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Analysis and Control of a Dynamic Model That Describes the Avoidance Behavior of Zooplankton on Phytoplankton Infected by Free Viruses

Lakshmi. N. Sridhar*

Chemical Engineering Department, University of Puerto Rico, Mayaguez, PR 00681, USA

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*Corresponding author: Lakshmi N. Sridhar, Chemical Engineering Department, University of Puerto Rico, Mayaguez, PR 00681, USA, Email: lakshmin.sridhar@upr.edu

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ABSTRACT

The effect of marine viruses on phytoplankton and zooplankton is highly nonlinear and complicated. The phytoplankton population is infected by external free viruses and zooplankton are affected by the consumption of infected phytoplankton. To minimize the infected phytoplankton and maximize the healthy zooplankton it is important to analyze and control the negative effects of the viruses. In this work, bifurcation analysis and multiobjective nonlinear model predictive control is performed on a dynamic model that describes the avoidance behavior of zooplankton on phytoplankton infected by free viruses Bifurcation analysis is a powerful mathematical tool used to deal with the nonlinear dynamics of any process. Several factors must be considered and multiple objectives must be met simultaneously. The MATLAB program MATCONT was used to perform the bifurcation analysis. The MNLMPC calculations were performed using the optimization language PYOMO in conjunction with the state-of-the-art global optimization solvers IPOPT and BARON. The bifurcation analysis revealed the existence of branch points limit points and Hopf bifurcation points. The Hopf bifurcation point, which causes an unwanted limit cycle, is eliminated using an activation factor involving the tanh function. The MNLMPC converged to the Utoia solution. The branch and limit points (which cause multiple steady-state solutions from a singular point) are very beneficial because they enable the Multiobjective nonlinear model predictive control calculations to converge to the Utopia point (the best possible solution) in the model.

Keywords: Bifurcation; Optimization; Control; Zooplankton; Phytoplankton

Background

Castberg, et al.¹ studied the microbial population dynamics and diversity during a bloom of the marine coccolithophorid Emiliania huxleyi (Haptophyta). Jacquet, et al.² performed a flow cytometric analysis of an Emiliana huxleyi bloom terminated by viral infection. Chattopadhyay, et al.³ researched the viral infection on the phytoplankton-zooplankton system using a mathematical model. Wilson, et al.⁴ showed that the isolation of viruses was responsible for the demise of an Emiliania huxleyi bloom in the English Channel. Chattopadhyay, et al.⁵, conducted preliminary experiments with population dynamics

models of three trophic levels. Singh, et al.⁶ studied the role of virus infection in a simple phytoplankton-zooplankton system. Bairagi, et al.⁷ showed that the virus replication factor may be a controlling agent for obtaining a disease-free system in a multispecies eco-epidemiological system. Evans, et al.⁸ showed that the viral infection of Emiliania huxleyi (Prymnesiophyceae) leads to elevated production of reactive oxygen species. Hilker, et al.⁹ demonstrated the existence of oscillations and waves in a virally infected plankton system. Gakkhar, et al.¹⁰ developed a mathematical model for viral infection in toxin-producing phytoplankton and zooplankton systems. Rhodes, et al.¹¹

