac{aL}{c} - F + \dfrac{1}{c}\right) + \dfrac{m}{bL} = 0 \end{cases}$$

$$\begin{cases} P = \dfrac{aL}{c} - F + \dfrac{1}{c} \\ Z = \dfrac{1}{b}\left(\dfrac{c}{L}P - \dfrac{1}{L}\right) \\ F = -\dfrac{b^2L(aL+1)}{mc^2} + \dfrac{aL}{c} \end{cases}$$

We now inject F in P and P in Z

$$P = \frac{b^2L(aL+1)}{mc^2} + \frac{1}{c}$$

$$Z = c\left(\frac{b^2L(aL+1)}{mc^2} + \frac{1}{c}\right) \cdot \frac{1}{L} - \frac{1}{L} = \frac{b(aL+1)}{mc}$$

So we found out coexistence equilibrium :

$$\boxed{\vec{X}_4 = \begin{pmatrix} P_4 \\ F_4 \\ Z_4 \end{pmatrix} = \begin{pmatrix} \frac{b^2L(aL+1)}{mc^2} + \frac{1}{c} \\ -\frac{b^2L(aL+1)}{mc^2} + \frac{aL}{c} \\ \frac{b(aL+1)}{mc} \end{pmatrix}}$$

For this equilibrium to be biologically relevant, we must ensure :

$$P_4 > 0, \quad F_4 > 0, \quad Z_4 > 0$$

1. $P_4 > 0$: obviously true if all parameters are strictly positive.
2. $Z_4 > 0$: always verified because $b > 0, a > 0, L > 0, m > 0, c > 0$
3. $F_4 > 0$: we verify the following condition :

$$-\frac{b^2L(aL+1)}{mc^2} + \frac{aL}{c} > 0$$

Multiplying both sides by mc^2 yields :

$$aLmc^2 > b^2L(aL+1)$$

We then obtain the existence condition :

$$\boxed{cma > b^2(aL+1)}$$

Thus, the equilibrium $\vec{X}_4$ exists if and only if this condition is satisfied.

We now aim to study the stability of the equilibria. For that, we need to compute the Jacobian matrix J :

$$J = \begin{pmatrix} \frac{d}{dP}\frac{dP}{dt} & \frac{d}{dF}\frac{dP}{dt} & \frac{d}{dZ}\frac{dP}{dt} \\ \frac{d}{dP}\frac{dF}{dt} & \frac{d}{dF}\frac{dF}{dt} & \frac{d}{dZ}\frac{dF}{dt} \\ \frac{d}{dP}\frac{dZ}{dt} & \frac{d}{dF}\frac{dZ}{dt} & \frac{d}{dZ}\frac{dZ}{dt} \end{pmatrix} = \begin{pmatrix} a - \frac{c}{L}F - bZ & -\frac{c}{L}P & -bF \\ \frac{c}{L}F & \frac{c}{L}P - \frac{1}{L} - bZ & -bF \\ bZ & bZ & bP + bF - 2mZ \end{pmatrix}$$

We now need to determine the characteristic polynomial of this matrix for each equilibrium point. To do so, we will use the general Sarrus rule, illustrated as follows :

$$\begin{vmatrix} a & b & c \\ d & e & f \\ g & h & i \end{vmatrix} = aei + bfg + cdh - ceg - bdi - afh$$

We then obtain the characteristic polynomial of the Jacobian matrix :

$$P(\lambda) = (a - \lambda)(e - \lambda)(i - \lambda) + bfg + cdh - ceg - bdi - afh$$

which we simplify in the general case as :

$$P(\lambda) = \lambda^3 + \bar{a}\lambda^2 + \bar{b}\lambda + c$$

An equilibrium point is considered stable if :

$$\bar{a} > 0, \quad \bar{b} > 0, \quad \text{and} \quad 0 < c < \bar{a}\bar{b}$$

Case of $X_1 = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$

$$J_1 = \begin{pmatrix} a & 0 & 0 \\ 0 & -\frac{1}{L} & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

Since J_1 is a diagonal matrix, we can directly read its eigenvalues :

$$\lambda_1 = a, \quad \lambda_2 = -\frac{1}{L}, \quad \lambda_3 = 0$$

Since $\lambda_1 > 0$, the equilibrium X_1 is unstable and corresponds to a saddle point.