showed that viral infections could act as a regulator of oceanic phytoplankton populations. Siekmann, et al. 12, I., developed an extension of the Beretta-Kuang model of viral diseases. Evans, et al.¹³ discussed the preferential grazing of Oxyrrhis marina on virus-infected Emiliania huxleyi. Evans, et al. 14 investigated the changes in Emiliania huxleyi fatty acid profiles during infection with the E. huxleyi virus and discussed the physiological and ecological implications. Rhodes, et al. 15 studied the influence of viral infection on a plankton ecosystem undergoing nutrient Chakraborty, et al. 16 discussed the role of enrichment. avoidance by zooplankton for survival and dominance of toxic phytoplankton. Samanta, et al. 17 studied the effect of enrichment on plankton dynamics where phytoplankton can be infected from free viruses. Rosenwasser, et al. 18 showed that rewiring host lipid metabolism by large viruses determines the fate of Emiliania huxleyi, a bloom-forming alga in the ocean. Gilg, et al. 19 demonstrated that differential gene expression is tied to photochemical efficiency reduction in virally infected Emiliania huxleyi. Malitsky, et al.20 showed that the viral infection of the marine alga Emiliania huxleyi triggers lipidome remodeling and induces the production of highly saturated triacylglycerol. Costamagna, et al.²¹ developed a model for the operations to render an epidemic-free hog farm infected by the Aujeszky disease. Vermont, et al.22 showed that Virus infection of Emiliania huxleyi deters grazing by the copepod Acartia tonsa. Biswas, et al.²³ modelled the avoidance behavior of zooplankton on phytoplankton infected by free viruses. This work aims to perform bifurcation analysis and multiobjective nonlinear control (MNLMPC) studies on a dynamic model describing the avoidance behavior of zooplankton on phytoplankton infected by free viruses²³. The paper is organized as follows. First, the model equations are presented, followed by a discussion of the numerical techniques involving bifurcation analysis and multiobjective nonlinear model predictive control (MNLMPC). The results and discussion are then presented, followed by the conclusions.

Model Equations²³

In this model, sv, iv, zv and vv represent the susceptible phytoplankton, infected phytoplankton, zooplankton and free viruses in the environment infecting the phytoplankton. The model equations are

$$\frac{d(sv)}{dt} = a(sv) \left(1 - \left(\frac{(sv + iv)}{k} \right) \right) - \frac{\alpha 1(sv)zv}{(d1 + sv)} - \frac{\beta(sv)vv}{(k1 + vv)}$$

$$\frac{d(iv)}{dt} = \left(\frac{\beta(sv)vv}{(k1 + vv)} \right) - \left(\frac{\alpha 2iv(zv)}{(d2 + iv + (\gamma sv))} \right) - \mu(iv)$$

$$\frac{d(zv)}{dt} = \left(\lambda 1 \frac{\alpha 1(sv)zv}{(d1 + sv)} \right) - \left(\lambda 2 \frac{\alpha 2iv(zv)}{(d2 + iv + (\gamma sv))} \right) - (\upsilon zv)$$

$$\frac{d(vv)}{dt} = b\mu(iv) - \frac{\beta(sv)vv}{(k1 + vv)} - \delta(vv)$$

The base parameter values are

 $\alpha 1 = 0.045$; d1 = 2; $\alpha 2 = 0.045$; d2 = 2; $\gamma = 3.8$; ; $\lambda 1 = 0.75$; $\lambda 2 = 0.61$; $\nu = 0.012$; $\alpha = 0.77$; k = 108; k1 = 3; $\beta = 0.65$; $\mu = 0.16$; b = 35; $\delta = 1.23$.

Bifurcation analysis

The MATLAB software MATCONT is used to perform the bifurcation calculations. Bifurcation analysis deals with

multiple steady-states and limit cycles. Multiple steady states occur because of the existence of branch and limit points. Hopf bifurcation points cause limit cycles. A commonly used MATLAB program that locates limit points, branch points and Hopf bifurcation points is MATCONT^{24,25}. This program detects Limit points (LP), branch points (BP) and Hopf bifurcation points(H) for an ODE system.

$$\frac{dx}{dt} = f(x, \alpha)$$

 $x \in \mathbb{R}^n$ Let the bifurcation parameter be α . Since the gradient is orthogonal to the tangent vector,

The tangent plane at any point $W = [W_1, W_2, W_3, W_4, ..., W_{n+1}]$ must satisfy

$$Aw = 0$$

Where A is

$$A = [\partial f / \partial x | | \partial f / \partial \alpha]$$

where $\partial f / \partial x$ is the Jacobian matrix. For both limit and branch points, the Jacobian matrix $J = [\partial f / \partial x]$ must be singular.

For a limit point, there is only one tangent at the point of singularity. At this singular point, there is a single non-zero vector, y, where Jy=0. This vector is of dimension n. Since there is only one tangent the vector

$$y = (y_1, y_2, y_3, y_4, ... y_n) \quad \text{must} \quad \text{align} \quad \text{with}$$

$$\hat{w} = (w_1, w_2, w_3, w_4, ... w_n) \cdot \text{Since}$$

$$J\hat{w} = Aw = 0$$

the n+1 th component of the tangent vector $W_{n+1} = 0$ at a limit point (LP).

For a branch point, there must exist two tangents at the singularity. Let the two tangents be z and w. This implies that

$$Az = 0$$

$$Aw = 0$$

Consider a vector v that is orthogonal to one of the tangents (say w). v can be expressed as a linear combination of z and w ($v = \alpha z + \beta w$). Since Az = Aw = 0; Av = 0 and since

w and v are orthogonal, $w^T v = 0$. Hence $Bv = \begin{bmatrix} A \\ w^T \end{bmatrix} v = 0$ which implies that B is singular.

Hence, for a branch point (BP) the matrix $B = \begin{bmatrix} A \\ w^T \end{bmatrix}$ must be singular.

At a Hopf bifurcation point,

$$\det(2f_{r}(x,\alpha)@I_{n})=0$$

@ indicates the bialternate product while I_n is the n-square identity matrix. Hopf bifurcations cause limit cycles and should be eliminated because limit cycles make optimization and control tasks very difficult. More details can be found in Kuznetsov^{27,28}.

Hopf bifurcations cause limit cycles. The tanh activation function (where a control value u is replaced by) ($u \tanh u / \varepsilon$) is used to eliminate spikes in the optimal control profiles²⁹⁻³². Sridhar³³ explained with several examples how the activation factor involving the tanh function also eliminates the Hopf bifurcation points. This was because the tanh function increases the oscillation time period in the limit cycle.

Multiobjective Nonlinear Model Predictive Control (MNLMPC)

The rigorous multiobjective nonlinear model predictive control (MNLMPC) method developed by Flores Tlacuahuaz, et al.³⁴ was used.

Consider a problem where the variables $\sum_{t_{i=0}}^{t_i=t_f} q_j(t_i)$ (j=1,

2..n) have to be optimized simultaneously for a dynamic problem

$$\frac{dx}{dt} = F(x, u)$$

 t_f being the final time value and n the total number of objective variables and u the control parameter. The single objective optimal control problem is solved individually

optimizing each of the variables $\sum_{t_{i=0}}^{t_i-t_f} q_j(t_i)$ The optimization

of
$$\sum_{t_{i=0}}^{t_i=t_f} q_j(t_i)$$
 will lead to the values q_j^* . Then, the

multiobjective optimal control (MOOC) problem that will be solved is

$$\min(\sum_{j=1}^{n} (\sum_{t_{i=0}}^{t_i=t_f} q_j(t_i) - q_j^*))^2$$

subject to
$$\frac{dx}{dt} = F(x, u);$$

This will provide the values of u at various times. The first obtained control value of u is implemented and the rest are discarded. This procedure is repeated until the implemented and the first obtained control values are the same or if the Utopia

point where (
$$\sum_{t_{i=0}}^{t_i=t_f} q_j(t_i) = q_j^*$$
 for all j) is obtained.

Pyomo³⁵ is used for these calculations. Here, the differential equations are converted to a Nonlinear Program (NLP) using the orthogonal collocation method
The NLP is solved using IPOPT³⁶ and confirmed as a global solution with BARON³⁷.

The steps of the algorithm are as follows

Optimize
$$\sum_{t=0}^{t_i=t_f} q_j(t_i)$$
 and obtain q_j^* .