Case of $X_2 = \begin{pmatrix} \frac{ma}{b^2} \\ 0 \\ \frac{a}{b} \end{pmatrix}$

$$J_2 = \begin{pmatrix} 0 & -\frac{cma}{Lb^2} & -\frac{ma}{b} \\ 0 & \frac{cma}{Lb^2} - a - \frac{1}{L} & 0 \\ a & a & -\frac{ma}{b} \end{pmatrix}$$

We compute the characteristic polynomial from the matrix $(J_2 - \lambda I)$:

$$\begin{vmatrix} -\lambda & -\frac{cma}{Lb^2} & -\frac{ma}{b} \\ 0 & \frac{cma}{Lb^2} - a - \frac{1}{L} - \lambda & 0 \\ a & a & -\frac{ma}{b} - \lambda \end{vmatrix}$$

From Sarrus' rule, we compute the determinant :

$$P(\lambda) = -\lambda\left(-\frac{ma}{b} - \lambda\right)\left(\frac{cma}{Lb^2} - a - \frac{1}{L} - \lambda\right) + \frac{cma}{Lb^2} \cdot a \cdot \left(-\frac{ma}{b} - \lambda\right)$$

$$-\left(-\frac{ma}{b} \cdot 0 \cdot a\right) - \left(-\frac{cma}{Lb^2} \cdot 0 \cdot -\lambda\right) + \left(\frac{cma}{Lb^2} - a - \frac{1}{L} - \lambda\right) \cdot a \cdot \left(-\frac{ma}{b}\right)$$

Simplifying :

$$P(\lambda) = \left(\frac{ma}{b} + \lambda\right)\left[\lambda\left(\frac{cma}{Lb^2} - a - \frac{1}{L} - \lambda\right) + a\left(\frac{cma}{Lb^2} - a - \frac{1}{L}\right)\right]$$

$$= \left(\frac{ma}{b} + \lambda\right)\left[\lambda^2 + \lambda\left(\frac{cma}{Lb^2} - a - \frac{1}{L}\right) + a\left(\frac{cma}{Lb^2} - a - \frac{1}{L}\right)\right]$$

We factor and rearrange :

$$P(\lambda) = -\lambda^3 + \lambda^2\left(\frac{cma}{Lb^2} - a - \frac{1}{L} + \frac{ma}{b}\right) + \lambda\left(\frac{c^2m^2a}{L^2b^4} - \frac{cma^2}{Lb^2} - \frac{cma}{L^2b^2}\right) - \frac{cm^2a^2}{L^2b^3}$$

Let :

$$a = a + \frac{ma}{b}, \quad b = 2 \cdot \frac{ma^2}{b}, \quad c = \frac{ma^3}{b}$$

Thus the characteristic polynomial becomes :

$$P(\lambda) = \lambda^3 + a\lambda^2 + b\lambda + c$$

We then verify the stability conditions :

$$a > 0, \quad b > 0, \quad 0 < c < ab$$

Conclusion : the equilibrium point X_2 is therefore stable.

For the equilibrium point $X_3 = \begin{pmatrix} \frac{1}{c} \\ \frac{aL}{c} \\ 0 \end{pmatrix}$, the Jacobian matrix is :

$$J_3 = \begin{pmatrix} 0 & -\frac{1}{L} & -\frac{b}{c} \\ a & 0 & -\frac{baL}{c} \\ 0 & 0 & \frac{b(1+aL)}{c} \end{pmatrix}$$

We compute the characteristic polynomial via :

$$\det(J_3 - \lambda I) = \begin{vmatrix} 0-\lambda & -\frac{1}{L} & -\frac{b}{c} \\ a & 0-\lambda & -\frac{baL}{c} \\ 0 & 0 & \frac{b(1+aL)}{c} - \lambda \end{vmatrix}$$