Minimize $\left(\sum_{t=0}^{n} \left(\sum_{t=0}^{t_i=t_f} q_j(t_i) - q_j^*\right)\right)^2$ and get the control values

Implement the first obtained control values

Repeat steps 1 to 3 until there is an insignificant difference between the implemented and the first obtained value of the control variables or if the Utopia point is achieved. The Utopia

point is when
$$\sum_{t_{i=0}}^{t_i=t_f} q_j(t_i) = q_j^* \text{ for all j.}$$

Sridhar³⁸ demonstrated that when the bifurcation analysis revealed the presence of limit and branch points the MNLMPC calculations to converge to the Utopia solution. For this, the singularity condition, caused by the presence of the limit or branch points was imposed on the co-state equation. If the minimization

of q_1 lead to the value q_1^* and the minimization of q_2 lead to the value q_2^* The MNLPMC calculations will minimize the function $(q_1-q_1^*)^2+(q_2-q_2^*)^2$. The multiobjective optimal control problem is

min
$$(q_1 - q_1^*)^2 + (q_2 - q_2^*)^2$$
 subject to $\frac{dx}{dt} = F(x, u)$

Differentiating the objective function results in

$$\frac{d}{dx_i}((q_1-q_1^*)^2+(q_2-q_2^*)^2)=2(q_1-q_1^*)\frac{d}{dx_i}(q_1-q_1^*)+2(q_2-q_2^*)\frac{d}{dx_i}(q_2-q_2^*)$$

The Utopia point requires that both $(q_1-q_1^*)$ and $(q_2-q_2^*)$ are zero. Hence

$$\frac{d}{dx_1}((q_1-q_1^*)^2+(q_2-q_2^*)^2)=0$$

The optimal control co-state equation³⁹ is

$$\frac{d}{dt}(\lambda_i) = -\frac{d}{dx_i}((q_1 - q_1^*)^2 + (q_2 - q_2^*)^2) - f_x \lambda_i; \quad \lambda_i(t_f) = 0$$

 λ_i is the Lagrangian multiplier. t_f is the final time. The first term in this equation is 0 and hence

$$\frac{d}{dt}(\lambda_i) = -f_x \lambda_i; \lambda_i(t_f) = 0$$

At a limit or a branch point, for the set of ODE $\frac{dx}{dt} = f(x,u)$ f_x is singular. Hence there are two different vectors-values for $\left[\lambda_i\right]$ where $\frac{d}{dt}(\lambda_i) > 0$ and $\frac{d}{dt}(\lambda_i) < 0$. In between there is a vector $\left[\lambda_i\right]$ where $\frac{d}{dt}(\lambda_i) = 0$. This coupled with the boundary condition $\lambda_i(t_f) = 0$ will lead to $\left[\lambda_i\right] = 0$ This makes the problem an unconstrained optimization problem and the optimal solution is the Utopia solution.

Results

When a is the bifurcation parameter, a branch point occurred at (sv, iv, zv, vv,a) values of (0;-0.608365; -4.948035; -2.769792; -7.887499) (Figure 1a).

a is bifurcation parameter

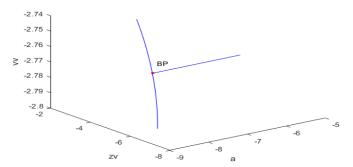


Figure 1a: a is the bifurcation parameter

When $\alpha 1$ is the bifurcation parameter, a branch point occurred at (sv, iv, zv, vv, $\alpha 1$) values of (3.792436; 14.728461; 0; 65.14051; 0.050878) (Figure 1b).

alpha1 is bifurcation paramter

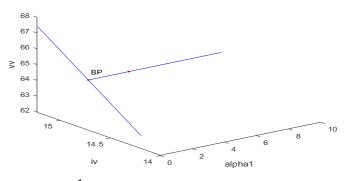


Figure 1b: α 1 is the bifurcation parameter.

When $\alpha 2$ is the bifurcation parameter, a Hopf bifurcation point occurs at (sv, iv, zv, vv, $\alpha 2$) values of (19.860109 1.388582 164.282223 2.055185 1.737406). This is indicated in the curve AB in (Figure 1c). When $\alpha 2$ is modified to $\alpha 2 \tanh(\alpha 2)/1.5$, the Hopf bifurcation point disappears. This is indicated in the curve CD in Fig. 1c. The limit cycle caused by the Hopf bifurcation is shown in (Figure 1d).

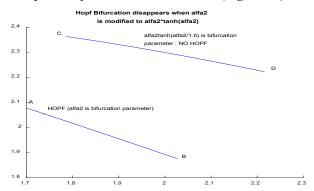


Figure 1c: $\alpha 2$ is the bifurcation parameter, a Hopf bifurcation point is present (curve AB). When $\alpha 2$ is modified to $\alpha 2 \tanh(\alpha 2)/1.5$, the Hopf bifurcation point disappears (curve CD)

When δ was used as the bifurcation parameter several limit points were found. One of them occurred at (sv, iv, zv, vv, δ) values of (0,0,0,310.688616,0). (Figure 1e).

limit cycle for Hopf Bifurcation

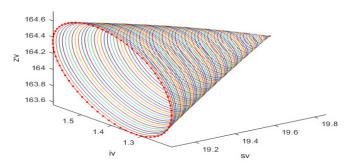


Figure 1d: Limit cycle for Hopf shown in Figure 1d.

delta is bifurcation parameter

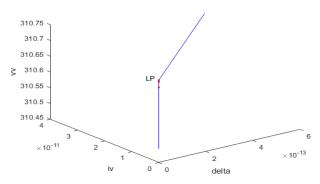


Figure 1e: The bifurcation parameter.

For the MNLMPC calculations, sv(0) = 200, vv(0) = 50,

$$zv(0) = 50$$
, iv (0) = 50, $\sum_{t_{i=0}}^{t_i = t_f} iv(t_i)$ was minimized and $\sum_{t_{i=0}}^{t_i = t_f} zv(t_i)$

was maximized individually and resulted in values of 50 and 400. The overall optimal control problem will involve the

minimization of
$$(\sum_{t_{i=0}}^{t_i=t_f} i\nu(t_i) - 50)^2 + (\sum_{t_{i=0}}^{t_i=t_f} z\nu(t_i) - 400)^2$$
 was

subject to the equations governing the model. This led to a value of zero (the Utopia

The MNLMPC values of the control variables, β was 0.000334. The various MNMPC figures are shown in (**Figures 2a-2b**). The control profiles of β exhibited noise and this was remedied using the Savitzky-Golay filter to produce a smoother control profile βsg . Both the noisy and smooth profiles ae shown in (**Figure 2c**).

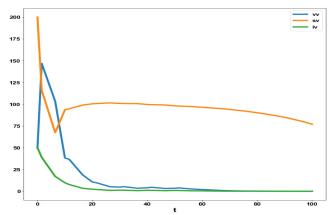


Figure 2a: MNLMPC (vv,sv,iv profiles).

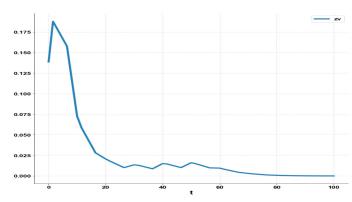


Figure 2b: MNLMPC (zv profile).

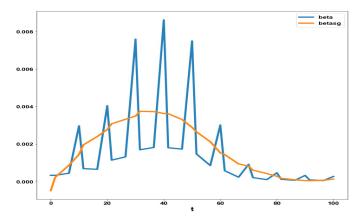


Figure 2c: (β (noise exhibited) βsg (noise eliminated)).

Discussion of Results

Theorem

If at least one of the functions in a dynamic system is separable into two distinct functions, a branch point singularity will occur in the system.