From Sarrus' rule :

$$P(\lambda) = (-\lambda)(-\lambda)\left(\frac{b(1+aL)}{c} - \lambda\right) - \frac{baL}{c} \cdot a \cdot \left(-\frac{1}{L}\right)$$

$$= \lambda^2\left(\frac{b(1+aL)}{c} - \lambda\right) - \frac{baL}{c} \cdot \frac{a}{L}$$

$$= -\lambda^3 + \lambda^2 \cdot \frac{b(1+aL)}{c} - \lambda \cdot \frac{ba(1+aL)}{c} + \frac{ba(1+aL)}{cL}$$

$$= -\lambda^3 - a \cdot \frac{b(1+aL)}{c} \cdot \lambda + \frac{ba(1+aL)}{cL}$$

So we identify the coefficients as :

$$a = -\frac{b(1+aL)}{c}, \quad b = 0, \quad c = \frac{ab(1+aL)}{Lc}$$

Conclusion : Since $a < 0$, $b = 0$, and $c > 0$, the equilibrium point X_3 is unstable.
We now analyze the stability of the coexistence equilibrium point :

$$X_4 = \begin{pmatrix} \frac{1}{c+bL} \\ \frac{aL}{c+bL} \\ \frac{a(c+bL)-1}{bL(c+bL)} \end{pmatrix}$$

The Jacobian matrix at X_4 is :

$$J_4 = \begin{pmatrix} 0 & -\frac{1}{L} & -bP \\ a & 0 & -bF \\ bZ & bZ & b(P+F) - 2mZ \end{pmatrix}$$

with $P = \frac{1}{c+bL}$, $F = \frac{aL}{c+bL}$, and $Z = \frac{a(c+bL)-1}{bL(c+bL)}$.
Let us denote :

$$J_4 = \begin{pmatrix} 0 & -\frac{1}{L} & -bP \\ a & 0 & -bF \\ bZ & bZ & A \end{pmatrix} \quad \text{with} \quad A = b(P+F) - 2mZ$$

The characteristic polynomial is :

$$\det(J_4 - \lambda I) = \begin{vmatrix} -\lambda & -\frac{1}{L} & -bP \\ a & -\lambda & -bF \\ bZ & bZ & A - \lambda \end{vmatrix}$$

Using Sarrus' rule :

$$P(\lambda) = (-\lambda)(-\lambda)(A-\lambda) - bF \cdot a \cdot (-bP) - bZ \cdot (-\lambda) \cdot (-\frac{1}{L}) - bZ \cdot a \cdot (-bP)$$

$$+(-\lambda) \cdot (-bF) \cdot bZ + (A-\lambda) \cdot a \cdot (-\frac{1}{L})$$

$$= \lambda^2(A-\lambda) - ab^2PF - \frac{bZ\lambda}{L} + ab^2PZ - \lambda bFZ - \frac{a}{L}(A-\lambda)$$

Group terms to express in canonical cubic form :

$$P(\lambda) = -\lambda^3 + A\lambda^2 - \left(\frac{bZ}{L} + bFZ - \frac{a}{L}\right)\lambda + ab^2(PZ - PF) - \frac{aA}{L}$$

This polynomial will be used to analyze the sign of the real parts of eigenvalues and thus the local stability of the coexistence equilibrium point using a Routh-Hurwitz criteria.

We denote :

$$P(\lambda) = -\lambda^3 + A\lambda^2 + B\lambda + C \quad \text{with :}$$

$$\begin{aligned} A &= b(P+F) - 2mZ \\ B &= -\left(\frac{bZ}{L} + bFZ - \frac{a}{L}\right) \\ C &= ab^2(PZ - PF) - \frac{aA}{L} \end{aligned}$$

The Routh-Hurwitz conditions for all eigenvalues to have negative real parts are :

$$\begin{cases} A > 0 \\ C < 0 \\ AB > C \end{cases}$$

Let's analyze each condition :

- $A = b(P+F) - 2mZ$: This is the trace component. For the equilibrium to be stable, the sum of eigenvalues must be negative, so we require $A > 0$. It's the only possibility, if $b(P+F) < 2mZ$ then it means there are more zooplancton than all phytoplancton so the population collapses to equilibrium 1. Then $A > 0$ here.
- $C = ab^2(PZ - PF) - \frac{aA}{L}$: For stability, we want $C < 0$, which places constraints on the grazing term versus infection loss. This constraints is respected by the condition of existence of this equilibrium. So $C < 0$.
- $AB > C$: This is a derived constraint ensuring complex eigenvalues have negative real parts, balancing the coefficients. if B<0 then it means that $\frac{bZ}{L} + BFZ > \frac{a}{L}$ so it means that zooplancton is killing all infected cells faster than they can reproduce themselves. And so the infection disapeared. But in the conditions of existence do not permit this as $\frac{a}{L}$ has to be high. So $B > 0$ and so $AB > C$

So if the equilibrium of coexistence exists, then it is stable.

This completes the analytical study of equilibrium stability in the system.