Proof

Consider a system of equations

$$\frac{dx}{dt} = f(x, \alpha)$$

 $x \in \mathbb{R}^n$. Defining the matrix A as

$$A = \begin{bmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \frac{\partial f_1}{\partial x_3} & \frac{\partial f_1}{\partial x_4} & \dots & \frac{\partial f_1}{\partial x_n} & \frac{\partial f_1}{\partial \alpha} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \frac{\partial f_2}{\partial x_3} & \frac{\partial f_2}{\partial x_4} & \dots & \frac{\partial f_2}{\partial x_n} & \frac{\partial f_2}{\partial \alpha} \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \frac{\partial f_n}{\partial x_3} & \frac{\partial f_n}{\partial x_4} & \dots & \frac{\partial f_n}{\partial x_n} & \frac{\partial f_n}{\partial \alpha} \\ \end{bmatrix}$$

 α is the bifurcation parameter. The matrix A can be written in a compact form as

$$A = \begin{bmatrix} \frac{\partial f_p}{\partial x_a} \cdot | & \frac{\partial f_p}{\partial \alpha} \end{bmatrix}$$

The tangent at any point x; ($z = [z_1, z_2, z_3, z_4,z_{n+1}]$) must satisfy

$$Az = 0$$

The matrix $\{\frac{\partial f_p}{\partial x_q}\}$ must be singular at both limit and branch points. The n+1 th component of the tangent vector $Z_{n+1} = 0$ at a limit point (LP) and for a branch point (BP) the matrix $B = \begin{bmatrix} A \\ z^T \end{bmatrix}$ must be singular.

Any tangent at a point y that is defined by $Z = [z_1, z_2, z_3, z_4, z_{n+1}]$) must satisfy

$$Az = 0$$

For a branch point, there must exist two tangents at the singularity. Let the two tangents be z and w. This implies that

$$Az = 0$$
$$Aw = 0$$

Consider a vector v orthogonal to one of the tangents (z). v can be expressed as a linear combination of z and w ($v = \alpha z + \beta w$). Since Az = Aw = 0; Av = 0 and since z and v are orthogonal, $z^Tv = 0$. Hence $Bv = \begin{bmatrix} A \\ z^T \end{bmatrix} v = 0$

which implies that B is singular where $B = \begin{bmatrix} A \\ z^T \end{bmatrix}$

Let any of the functions $\mathbf{f}_{_{\mathbf{i}}}$ are separable into 2 functions $\phi_{_{\mathbf{i}}},\phi_{_{\mathbf{2}}}$ as

$$f_i = \phi_1 \phi_2$$

At steady-state $f_i(x,\alpha)=0$. Hence either $\phi_1=0$ or $\phi_2=0$ or both ϕ_1 and ϕ_2 must be 0 implying that the two branches $\phi_1=0$ and $\phi_2=0$ will intersect at a point ϕ_1 and ϕ_2 are 0.

Here, B will be singular as one row row in this matrix would be

However,
$$\left[\frac{\partial f_i}{\partial x_k} \middle| \frac{\partial f_i}{\partial \alpha}\right]$$

$$\left[\frac{\partial f_i}{\partial x_k} = \phi_1(=0)\frac{\partial \phi_2}{\partial x_k} + \phi_2(=0)\frac{\partial \phi_1}{\partial x_k} = 0 (\forall k = 1..., n)$$

$$\frac{\partial f_i}{\partial \alpha} = \phi_1(=0)\frac{\partial \phi_2}{\partial \alpha} + \phi_2(=0)\frac{\partial \phi_1}{\partial \alpha}\right] = 0$$

This implies that every element in the row $\left[\frac{\partial f_i}{\partial f_i} \middle| \frac{\partial f_i}{\partial f_i} \middle]$ would be 0 and hence the matrix B would be singular, approximately a branch point.

When a is the bifurcation parameter, a branch point occurred at (sv, iv, zv, vv,a) values of (0;-0.608365; -4.948035; -2.769792; -7.887499).

Here, the two distinct functions can be obtained from the first ODE in the model

$$\frac{d(sv)}{dt} = a(sv) \left(1 - \left(\frac{(sv + iv)}{k} \right) \right) - \frac{\alpha 1(sv)zv}{(d1 + sv)} - \frac{\beta(sv)vv}{(k1 + vv)}$$

The two distinct equations are

$$sv = 0$$

$$a\left(1 - \left(\frac{(iv)}{k}\right)\right) - \frac{\alpha 1zv}{(d1)} - \frac{\beta vv}{(k1 + vv)} = 0$$

With sv=0; a = -7.887499; iv = ;-0.608365; zv=-4.948035; vv=-2.769792; k = 108; alfa α 1 = 0.045; d1 = 2; β = 0.65; k1=3; both the distinct equations are satisfied, validating the theorem.

When $\alpha 1$ is the bifurcation parameter, a branch point occurred at (sv, iv, zv, vv, $\alpha 1$) values of (3.792436; 14.728461; 0; 65.14051; 0.050878)

Here, the two distinct functions can be obtained from the third ODE in the model

$$\frac{d(zv)}{dt} = \left(\lambda 1 \frac{\alpha 1(sv)zv}{(d1+sv)}\right) - \left(\lambda 2 \frac{\alpha 2iv(zv)}{(d2+iv+(\gamma sv))}\right) - (\upsilon zv)$$

The two distinct equations are

$$zv = 0$$

$$\left(\lambda 1 \frac{\alpha 1(sv)}{(d1+sv)}\right) - \left(\lambda 2 \frac{\alpha 2(iv)}{(d2+iv+(\gamma sv))}\right) - v = 0$$

With

 $\alpha 1 = 0.050878$; d1 = 2; $\alpha 2 = 0.045$; d2 = 2; $\gamma = 3.8$; ; $\lambda 1 = 0.75$; $\lambda 2 = 0.61$; $\upsilon = 0.012$; sv = 3.792436; iv = 14.728461; zv = 0; vv = 65.14051

both the distinct equations are satisfied, validating the theorem.

When $\alpha 2$ is the bifurcation parameter, a Hopf bifurcation point occurs at (sv, iv, zv, vv, $\alpha 2$) values of (19.860109 1.388582 164.282223 2.055185 1.737406). When $\alpha 2$ is modified to $\alpha 2 \tanh(\alpha 2)/1.5$, the Hopf bifurcation point disappears. This validates the analysis of Sridar³³.

It is seen that the presence of the limit and branch points are beneficial because it allows the MNLMPC calculations to attain the Utopia solution, validating the analysis of Sridhar³⁸.

Conclusions

Bifurcation analysis and multiobjective nonlinear model predictive control (MNLMPC) studies were conducted on a dynamic model that describes the avoidance behavior of zooplankton on phytoplankton infected by free viruses. The bifurcation analysis revealed the existence of branch points, limit points and Hopf bifurcation points. in the model. The branch and limit points (which cause multiple steady-state solutions from a singular point) are very beneficial because they enable the Multiobjective nonlinear model predictive control calculations to converge to the Utopia point (the best possible solution). It is proven (with computational validation) that the branch points were caused by the existence of two distinct separable functions in one of the equations in each dynamic model. A theorem was

developed to demonstrate this fact for any dynamic model. The Hopf bifurcation point that causes an unwanted limit cycle is eliminated using an activation factor involving the tanh function. A combination of bifurcation analysis and Multiobjective Nonlinear Model Predictive Control (MNLMPC) for a dynamic model that describes the avoidance behaviour of zooplankton on phytoplankton infected by free viruses is the main contribution of this paper.

Data availability statement

All data used is presented in the paper.

Conflict of interest

The author, Dr. Lakshmi N Sridhar, has no conflict of interest.

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